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Assessing the Relative Utility of Models of Vegetation Dynamics for the Management of Sagebrush Steppe Rangelands

Paul E. Hosten

Utah State University

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ASSESSING THE RELATIVE UTILITY OF MODELS OF VEGETATION DYNAMICS FOR THE MANAGEMENT OF SAGEBRUSH STEPPE RANGELANDS

PAUL E. HOSTEN

1995
ASSESSING THE RELATIVE UTILITY OF MODELS OF VEGETATION DYNAMICS
FOR THE MANAGEMENT OF SAGEBRUSH STEPPE RANGELANDS

by

Paul E. Hosten

A dissertation submitted in partial fulfillment of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Range Science

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1995
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Paul E. Hosten
PREFACE

When I first started working on this dissertation, I focussed on the relative importance of different kinds of benchmarks/monitoring points associated with monitoring rangeland condition. It was only as my work progressed that I realized that the choice of benchmark depended heavily on the model of vegetation dynamics underlying the range condition and trend assessment process. I thus changed the focus of my project to examine more closely different models of vegetation dynamics that might be used in range management. In this dissertation, I review popular models of community-level vegetation dynamics, examine some of the assumptions and concepts underlying some of the most important models, determine the requirements of such models by the range profession, and finally, suggest how this might affect the location of benchmarks and monitoring points. All this is related to three empirical field studies within sagebrush steppe (Chapters 4, 5, and 6). The following flow diagram indicates the logical order of chapters, and the location of the above topics.

All materials (raw data and photos) used in Chapter 4 are archived in special collections at the Utah State University Library.
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ABSTRACT

Assessing the Relative Utility of Models of Vegetation Dynamics for the Management of Sagebrush Steppe Rangelands

by

Paul E. Hosten, Doctor of Philosophy
Utah State University, 1995

Major Professor: Dr. Neil E. West
Department: Range Science

The literature, long-term temporal data sets, and spatial data points surrounding livestock watering points within rangeland communities were used to examine common assumptions and concepts used in models of vegetation dynamics. Of the stability concepts examined, the constancy concept was invalidated using long-term relict area data, whereas long-term data following disturbance indicated that sagebrush-dominated areas could be considered as resilient under the circumstances examined. Piosphere as well as relict and post-disturbance data indicated that the individualistic notion of vegetation change was favored. Species showing the most predictability (based on repeatability of abundance curves, and spatial and temporal serial correlations) were sagebrush and cheatgrass, specifically in their response to fire. Bunchgrasses were characterized by their persistence in abundance under all circumstances (grazing disturbance and fire disturbance) except long-term absence of fire. This, together with the support of the individualistic notion of plant community change, suggests examining change on a vital attributes basis within a kinetic framework.

It was found that most models of vegetation dynamics could be validated, because of the multivariate nature of the data examined. A closer examination of the requirements of range management for a model to be used as a basis for range condition and trend analysis determined that three basic model types are needed by range managers: First, a conceptual model for marrying divergent perspectives of different rangeland user groups; second, mechanistic models for the exploration of vegetation dynamics; and third, expert systems for information transfer. Further emphasis was placed on deriving a suitable conceptual model subscribing to the
objective of linking vegetation dynamics, range management, and monitoring within sagebrush-dominated areas. Important characteristics (derived from the data sets examined) included in this model are the recognition of static and dynamic plant communities, swathes of change rather than predefined pathways, the individualistic nature of change, and the recognition of spatial heterogeneity. Predictability at various scales was incorporated by focusing on cheatgrass and sagebrush, since these species indicated the most repeatable dynamics observed in the data sets, and were "common denominator" species (thus overcoming the problem of spatial heterogeneity). The undesired effects of cheatgrass and sagebrush on other growth-forms suggest that monitoring and managing these undesired species may be a proactive way of managing for a desired plant community incorporating a balance of growth-forms.
CHAPTER 1
INTRODUCTION

The range management profession has a long history of using models of vegetation dynamics for management purposes. Such models are used to predict changes in plant communities concomitant with livestock grazing. The necessity for such predictive models arises from the need to give managers a formula by which to make the correct decisions. Faith in the science underlying models, as well as their adoption and preservation by government agencies, fosters continued use of outdated models (Joyce 1993). Outdated models pose a threat to management (Niering 1987) and to monitoring on which good management is dependent (Friedel 1991). Monitoring of our rangelands is essential if we are to adequately gauge temporal changes in our plant communities relative to management objectives. The following discussion of how the Clementsian model of vegetation dynamics has been used in range management in the U.S. will make the need apparent for a revision of models of vegetation dynamics.

The classical Clementsian model assumes a stable plant community at the endpoint to succession (climax), where individual species are in equilibrium with their environment (Figure 1.1). Any disturbance (anthropogenic, or natural) is thought to result in a linear displacement of the plant community from its climax. The decision-making process in range condition analysis under the climax theory is summarized in Figure 1.2.

Cessation of disturbance is assumed to allow the plant community to return to its stable endpoint. Such a model holds intuitive appeal to range managers, where livestock grazing activities are seen as the disturbance displacing vegetation from the endpoint plant community. Relict areas have been assumed to be at climax, and therefore in the best range condition. The model instructs us that the primary management tool for achieving high range condition is simply the cessation of the grazing disturbance (Stafford Smith and Pickup 1993). Range condition, forage production, biodiversity, watershed protection, etc., are also assumed to be linearly related to the Clementsian successional sequences with maxima at the climax.

\footnote{Many concepts used in models of vegetation dynamics have been questioned. A full discussion is provided at the end of this chapter.}
Fig. 1.1. The relationships between successional tendency, disturbance intensity, and range condition for a Clementsian model showing linear species replacement.

Fig. 1.2. Generalized scheme for the traditional ecological approach to range condition (after Risser 1989).
The Clementsian model has been detrimental by blinding several generations of range managers and scientists to: (1) changing circumstances such as climate and environmental changes, or the introduction of new plant species into the local community (Svejcar and Brown 1991); (2) alternative management tools (a point which Savory [1988] has made clear); (3) using windows of opportunity (rare co-occurrences of environmental and management-controlled conditions [Westoby et al. 1989a, b]); and (4) misguided information that succession and regression (retrogression) follow the same pathway (Noy-Meir and Walker 1986, Friedel 1991). Additional problems are the questionable assumptions of an inverse relationship between range condition and disturbance (Smith 1989) and that climax is said to represent the most desirable condition possible for a plant community.

In spite of these problems, there is a general consensus that rangelands in the United States have improved since passage of the Taylor Grazing Act and subsequent Clementsian-based management (Box and Sisson 1975). However, dissatisfaction with the Clementsian model is forcing range managers and scientists to consider alternative models (Pickett and McDonnell 1989, Laycock 1992). Thus, the National Academy of Sciences (NAS) (1994) advocates "... a coordinated research effort ... to develop, test, and employ new models of rangeland change that incorporate the concept of ecological thresholds" (page 11). While this supports the search for alternative models (a major objective of this dissertation), the assumption of thresholds remains unvalidated. It is thus important that the logic and assumptions underlying such models be examined, and that alternative models be validated before their general adoption as a basis for range condition and trend analysis. This need has led to the definition of the primary objectives of this dissertation.

**Primary Objectives**

Since the number of possible models describing vegetation dynamics is limited only by one's imagination, the first objective of this dissertation is to determine which of the available models are most successful in describing vegetation dynamics in the sagebrush steppe region. A second objective is to determine the requirements of a model describing vegetation dynamics in sagebrush steppe from a range management perspective. This will allow a more objective choice of models for predicting vegetation dynamics in managed sagebrush steppe rangelands. Finally, since monitoring plays an integral role in
rangeland management, an assessment of choice of benchmark and monitoring protocol relative to model choice will be made.

Considerable description of existing models of vegetation dynamics, their assumptions, and the concepts involved are required before the primary objectives can be broken down into sets of research hypotheses. Concepts such as stability and equilibrium have evoked much discussion in the discipline of ecology, and are deeply embedded in many models of vegetation dynamics. Due to the vast extent of this literature, full inclusion with model descriptions would decrease readability of this section considerably. These concepts are therefore addressed separately at the end of this chapter.

**Description of Models and Concepts**

The word "model" may evoke thoughts of mathematical equations representing mechanisms. In reality, simple verbal and nonmechanistic descriptions, providing a framework for ideas, may also pass for a model. The multivariate nature of data in vegetation science prompts mathematical terminology to aid the description of models as well as methods employed to describe pertinent data and their manipulation. Figure 1.3 thus introduces terminology used in this dissertation.

Each matrix [ ] represents presence or abundance of species, life or growth forms, or any other multivariate representation of a stand sample representing a plant community of interest. The collection of matrices represent data along spatial or temporal gradients. In this dissertation, sites with constituent stands of vegetation are said to represent objects, while species (or any other categories within communities) are called the attributes. In general, models of vegetation dynamics attempt to describe relationships between objects. In doing so, many different assumptions have been made. Pathways of change have usually been regarded as repeatable. Models may assume single pathways, or multiple pathways, each with their own end points. Stable states associated with discrete transition might be considered as an alternative to models incorporating pathways with continuous change. Assumptions are also made about attribute behavior. For example, species belonging to the same growth/life form may react to the environment similarly; or, the fluctuation of plant species abundance along environmental gradients may occur as a Gaussian curve. Some of the more esoteric assumptions may involve stability, equilibrium, and chaos theory.
A few models may relate plant community change to strict observation, but most prescribe mechanisms operating within the organismal, population, community, landscape, or ecosystem criteria. There are few models considering multiple criteria. A few examples of criteria specifically pertinent to sagebrush steppe rangelands are

1. organismal--fire and grazing tolerance, life strategy
2. population--plant demography, seedbank maintenance
3. community--competition, mutualism, facilitation, deterministic succession, keystone species, functional groups
4. ecosystem--relation of vegetation to soils and other parts of the abiotic environment.

Models of Vegetation Dynamics

\[ [A]_1, [B]_2, [C]_3, \ldots [Y]_k, [Z]_n \]

\[
\text{transition} = \text{pathway}？
\]

A to Z represent the communities found along the spatial and/or temporal continuum 1 through n. Square brackets [ ] indicate multivariate data collected as required for community analysis.

Vegetation science attempts to describe pathways between spatial and/or temporal endpoints. Pathways may be attributed to:

1. organismal criteria
2. population criteria
3. community criteria
4. landscape criteria
5. ecosystem criteria
6. environmental variability
7. observation of the norm
8. combinations of the above

Fig. 1.3. Terminology employed and focus of models of vegetation dynamics introduced in this chapter. [X] represents a matrix of species abundances representative of a community landscape--soil transport, hydrologic cycle, insolation, patchiness, disturbance pattern, connectivity

---

2 Allen and Hoekstra (1992) use the word criterion instead of level of organization to emphasize the scale-independence of these concepts.
Models describing patterns of vegetation dynamics may focus on criteria representing ecosystem functions (transfers of nutrients and energy) and processes (for example, photosynthesis, grazing), mechanisms (such as competition and facilitation), or observed dynamics (commonly noted for particular vegetation types). This will be emphasized within descriptions of individual models of vegetation dynamics. Some of the above mechanisms are difficult to measure in an applied situation; I will refer to these as phenomenological. A classification of the models of vegetation dynamics is necessary in order to present material in a coherent fashion.

Classification and Organization of Existing Models of Plant Community Dynamics

The study of plant community dynamics sits comfortably within the following definition of vegetation science from Austin and Smith (1989, page 35): "The study of those processes which determine the patterns of composition and emergent properties observed in vegetation". This definition applies to both spatial and temporal patterns. Existing models of vegetation patterns can be restricted to the temporal or spatial domains only, while others consider both dimensions simultaneously. At times, it is difficult to separate the spatial and temporal components in certain models. In fact, natural experiments in the form of space-for-time substitutions (Pickett 1985) have often been used to speculate about long-term temporal trends. Austin (1985) saw the lack of discernment between spatial and temporal components as a major weakness in vegetation science up to that point.

Many classifications of models of vegetation patterns are possible. Since the separation of spatial and temporal patterns is a major issue in vegetation science, I will describe the existing models within this framework. Table 1.1 lists some of the models mentioned in this dissertation. This list is not intended to be comprehensive, but rather to cover the spectrum of available models for the reader’s benefit and also to aid in the selection of model requirements from a range manager’s perspective.
Table 1.1. A summary of characteristics for models used in plant community dynamics. (res=resources, climate, man=management, - indicates all possible criteria)

<table>
<thead>
<tr>
<th>Models of Vegetation Dynamics</th>
<th>CRITERIA</th>
<th>Organismal Population</th>
<th>Mechanistic Phenomenological</th>
<th>Predefinition of Communities and Pathways</th>
</tr>
</thead>
<tbody>
<tr>
<td>[A], [B] .. [N]</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Temporal Models:**

- **Clementsian model**
  - C(C)
  - M,C
  - D
  - References: Clements (1916, 1928)

- **Gleason**
  - C(C)
  - M,C
  - N
  - References: Gleason (1926)

- **Tansley**
  - C(C)
  - M,C
  - N
  - References: Tansley (1929)

- **Egler**
  - C(C)
  - M,C
  - N
  - References: Egler (1934), Wilson et al. (1992)

- **Connell & Slatyer**
  - C(C), C(O)
  - M,C
  - N
  - References: Connell & Slatyer (1977)

- **Pickett et al.**
  - C(C)
  - M
  - N
  - References: Pickett et al. (1987)

- **Vital attributes**
  - C(O)
  - M
  - N
  - References: Noble & Slatyer (1980)

- **Resource ratio hyp.**
  - C(O, res.)
  - M
  - N
  - References: Tilman (1985)

- **Grimes's model**
  - C(C, res.)
  - M,C
  - N
  - References: Grime (1977)

- **Multiple-stable-states**
  - C(O, C, res, cli, man.)
  - P,C
  - D
  - References: Westoby et al. (1989a, b)

- **Combination of multiple-stable-states & continuum**
  - C(O, C, res, cli, man.)
  - P,C
  - D
  - References: Friedel (1991)

- **Degradation models**
  - C(C,-)
  - P,C
  - D
  - References: See text

- **Resource modelling**
  - P(O, res)
  - M
  - N
  - References: See text

- **Forage production models**
  - P(C(O, res)
  - M
  - N
  - References: See text

- **Centripetal or chaotic models**
  - C(cli)
  - P
  - N
  - References: Ellis & Swift (1988)

- **Markov chains**
  - C,P(-)
  - P
  - N
  - References: See text

- **Linked models**
  - C,L,P(O, cli, res)
  - M
  - N
  - References: See text

**Spatial Models**

- **Continuum**
  - C,P(res)
  - M
  - N
  - References: Austin & Smith (1989)

- **Pisosphere models**
  - C(O)
  - P
  - N
  - References: Andrew (1988)

**Spatial & Temporal Models:**

- **Whittakers' climax pattern hypothesis**
  - C(C)
  - M,C
  - D
  - References: Whittaker (1974a)

- **Dynamical systems**
  - C(O)
  - M,C
  - N
  - References: Roberts (1987)

- **Ecological field theory**
  - C(O, res, cli)
  - M
  - N
  - References: Walker et al. (1989)

- **Extension of FATE**
  - C(O)
  - M
  - N
  - References: Moore & Noble (1993)

- **Models in artificial landscapes**
  - C, E(O, L, E)
  - M
  - N
  - References: Turner et al. (1993b)

- **GIS & remote sensing based models**
  - C, E(O, L, E)
  - M,P
  - N
  - References: Roberts (in press a, b)

**Temporal Models**

**Clementsian-Derived Models**

Several variants of the Clementsian model exist (Whittaker 1974a). A common criticism of Clementsian models is their rigidity in defining a single climax. However, most authors, including Clements, identified alternative communities under the guise of proclimaxes, subclimaxes, and other designations. Walter
(1962) decided that the climax could only be found on local homogenous areas. This, as do the following views, constitutes a polyclimax view. On a similar theme, Dansereau (1957) considered that succession involved release from local climatic control (by topography, parent material, biotic interaction, etc.) so that the climax could only be found on flat, homogenous, and disturbance-free areas. Braun (1956) and Oosting (1956) recognized topographic and edaphic climaxes that would converge on a single climax, given sufficient time. They considered that, in practice, these could be viewed as separate community types. Some view the definition of alternative communities and pathways as the recognition that the Clementsian model lacks reality. Recently, new models incorporating several alternative communities and pathways of attaining these "states" have been devised (for example, Huschle and Hironaka 1980).

**Opposing Gleasonian and Tansleyian Views**

Instead of subscribing to the view that all vegetation of a region moves towards a climax, Gleason (1926) proposed that vegetation change occurred individualistically. That is, different species changed their distribution and abundances independently of one another. The occurrence of this phenomenon is of great interest to vegetation scientists and still provides inspiration for articles (for example, Leps 1991). Tansley (1929, 1935) adopted a more holistic perspective and considered it essential that environment, flora, and fauna be viewed together to gain an understanding of observed vegetation dynamics within an ecosystem context.

**Egler's Complete and Preemptive Initial Floristics**

While Clements believed that succession resulted in species replacement, Egler (1954) emphasized that all, or most, species observed through time were initially present (perhaps in the form of propagules). Changes in dominance simply represented differential growth and structure (Wilson et al. 1992). Preemptive initial floristics refers to situations where the first plants at a site dominate and influence vegetation dynamics for a long time (Wilson et al. 1992).

While the above views are often seen as antagonistic, it is feasible that all perspectives are indeed valid. Differences may arise from the use of alternative scales and perspectives of observation, or observation within vegetation types showing different dynamics (Allen and Hoekstra 1992). Aspects of the above
conceptual models are emphasized in most of the more recent models of vegetation dynamics discussed here (Table 1.1).

**Connell and Slatyer (1977) versus Pickett et al. (1987)**

In many respects, the models offered by Connell and Slatyer (1977) and Pickett et al. (1987) reflected a restatement and continued evolution of the Clementsian model. Connell and Slatyer (1977) proposed three models (tolerance, inhibition, and facilitation), of which the latter conforms with the classical Clementsian model (MacMahon 1980). General causes of succession in the Clementsian model are nudation, migration, ecesis, competition, and reaction. Connell and Slatyer (1977) maintained these "pathways" (their terminology) in the form of facilitation, tolerance, and inhibition (Burrows 1990).

Pickett et al. (1987) criticized these notions as lacking testability, and commented on the difficulty of discerning between inhibition and tolerance. Pickett et al. (1987) listed site availability, differential species availability, and differential species performance as general causes. They also contributed an extensive list of contributing causes with modifying factors affecting successional pattern. Thus, disturbance is seen as a cause of site availability and size, severity, timing, and dispersion of disturbance as modifying factors. Similarly, dispersal, propagule pool, and resources available are seen as causes of differential species availability, while ecophysiology, life history strategy, environmental stress, competition, allelopathy, herbivory, predation, and disease cause differential species performance. Numerous autecological, synecological, and environmental factors are listed as modifiers of the latter two general causes. There is no doubt that Pickett et al. (1987) developed a more satisfying theoretical framework for understanding vegetation dynamics. Consideration of these "natural phenomena" places the work by Pickett et al. (1987) within the "kinetic concept" (Burrows 1990) of vegetation dynamics.

**Vital Attributes (Noble and Slatyer 1980)**

The Clementsian and facilitation models of Connell and Slatyer (1977) emphasized community phenomena. Noble and Slatyer (1980) made more use of life history characteristics, reflecting species' autecology. The incorporation of such species-specific attributes is considered fundamental to developing concepts deterring from classical deterministic model types (Cattelino et al. 1979). Several generalizations
are made within the model. These are: that species recover after disturbance through propagules and resprouting; that there is a pulse of recruitment following disturbance characterized by increased growth and decreased competition; that after initial growth, recruitment slows down, and that once a plant is established, it is difficult to displace; that there is a repression of recruitment of additional species; and that long-lived species that can propagate in the presence of others tend to dominate.

In this model, three main groups of "vital attributes" pertinent to a disturbed site are emphasized: the method of arrival at the site; the ability to establish; and the time taken for the species to reach crucial life stages. The model also defined three major life stages--the juvenile, mature, and propagule (sexual or asexual), and the recognition that if the adult population is lost and no propagules exist, the species may become locally extinct. The model is applied by classifying species in terms of the first two vital attributes. Replacement sequences following disturbance are then generated by considering the following aspects of the third vital attribute: the time taken for a species to reach reproductive maturity following disturbance, the life span of the species under undisturbed conditions, and the time taken for propagules to be lost from the system. The model permitted multiple successional pathways in areas disturbed by frequent fire (Cattellino et al. 1979), a characteristic that may make this model particularly suited to the sagebrush steppe milieu.

This model has been incorporated in a computer algorithm called FATE (Functional Attributes in Terrestrial Ecosystems--Moore and Noble 1990). As the name implies, the model examined succession at the data resolution of functional groups. Their computer algorithm is divided into three submodels: (1) a life history submodel based on Harper (1977) and incorporating propagules, germinants, immature and mature plants; (2) the competition submodel which requires the ordering of plant groups in terms of competitive relationships for the single "dominant environmental resource" (or several resources showing a gradient in the same direction); and (3) a submodel that deals with disturbance (fire, storms, and episodic grazing) and requires the proportion of each functional group destroyed in such an event. Partial or complete destruction of plants results in the liberation of resources and initiates species/group replacement.

Slatyer (1976) noted several advantages and disadvantages to life-history-based models. Amongst the advantages are the fact that such models have modest data requirements that can be drawn from practical rangeland or forest experience. Since these models are based on autecological data, long historical runs of
information are not necessary. The models are amenable to experimentation such as harvesting, various disorders, and the incorporation of new species. The prime disadvantage is the computer time required, especially for species-rich communities.

The Resource Ratio Hypothesis

Tilman's (1985) model, employing his Resource Ratio Hypothesis, is applied to plant species that are dominant at some time in the successional trajectory. This model is based on interspecific competition for resources and the long-term supply of these resources. This has commonly been applied to explain spatial gradients. Tilman (1985) related temporal succession directly to the requirements of species for limiting resources and the change in resource availability through time. Tilman (1988) incorporated random disturbance within the above framework in a computer algorithm called ALLOCATE. Different life histories, including growth allocations, are emphasized in explaining differential species performance under different conditions of resource availability and disturbance. In this sense, the model is similar to the Vital Attributes Model and subscribed to Pickett et al.'s (1987) theoretical framework.

Grime's Life-Strategy Model

Grime (1977) used life histories and assumptions concerning the relationship between competition and plant traits to explain vegetation dynamics. The three basic life strategies recognized are ruderals, stress tolerators, and competitors. Ruderals show greater reproductive effort and growth rates than the other categories of life strategies. Tolerators are the converse of ruderals and, thus, are found in unproductive and undisturbed habitats. Competitors show low reproductive effort but high growth rates and are found in undisturbed but productive habitats.

Other models incorporating life histories abound, for example, STEPPE (Coffin and Lauenroth 1990), and ZELIG (Urban et al. 1991), a forest model derived from FORET (Shugart and West 1977, Shugart 1984). As an example of their utility, STEPPE and ZELIG were used to make comparisons of ecosystem response to spatial and temporal variability in the environment (Coffin and Urban 1993).
Multiple-Stable-States Models

The State-and-Transition Model (Westoby et al. 1989a, b) is the best known Multiple-Stable-States Model within the range management discipline. This model lends itself to both the temporal and spatial domains, although the former is emphasized. It was developed to summarize information (management and environmental) relevant to vegetation changes under conditions of livestock grazing. It was developed as an alternative to stability and equilibrium-based models. This model recognizes discrete states (stable plant communities on a site showing little change in soil resources) separated in time by rapid community change (relative to annual fluctuation). Change is triggered by overcoming thresholds. Thresholds combine both environmental and management criteria. From a livestock management point of view, the threshold can be seen as variable and dependent on climate. The model allows for opportunistic management through manipulation of livestock stocking rates, seasonality of grazing, and other forms of management in conjunction with stochastic climatic events to change system state. This model has been greeted with considerable enthusiasm by the range management community (Friedel 1990, 1991, Laycock 1991, Bormann and Pyke 1994) and is being considered as an alternative to the Clementsian model as a basis for range condition analysis (NAS 1994, West et al. 1994).

Several attempts have been made to incorporate sagebrush steppe vegetation dynamics within multiple-stable-states models. West (in press) incorporated the combination of climatological effects, livestock grazing, and management within a State-and-Transition model for sagebrush steppe vegetation (Figure 1.4). Miller et al. (1994) considered sagebrush steppe vegetation to fall within three stable states. These are discussed further under the section "A General Description of the Sagebrush-Dominated Vegetation Types."

Combination of Multiple-Stable-States and Continuum Concepts

Friedel (1991) suggested that severe impacts (disturbances) in the form of extended heavy grazing can cause ecosystems to cross thresholds into a new domain. Unlike stable state, the word "domain" implies that change in composition is possible within a defined vegetation compositional space. Factors such as variation in climate and mild herbivory and disease levels may be responsible for this change in composition.
This recognizes that disjunct changes in vegetation composition can occur, as well as more benign fluctuations and trends due to less severe climate, fire, and grazing impacts.

Degradation Models

Several degradation models specific to range management have been proposed. One South African example has been incorporated within an expert system using ordination techniques to detect trends (Bosch and Booysen 1992). In this case, the degradation model is built by assuming a space-for-time relationship. A suite of sites, ranging from good condition to degraded, is used to define the degradation process. Monitored sites are considered relative to this model by comparison within ordination space.

In a second model, the stepwise model of degradation (Milton et al. 1994), the degradation process occurs in several disjunct steps, each associated with increasing costs for rehabilitation. The first step is characterized by changing demography of the fodder plants, while the second step is identified by the process of loss of plant diversity and productivity. The third and fourth steps show reduction and eventual loss in plant cover and associated acceleration in soil erosion.

![Diagram of multiple-stable-states model for sagebrush-dominated vegetation derived from West 1995](image-url)
While the Bosch and Booysen (1992) model involved the classification of species into increasers, decreasers, and invaders, and appeared inflexible (deterministic) in that a specific community is classified as degraded, it remained very flexible. This is so because multiple degradation sequences could be incorporated within the model and analytical environment (O.J.H. Bosch, pers. comm.). Milton et al. (1994) considered not only plant community composition but also incorporated demography, plant diversity, plant cover, and soil loss processes, all of which are important to the degradation issue.

Resource-Based Models

Many resource-based models exist, most of which are founded on tracking water, nutrient, and light relationships to individual plant species. Smith and Huston (1989) published "Theory of the Spatial and Temporal Dynamics of Plant Communities" based on the effect of these parameters on plant life histories. Three sets of constraints were examined: both extremes of water availability, light availability; and a combination of water and light availability. The model is said to be able to examine diverse phenomena (both temporal and spatial) at several criteria of system organization ranging from organismal through population, community, and landscape criteria. In general, physiological models examining any possible variable of interest can be found. For example, Milchunas et al. (1988) presented a model of the interactions of environmental moisture with evolutionary history of grazing to explain grazer-grassland interactions over a range of grassland communities.

The heightened interest in the effect of elevated carbon dioxide in the atmosphere has spawned several models examining the effect of $CO_2$ on plants (Comins and Mcmurtrie 1994). There is no doubt that these models are plausible, but their consideration as models describing vegetation dynamics from a range management perspective is not likely, since they do not serve the usual objectives of describing vegetation dynamics following grazing and other disturbances important to rangelands such as sagebrush steppe.

Forage Production Models

Numerous models examined forage production relative to rainfall and soil moisture budgets (Stafford Smith and Pickup 1993). Many of these do so on a physiological basis and do not consider dynamics beyond the lifespan of the plants of interest (Stafford Smith and Pickup 1993). Such models therefore suffer the same
shortcomings (from a range management perspective) as did physiological models. These models are generally simulation models (for example, Seligman and Van Keulen [1989], the FORAGE [Baker et al. 1991] submodel of SPUR, a general rangeland production and utilization model [Hanson et al. 1988]). The SPUR model is based on the ELM (Ecosystem Level Model, Innis 1978, Parton 1978) and the grassland models developed by Parton et al. (1978) and Detling et al. (1978). Simulation modelling of currencies (energy, carbon, or any particular nutrient) have also been extended to plant populations in exploited environments. Thus, the concept of sustainability in terms of maintaining plant populations continuously being harvested has been considered within economic models (Levine 1988).

**Centripetal or Chaotic Models**

These models were developed to describe vegetation dynamics within systems governed by high climatic fluctuation. In such areas, plant communities are not primarily controlled by herbivores, but largely by the variation in amount and seasonality of precipitation. This contrasts with the notion that the expression of vegetation is governed by mean rainfall as in older equilibrium-based models (using the intuitive balance between plants and their environment as the definition of equilibrium). It is possible that the coefficient of variation of mean annual rainfall may exceed 30% (the yardstick determined by Ellis and Swift 1988) in defining nonequilibrium-based models, but other factors also need to be considered if nonequilibrial systems are defined from the perspective of the western ranch manager. To nomadic pastoralists, the ability to survive dire conditions by moving makes the concept of nonequilibrium of little importance.

Much research has been conducted in the sagebrush steppe system (Blaisdell et al. 1982, Tisdale and Hironaka 1981, West 1979, 1983b, 1988, in press), and yet frequent marked changes in the abundance of major species have not been demonstrated. Another factor is the ability of human beings to overcome climatic constraints using high-energy technological means. Hauling water and storing feed through seasonal or between-year stochastic constraints are examples of this.

Although the existence of nonequilibrial systems has forced managers to consider new constraints on the expression of vegetation, these patterns have not yet been demonstrated to operate within the sagebrush
steppe system. Consequently, the centripetal or chaotic nonequilibrial systems (seen as distinct from the State- and-Transition nonequilibrial model) will not be considered further in this dissertation.

**Markov Chain-Based Modelling**

Successional models classified under this heading are predictive, nonmechanistic, and based on Markovian matrices. Building such models requires the definition of different states (that could be defined from cluster analysis) and probabilities of moving from one state to another. Both continuum and discrete community concepts can be accommodated through the careful definition of these states.

For several reasons these models are unsuitable for range management, for example, the difficulty in defining states, the difficulty in collecting the required data, and the lack of flexibility in accommodating change. Entirely new data sets would need to be collected to accommodate the arrival of a new species. Usher (1981) reviewed the above disadvantages and others in more detail. One of the major disadvantages of such models is the assumption that future behavior is entirely dependent on the present state (Slatyer 1976). In spite of these limitations, Rego et al. (1993) presented a recent and insightful example of modelling plant community dynamics using such techniques.

More recently, Semi-Markov Models have been developed as an extension of the above. Such models incorporated biological models of succession and disturbance to define community states and have been considered to be of interest to land managers (Moore 1990). Moore (1990) incorporated the Vital Attributes Model to determine: the probability that a particular stand would still exist at a given time, the extinction times for individual species, and the optimal use of prescribed disturbances. The Semi-Markov Model appeared to have preserved the major advantage of Markov Models (predictability) while overcoming many of the disadvantages mentioned above.

**Linked Models**

A few attempts have been made to link models simulating different attributes (species, resources and disturbance regimes) within a single computer program. For example, consider a model by Lauenroth et al. (1993). The authors linked several simulation models to incorporate vital attributes and the modelling of ecosystem functioning. Although vital attributes are generally based on limited resources, they do not achieve a
simulation of important functional currencies. Nevertheless, this approach allowed the comparisons of different ecosystem types. In another example, Levine et al. (1993) developed FED (Forest Ecosystem Dynamics), which linked submodels of soil processes, forest growth and succession, and radiative transfer.

**Spatial Models**

Many features of spatial models show a mutual interchange of ideas with temporal models. This includes continua of change versus discrete steps of change in either plant populations or communities. Changes in the spatial domain are generally considered to be resource-based and most easily understood from an individualistic perspective. Hence, the predominance of vital attribute and resource simulation models are based on resource currencies involved in system constraints. Some authors examined spatial patterns to invoke particular metapopulation models, but since these imply dynamics over time, they are considered here under the heading of "Spatio-Temporal Models in Artificial Landscapes."

**Continuum Models**

The spatial continuum models have much in common with the temporal continuum models. Only the postulated mechanisms held responsible for the model functioning differ.

Austin and Smith (1989) reviewed three basic views of continuum theory. First, Gleason's (1926) "individualistic continuum" considered species abundance optima and their limits as independently distributed along the ecological gradient. Second, Gauch and Whittaker (1972) considered major species to be regularly distributed along gradients, with optima for major species as evenly spaced, while those for minor species as independently spaced. Third, a stratal continuum described continua for each stratum of vegetation. In this case, species distribution may be regular or irregular, and strata may be correlated or uncorrelated (Austin 1985). Austin and Smith (1989) presented a new continuum model. They identified 3 kinds of environmental gradients: indirect (= complex gradients); resource (defined by water, light, carbon dioxide, essential nutrients, etc.); and direct (soil pH and air temperature). They noted that indirect gradients cannot be extrapolated beyond the spatial and temporal bounds of data collection. Species richness was defined as bimodal (as a result of biotic conditions). Species dominance was described as trimodal. Standing crop was hypothesized to be
unimodal. The model was able to accommodate four sets of theoretical concepts thought to be responsible for vegetation patterns:

1. Species response curves (Mueller-Dombois and Ellenberg 1974);
2. Grime’s primary strategies for species survival (Grime 1977);
3. Tilman’s nutrient ratios (Tilman 1982); and
4. Light/nitrogen gradients (Tilman and Bazzaz cited in Austin and Smith 1987).

Piosphere Models

Several papers have illustrated the presence of landscape-scale piosphere effects (Andrew 1988). Piospheres are defined as changes in plant cover (or species composition) due to a grazing gradient, usually from a watering point outwards. Such gradients in vegetation parameters have been verified using ground-collected data as well as remotely sensed data. The fact that such effects are found around numerous watering points in areas of homogenous vegetation and topography implies that such a model may be predictive within the spatial domain.

Combined Spatial and Temporal Models

The development of combined spatial and temporal models shows a definite evolution. Initial attempts combined constituent models from the spatial and temporal domains. The development of spatio-temporal models generally shows all possible combinations of spatial and temporal models. More recent and sophisticated models are able to incorporate the interaction of mechanisms specific to the spatial and temporal domains. Landscape models incorporating disturbance, vital attributes, limiting resources, and community constraints appear to be at the forefront of this evolution. The first spatio-temporal model described is Whittaker's Climax Pattern Hypothesis.

Climax Pattern Hypothesis

Whittaker (1974a) developed his "Climax Pattern Hypothesis" from continuum models existing at the time. Whittaker outlines several important points to his model:

1. Plants respond to the environment individualistically;
2. The landscape forms a complex pattern of environmental gradients;
3. Plant communities tend towards a climax at each point on the landscape;
4. Differences in the environment along a gradient result in a continuum of communities;
5. Since environmental gradients may be complex, so are the resultant plant communities;
6. Of all the communities, there is a prevailing community considered to be the climax community of the landscape.

Spatial and Temporal Resource-Based Models

Smith and Huston (1989) presented a model examining spatial and temporal patterns on a cost/benefit basis regarding physiological and life history constraints on the use of two or more resources. They maintained that plant functional types based on the above concepts can explain both spatial and temporal patterns, and that such a model can be used to examine phenomena at the full range of criteria. Such models represent coenoclines in both space and time (White 1979).

Dynamical Systems Theory

The Dynamical Systems Theory considers the vegetation and environment to be coupled somewhat like the Clementsian and Tansleyian "reaction" concept. The model included both continuum and community criteria while incorporating disturbance as part of the larger perspective. Roberts (1987) described two complementary n-dimensional spaces, vegetation composition space and environmental space. Species are described to have an ecological amplitude occupying a subvolume of ecological space. The shape and position of this space is dependent on the species and the way in which the environment is measured (e.g., synecological versus autecological, or physiological measures).

The initial trajectory depends on the species that find themselves at the study site and their life history traits. Thereafter, the trajectory is dependent on the vegetation-environment coupling, incorporating either positive or negative feedbacks. Environmental space may thus change so that species can no longer be accommodated, resulting in changes in the community. Species influence each other through environmental space. This can be translated into a vector acting upon the position of the site within environmental space. Environmental factors are classed as plastic (e.g., light), if they can change rapidly but can also return to
former values at short notice (after an acute disturbance), or elastic (resistant to change). The n-dimensional vector summation of vegetation reaction, environmental elasticity, and plasticity results in the trajectory.

Ecological Field Theory

A second model/theory with a firm mechanistic base is that of Ecological Field Theory (Walker et al. 1989). Plant spatial influences are seen as "pulsating geometric zones" around individual plants. This pulsating characteristic allows for changes in field intensity, and influences the surface, and, thus, the intensity of interaction between plants. Fluctuation allows for the establishment or death of plants on either an individual or functional basis, depending on prevailing environmental conditions. Important factors (soil resources and microclimatic factors) are combined into a single resource index. This model therefore places more emphasis on resources than autecological characteristics.

Spatial Expansion of FATE

Moore and Noble (1993) enabled the modelling of plant community dynamics at larger than stand scale by using FATE to generate replacement sequences. The sequences are then assumed to be repeatable pathways, and used as required over the spatial domain in place of full-scale simulation. This allowed the effects of large-scale disturbances to be modelled at the ecosystem level.

Spatio-Temporal Models in Artificial Landscapes

Several landscape-level models operating over artificial landscapes have been developed (Baker 1989, Turner et al. 1993b, 1994). These include many topics, including simulation models of winter foraging by large ungulates (Turner et al. 1993b). Recently, Roberts (in press a, b) used vital attributes adapted for the forest environment to model forest stands, focusing on seed distribution and disturbance propagation.

Geographic Information Systems and Remote Sensing-Based Models

Although indices based on different wavelengths of reflected radiation for estimating various vegetation parameters from remotely sensed imagery could be viewed as models, they are more commonly considered as tools. These and other indices measuring factors other than biotic are used for monitoring or
exploratory purposes. It is only when remotely sensed data are combined with Geographic Information Systems (GIS) that predictive models are formulated. Usually ground truthing the remotely sensed data is used for validation of the model. The most common ecological models formulated within the GIS environment are those determining the habitat for various plants and animals or those predicting the spread of invasive species. Software and hardware systems linking GIS and a spatial modelling package have been developed (Costanza and Maxwell 1991). A specific forest successional model based on vital attributes developed by Roberts (in press a, b) was incorporated within a GIS-based system and used successfully to model landscape vegetation dynamics of Bryce Canyon National Park. Another recent model, ECOLECON (an Ecological-Economic model for species conservation in complex forest landscapes), is also spatially explicit via linkage to a GIS system (Liu 1993).

Expert Systems

Noble (1987) predicted that expert systems could have considerable impact in ecology, particularly in applied disciplines. Expert systems are not explicit models, although they may incorporate models. Rather, they aid the making of decisions or validate them (Noble 1987). The apparent artificial intelligence stems from concepts, principles, or just general "rules of thumb" that are stored within the algorithms. Interaction with the user will yield different responses dependent on the prevailing situation. Expert systems are not limited to computer technology but may be communicated in the form of wall charts and manuals (Stafford Smith and Foran 1990).

Several examples of expert systems can be found within the range management discipline. Some examples are RANGEPACK (Stafford Smith and Foran 1990), SHRUBKILL (Ludwig 1990), RSPM (Resource Systems Planning Model [Stuth et al. 1990]), and SPUR (Simulation of General Grassland Model [Hanson et al. 1988]). Such expert systems may incorporate information from diverse disciplines such as economics, vegetation dynamics, management of herd dynamics, and may even aid the design of pastures.

A South African expert system (ISPD) uses multivariate techniques to determine trends within plant community data, which are consequently interpreted on the basis of a degradation model (Bosch and Kellner
1991). This monitoring approach allows managers to discern changes in plant communities that herald more serious deterioration and thus take remedial steps.

**General Discussion of Models**

Although the models examined do not constitute a complete list, several observations can be derived from Table 1.1. The bases of models examined show considerable variation in terms of the criteria identified by Allen and Hoekstra (1992). Environmental, climatic, or resource variables operating at even larger spatial scales may be harnessed as driving forces or constraints within these models. The particular criteria utilized in a model reflect the developers' interest and/or background. In many cases, a hierarchical approach is assumed in identifying mechanisms at a lower level of organization than that of the phenomena considered. Thus, population dynamics of a collection of species may be seen as driving community dynamics and ignoring community-level functions. Criteria from different levels of organization are rarely considered to act in tandem to explain the phenomenon of species replacement. This can only be seen as a deficiency, since applied ecologists have shown that the interaction of processes can be important in determining replacement sequences.

Also of interest is the pattern of incorporation of concepts within the temporal, spatial, and spatio-temporal domains considered. All three possibilities include models showing individualistic versus community dynamics, or continuum versus discrete dynamics.

Consideration of the full range of models available also gives one an impression of what the future evolution of models of vegetation dynamics may be within the realm of land management. With the advances in computer technology, it is apparent that more powerful spatio-temporal models utilizing GIS, remote sensing, and any of the constituent models discussed will become increasingly important. Instead of relying on a particular model, land managers will probably run a number of different models to aid decision making. Incorporation of remote sensing and GIS will enable models to be applied with greater realism. For example, disturbance submodels will be applied in such a way as to take heed of topography and other natural barriers. Past history will be incorporated within a management tool. Management relative to recent stochastic disturbances will be quickly and efficiently reassessed. Thus, flexible management of landscape diversity,
maintenance of corridors for wildlife, maintenance of firebreaks, or other management objectives will be possible. It becomes necessary at this point to discuss stability and equilibrium concepts inherent in some of the above-mentioned models.

**Stability and Equilibrium**

Many believe the concepts of stability and equilibrium to be central to ecological theory. Debates relating species' richness, the nature of foodwebs, and other phenomena to stability are ongoing. Since these are such important concepts, they usually have been incorporated as basic assumptions in models of vegetation dynamics. Other models highlight the lack of stability and equilibrium. Several authors even discourage the use of these concepts entirely (Peters 1991, Pimm 1991, Botkin 1990). Reasons for this dissension will become apparent in the ensuing discussion.

Equilibrium and stability are two closely tied ecological concepts. Botkin (1990) used an analogy to distinguish between them: a metal rod balanced on its end as an example of a system that is in equilibrium and yet unstable. Balls on a billiard table and in the corner pouches can both be viewed as in equilibrium, but the balls in the pouches are more stable than those on the table. Equilibrium can thus be viewed as a condition of constancy or a lack of change. This overlaps with one of the more commonly used nuances of stability, as the following summary will show.

**Stability**

The concept of stability is known for its varied use of several criteria. Several papers attempted to trace the history of development of this term (Noy-Meir 1974, Orians 1974, Whittaker 1974a, Walker 1989, Pimm 1991) but often ended in a quagmire of cross-references. Certainly, the numerous definitions of stability are an indication of the broad meaning of this term. For example, Orians (1974) listed 7 definitions, while Whittaker (1974b) listed 13. Papers dealing with this concept are too numerous for a comprehensive review here. For this reason, I will concentrate on papers that attempt to summarize divergent views, or papers that offer particular insight to the problem applied to rangeland plant communities.
Botkin (1990) referred to 3 alternative concepts of stability important to ecology prior to the 1980s: (1) static equilibrium, or absolute constancy of abundance, of all species over time; (2) quasi-steady state stability encompassing variation that is persistent but small enough to be ignored; and (3) classical static stability by systems showing constancy unless disturbed, and an ability to return to the previously defined state of constancy after disturbance. Walker (1989) described two major themes of stability still in use today: that of constancy, referring to "the degree of change in the abundance of the system's components over time"; and that of persistence of species over time. This followed Margalef's (1969) introduction of "adjustment or lability" versus "conservatism, endurance, or persistence."

Other papers attempted to break down stability into distinct components. Webster et al. (1975) defined resistance and resilience as components of relative stability. Resistance was defined as inversely related to the maximum amplitude of the measured parameter following disturbance, thus corresponding to previously described constancy or steady state models of stability. Resilience was directly related to the rate of recovery of a community following disturbance. Connell and Sousa (1983) stated that the first instance is equivalent to inertia, persistence, and resistance, or simply lack of change of numbers, which has been termed as constancy, conservatism, endurance, and persistence. Terms applying to the second component are adjustment, elasticity, and resiliency.

Westman and O'Leary (1986, page 180) defined several components of resilience:

1. elasticity--"rate of recovery following disturbance";
2. amplitude--"threshold of disturbance beyond which recovery to the original state no longer occurs";
3. malleability--"extent of alteration of the new stable-state from the original";
4. damping--"extent and duration of oscillation in an ecosystem parameter following disturbance."

In addition, two kinds of disturbance are identified: chronic perturbation, referring to gradual loss of phytomass (for example, due to grazing); and acute perturbations, defined as instantaneous loss of phytomass (for example, by fire). The aforementioned components are applicable to both chronic and acute perturbations. A fifth component, hysteresis ("degree to which the path of restoration is a mirror image of the path of degradation") (Westman 1978, page 705), is applicable to chronic perturbations only. Westman (1986) gives a complete overview of these and other terms, including synonyms.
Orians (1974) specified 4 different forms of community stability: (1) constancy (the lack of change of some parameter within a system), (2) persistence (the time length of survival as determined by the parameter measured), (3) inertia (the ability of a system to resist and recover from external disturbances), and (4) elasticity (the speed with which a system returns to its former state).

The above concepts, together with a few others, are graphically depicted in Figure 1.5. Figure 1.5a features a chronic disturbance (for example, grazing). In this case, no threshold of disturbance is reached, and the system recuperates to its former state. Note that a delay occurs between initiation of the disturbance and reaction by the attribute measured. The boxed area depicts hysteresis--recovery appears to be a reversal of degradation. Figure 1.5b (a hypothetical acute disturbance) illustrates what occurs when a threshold is overcome. The system moves to a new state, and the attribute measured stabilizes around a new mean.

Malleability is measured as the difference between the two stable states for the attribute measured. The amplitude is larger than the malleability and is a measure of the change of the attribute at the point of maximum deviation from the original state. Note that with the acute disturbance there is no time delay between application of the disturbance and manifestation of the disturbance.

It has been argued that these views of stability reflect the ongoing influence of classical Clementsian ideas. Orians (1974) graphically depicted these concepts in two dimensions, more easily understood from the perspective of nonlinear models of vegetation dynamics. Lewontin (1969) considered attractors and basins of attraction. On the same theme, Crowley (1992, page 246) proposed the following definition of dynamics: "a tendency for population densities to avoid dynamic boundaries (boundedness), or to approach a dynamic attractor." Since plant or animal densities may wander within, but rarely exceed, bounds, it implies that such bounds would be difficult to measure empirically. This definition does appear to be more valid for multiple-stable-states situations. Furthermore, Crowley (1992) supplied computer algorithms to determine stability based on random walk and randomization techniques. Yet another definition of stability is given by Noy-Meir (1974, page 220) as "the set of attributes of a system which minimize the magnitude, duration, and irreversibility of the changes in its own state resulting from external changes or disturbances." Thus, DeAngelis and Waterhouse (1987) summarized factors that have been perceived to increase stability of equilibria in mathematical models. These are functional interactions between species, disturbance patterns
that disrupt adverse feedback loops, integration of smaller scale units into larger units, compensatory mechanisms operating on low populations, and the moderating effects of spatial extent and heterogeneity.

The diagrammatic representation (Figure 1.5) and definitions of components of resilience emphasize the fact that stability can only be determined after a disturbance, as intuited by Waide (1988) and Connell and Slatyer (1977). This is in contrast to equilibrium, for which there are several definitions, all implying lack of change and generally measured as such.

**Equilibrium**

The concept of stability has been confounded with the issue of equilibrium or nonequilibrium. Botkin (1990) defined an equilibrium as a condition of constancy which may be stable or unstable. Systems which return to steady state are reputed to be in equilibrium. This has been extended to systems returning to a previously identified trend (Pers. comm., Monica Turner 1993).

![Diagram](image)

Fig. 1.5. A graphic description of the components of resilience (stability) (N.E. West, pers. comm. 1992).
Within range management, an equilibrial model has been central to range condition analysis for many decades. Range condition is considered to be inversely related to livestock impact. Congruous with the Clementsian successional model, any disturbance by livestock reduces range condition from a maximum observed for undisturbed "climax" vegetation. Removal of this disturbance allows the system to return to a pristine state or that of high range condition (conforming to the resilience concept of stability). Range management aims at balancing livestock presence with the maintenance of an acceptable range condition, thus subscribing to an equilibrial perspective of the system.

Recently, nonequilibrial models have been advocated within range science. Some of these models stem from observation of pastoral systems in Africa. The systems are judged to be in equilibrium or nonequilibriu on the basis of whether abiotic or biotic (more specifically, livestock) factors control the expression of vegetation. Generally, phytomass has been used as an index to determine equilibrium versus nonequilibriul conditions. Nonequilibriul models are contrary to traditional models in that phytomass shows high fluctuation unconstrained by livestock. I see several problems with these notions, since some of these problems also apply to stability. These will be addressed in the general discussion.

A second common conception of an equilibrial system is one in which density-dependent dynamics are found to occur. Chaotic or centripetal models define systems where this is found not to occur. The recent rapid development of landscape ecology has led to the development of new equilibrial concepts at larger spatial scales. Such definitions of equilibrium consider patch disturbance balanced by vegetation regrowth (Sprugel 1991). Sprugel (1991) listed 3 instances that may result in nonequilibriul dynamics: (1) when the spatial scale of disturbance is similar or greater than the area being considered (explored in greater detail by Turner et al. 1993a); (2) when unique events of the past impact the dynamics of the variable being considered (the author gives the example of a pathogen outbreak from which eastern hemlock populations have taken millennia to recover from); and (3) when the most commonly considered reason for nonequilibriul is due to climatic variability. Such examples emphasize the fact that plant communities exhibiting nonequilibriul dynamics may be very difficult to define because of their dynamic nature (Sprugel 1991).
General Discussion of the Concepts of Stability and Equilibrium

Clearly, Peters (1991) was correct in stating that the concepts of stability and equilibrium were indeed concept clusters. Lack of tight definition has resulted in a broad interpretation of these concepts. The public, as well as scientists, have grasped these simple notions as central to vegetation dynamics. Some studies have shown that plant communities are far from static. For example, North American plant communities may still be adjusting from the recent "Little Ice Age" (Tausch et al. 1993, Nowak et al. 1994). From that point of view, we realize that the development of vegetation types has been linked to climate change within the Holocene. New concepts of vegetation dynamics are needed to explain the more changeable nature of plant communities.

Several additional problems that are applicable to both stability and equilibrium are discussed further.

Several authors have implied that definitions of stability need to be more specific. Noy-Meir (1974) listed 4 important factors that should be considered when measuring stability: (1) the choice of attributes that best define the state and can be used for measuring it; (2) the time scale; (3) the benchmark against which stability is measured; and (4) the particular aspect of stability considered to be of importance.

Waide (1988) listed 4 reasons for the confused use of the term stability: (1) the fact that many have viewed systems isolated from their environment; (2) the view of systems exclusively from human spatio-temporal scales; (3) the extrapolation of population and community dynamics to ecosystem dynamics; and (4) the continued imposition of notions of stability derived from Clementsian models of succession.

Stability has been linked to single variables as well as to community measures. For example, stability is often linked with diversity, either as the outcome of stability or giving rise to stability (Walker 1989). Attempts to unravel these relationships are ongoing (for example, Frank and McNaughton 1991). Stability is scale-dependent, both in space (Waide 1988) and time--even systems under nonequilibrium conditions can be considered as stable at short time scales (Williamson 1987).

The concepts of community compositional stability, equilibrium, and similarity can be viewed as multivariate (considering species as variables) and multidisciplinary since interactions within and between fauna and flora as well as soils, climate, geology, and other disciplines can be expected (White 1979). The above concepts should also be considered as specific to the scale at which the work was executed and variables
measured. This implies that systems seen to be stable and at equilibrium at a certain scale may be unstable and nonequilibrial at another scale. This is not a new concept; several authors (Tongway and Ludwig 1990, Pickup 1985) considered system instability at a small scale (erosion cells) as intrinsic to system stability at larger scales. Consequently, instability at one spatial or temporal scale should not be viewed as contradictory or affirmatory at another.

Peters (1991) advised scientists not to use the stability/equilibrium concepts at all. An alternative solution would be to refer directly to the variable(s) being measured, while referring to the particular framework of stability and defining the spatial and temporal scales at which the variable was examined. Other restrictions discussed would still apply.

**A Restatement of the Objectives and Research Hypotheses**

The project proposal written prior to data collection listed specific objectives and predictors for stated hypotheses. With time, I realized that this project was more exploratory in nature and employed exploratory analytical tools to the extent that using predictors was not always valid. However, these hypotheses were useful in directing research and are mentioned within chapters dealing with specific projects. The initial scheme outlined alternative hypotheses, which are preserved within the structure of Table 1.2. A restatement of the objectives follows.

1. To examine the relative utility of models for describing sagebrush steppe vegetation dynamics by assessing the validity of the primary assumptions and concepts involved (stability, equilibrium, polyc1imax versus monoclimax views, continua of change versus discrete change, individualistic change versus community change, Gaussian response of individual plant species, the concept of hysteresis, etc.).

All of these concepts are explored at the spatial and temporal scales delimited by the data sets (see site descriptions for this). Where possible, these concepts are examined for both single species as well as for communities. The perspective of stability examined is that of the ability of populations and communities to return to a semblance of that preexisting the disturbance event (a definition strongly implied by the Clementsian Model). In addition, the relict areas afforded an opportunity to examine the constancy definition of equilibrium/stability as implied by the Clementsian Model and predefined climax community.
The Mills data set (Chapter 5) will also allow the testing of the resilience model of stability. Although later models of Clementsian succession allowed multiple pathways, the concept of hysteresis will also be examined.

Because of the difficulty of defining stable states, the examination of the notion of stability from the State-and-Transition Model will not be more than a rationalization. Distinct clusters of points for any long-term or spatial trends will be taken as evidence for alternative stable states (or possibly polyclimax). A single cluster of points will be taken as defining a single stable state (monoclimax), while trends will be taken to imply that the concept of stable states does not hold, if the range of change is large enough.

Table 1.2. Summary of studies dealing with the discussed concepts and assumptions. Columns represent separate studies, while rows represent major assumptions, concepts, or characteristics examined.

<table>
<thead>
<tr>
<th>Assumptions/Concepts Tested(^1)</th>
<th>Temporal Data Within Relicts (Ch. 4)</th>
<th>Temporal Data Following Disturbance (Ch. 5)</th>
<th>Piosphere Study (Ch. 6)</th>
<th>All Passey et al. Sites (Integrated)</th>
<th>Literature Review (Ch. 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stability</td>
<td>Indirectly</td>
<td>Yes – resilience model</td>
<td>Indirectly</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Equilibrium</td>
<td>Yes</td>
<td>No</td>
<td>Indirectly</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Continual vs. discrete change</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Individualistic vs. commun. change</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Hysteresis</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Repeatability of autocorrelations</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Repeatability of species response curves</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Similarity of relict to grazed areas</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
</tbody>
</table>

\(^1\) The above factors will be examined at the data resolution of individual species and community resolutions where possible. Several of the columns of Table 1.2 correspond to major chapters of this dissertation.
Reexamination of the the various Passey et al. (1982) data sets (Chapter 4) will allow the determination of whether community changes occur through the concerted change of species or on a more individualistic basis. The nature of change of individual species in the spatial and temporal domain will also give an indication of whether such changes are in the form of continua or discrete "jumps." These discussions will be considered in the light of other data gleaned from the literature.

The presence or absence of trends, and the nature of trends within relict areas, if present, will give an indication of the presence of equilibria. If the Mills data (Chapter 5) show an ability of plant communities to return to a semblance of their predisturbance composition, this will be taken as evidence of equilibrium also.

Since the above factors distinguish primarily between Clementsian-based models and others, the various data sets will be used to check predictions of the most favorable models surviving the above scrutiny.

2. To determine the requirements of a model describing vegetation dynamics in sagebrush steppe from a range management perspective, and to determine if any of the existing models meet the above requirements.

3. To discuss the location of monitoring points and benchmarks relative to model choice, representability, and availability of monitoring points and benchmarks to the grazed areas.

Additional chapters dealing with a general discussion of the perceived needs of the range management profession are presented for a better general model of vegetation dynamics, a description of vegetation dynamics within the sagebrush steppe type, methodology, and a final chapter integrating results from individual studies to test the questions outlined in the above table.
CHAPTER 2
ACCOMMODATING THE NEEDS OF RANGE MANAGEMENT
AND ECOLOGICAL THEORY IN MODELS
OF VEGETATION DYNAMICS

This chapter fulfills the second objective defined in Chapter 1, namely: to determine the requirements of a model describing vegetation dynamics in sagebrush steppe from a range management perspective, and to determine if any of the existing models meet the above requirements.

Table 1.1 indicated a diversity of models that could potentially be used in range management. It is therefore necessary to define the requirements of range managers for such models. I determined that models could be classified into one of three possibilities: simulation models used for research, conceptual models explaining ecosystem functioning relative to management, and expert systems for technology (information) transfer. This classification reflects broad requirements of range managers for models of vegetation dynamics.

The complexity of simulation models precludes their use by managers, but researchers might find them useful for exploring different management options, or regimes of management application. The need for a conceptual model stems from the requirement of a conceptual basis to avert conflicts between different rangeland user groups, and to establish an ecological basis for range management. This necessitates the definition of the rangeland degradation issue in terms used and understood by all rangeland user/interest groups. The final requirement is that of a vehicle used to convey guidelines for the management of rangelands to achieve particular management objectives. This requirement is fulfilled by expert systems, to be used by government agencies, other institutions, and private landowners involved in land management. From an academic perspective, more specific demands placed on models can be of a practical or theoretical nature.

Practical Demands of Models

Practical demands include that the model be heuristic, predictive, and flexible in encompassing a changing environment or new management tools. Joyce (1993) noted that, for any model to be acceptable, the methods for data collection and processing to assess changes in plant community need to be stipulated. That
the model be heuristic is most easily understood from the perspective of the user. Range managers need to be able to understand and apply the model with a minimum of training in ecology. Yet the model needs to incorporate enough science and current knowledge of vegetation dynamics of the pertinent plant communities in order to be favorably appraised by more discerning users, extension agents, and academics.

**Theoretical Demands of Models**

Models must reflect current ecological theory and yet stay away from concepts that may gain or lose favor dependent on vogue. Examples of such concepts include stability and equilibrium. Recent ecological literature also indicates a need for incorporating principles of ecology within the land management structure. This includes the consideration of multiple spatial and temporal scales and all major sub-disciplines of ecology pertaining to the criteria (Allen and Hoekstra 1992) defined in Chapter 1. Many concepts derived from organismal, population, community, landscape, and ecosystem criteria are already being used in range management and are incorporated within existing models of vegetation dynamics. The requirement for predictability implies the careful choice of variables and concepts to be considered in a model. For example, phytomass production may not be predictable because of the lack of predictibility of rainfall. However, species replacement after a specific disturbance event (including extreme climatic events) may be more predictable.

When considering the different broad requirements of models of vegetation dynamics based on use (exploratory, conceptual, expert system), it becomes apparent that the choice/construction of model also depends on particular circumstances of model application. Table 2.1 attempts to define the general requirements of models used for exploration versus conceptual models used for management. Expert systems serve to transfer information to the land manager, adhering to the framework of the conceptual model.

**The Use of Expert Systems**

Expert systems are often thought of as complicated computer algorithms, but they need not be so. For example, management tools derived for manipulating vegetation could be graphically represented as in Figure 2.1. Management tools for both increasing and decreasing selected community attributes could be summarized in matrices such as Table 2.2. In these cases, emphasis is places on growth-forms (the habit of a plant
determined by its appearance of branching and periodicity [McGraw-Hill 1984]), but the consideration of other attributes is equally valid.

This example checklist enables consideration of undesirable consequences on other attributes. Careful consideration and combination of the above rules pertinent to the discussed criteria, together with (or without) environmental fluctuation, may yield new opportunistic management tools. These rangeland manipulations could be presented in the form of a document compatible with tables such as the above, on a cell-by-cell basis.

**Table 2.1. The requirements for models of vegetation dynamics as perceived from a range management perspective.**

<table>
<thead>
<tr>
<th>General List of Practical and Theoretical Demands</th>
<th>Exploratory Model of Vegetation Dynamics</th>
<th>Conceptual Model of Vegetation Dynamics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heuristic</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Predictive</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Flexible</td>
<td>Yes—no predefined pathways</td>
<td>Only in terms of an understanding and communities that the conceptual model may change as circumstance varies</td>
</tr>
<tr>
<td>Incorporating the concepts of stability and equilibrium</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Mechanistic versus phenomenological</td>
<td>Mechanistic</td>
<td>Phenomenological</td>
</tr>
<tr>
<td>Multiple temporal scale</td>
<td>Yes</td>
<td>In a qualitative sense only</td>
</tr>
<tr>
<td>Multiple spatial scale</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Combined temporal and spatial scale</td>
<td>Yes</td>
<td>Emphasis on temporal</td>
</tr>
<tr>
<td>Multiple criteria</td>
<td>Yes</td>
<td>Yes—in terms of &quot;buzzwords&quot; *1</td>
</tr>
</tbody>
</table>

*1 buzzwords commonly used by the public encompass multiple criteria*
Fig. 2.1. A framework for considering management tools for the maintenance of plant community management objectives for sagebrush steppe through growth-form groups and individual species.

Table 2.2. An example tabular summary of the effects of different management tools on growth-form groups for sagebrush steppe vegetation

<table>
<thead>
<tr>
<th>Rangeland Manipulation</th>
<th>Shrub</th>
<th>Bunchgrass</th>
<th>Forbs</th>
<th>Native Annuals</th>
<th>Exotic Annuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early spring grazing 1</td>
<td>+</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Spring/summer grazing 1</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Fall grazing 2</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>year-round grazing 1</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Spring fire</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Summer fire</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Fall fire etc.</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>

Note: This table is an example of the possible utility for a particular form of data organization, and should not be interpreted strictly in terms of biology (+ = increase in growth-form; - = decrease in growth-form; and 0 = no perceptible change; 1 = grazing by cattle, 2 = grazing by sheep)
Such sets of management tools could be incorporated within the framework of any model consequent to objective one. Figure 2.1 and Table 2.2 are alternative representations of this idea. For example, if the analysis of data within this dissertation indicates that a multiple-stable-states model is warranted for the sagebrush steppe vegetation, then different versions of Figure 2.1 or Table 2.2 could be prepared to suit the situation within each state (Figure 2.2). Apart from having to fit management tools to specific models of vegetation dynamics, other problems regarding applied use abound.

**Temporal Versus Spatial Pattern**

One of the major problems in vegetation dynamics has been the accommodation of spatial and temporal patterns within a single model. The two have often been confused, and their disentanglement is of prime importance to vegetation science and range management. Spatial dimensions of vegetation modelling
are still developing, particularly within the subdiscipline of landscape ecology. Recently, spatio-temporal models have employed GIS, remote-sensing, and sophisticated hardware (Chapter 1). As this technology develops into new management tools, more realistic spatial integration will develop, together with the ability to incorporate new remotely sensed satellite imagery in monitoring efforts.

**Temporal and Spatial Scale**

The diagrammatic representation of model description (Figure 2.3) indicates not only the need to define vegetation type (sagebrush steppe) but also the spatial and temporal bounds of the model. From the management perspective, temporal bounds should accommodate vegetation changes within a management time frame. If management tools are used, reasonable changes in plant communities should be expected within 5 years, the minimum time period over which management could hope to be effective.

The spatial demands of a model are more complex. Traditional range management deals with vegetation from a minimum of the area covered by a homogenous stand of vegetation, to a maximum of a grazing allotment on public land incorporating various ecological sites. Other user and interest groups are forcing the consideration of management at alternative scales.

The temporal and spatial scales at which ecosystem functioning is studied are usually longer and larger than those of traditional management concerns. Although no long-term ecosystem functioning-based studies have been completed in the sagebrush steppe vegetation type, indications from other systems are that the temporal scale may extend through many decades (Bormann and Likens 1979). Spatial scale for considering ecosystem functioning has usually been intuited at the watershed level. Watersheds may accommodate several allotments, implying a spatial scale larger than that at which the range manager usually operates.

Theoretical demands accommodate management demands at the rancher's level but require an extension of the upper spatial and temporal bounds. A combination of spatial and temporal demands can only be met if the structure of land ownership and management are changed. Since this is not likely in the foreseeable future, an alternative strategy needs to be implemented.

Thus far, the only solution that I perceive is through the creation of linked models operating at
different scales—the larger model meeting larger-scale theoretical demands, while the smaller model is aimed at aiding smaller-scale management decisions (Figure 2.3). Strong links between the models are required to meet theoretical demands and to facilitate data sharing.

Integration of models facilitates the exchange of information. Vegetation abundance data collected for model A could be incorporated into a layer of the GIS constituting model D. This information could then be used to obtain groundtruthing for remotely sensed data. Feedback from model D to model A is in the form of constraints. These constraints might be the imposition or delay of management tools applied at the scale pertinent to model A. With this communication between models, a variety of larger-scale management demands can be enacted. These may include the enforcement of larger spatial scale disturbance patterns, the formation of corridors for migrating fauna, management for optimal biodiversity, or whatever other demands are placed on the management system by changing circumstances.

Much of the framework for the implementation of models A-D is already in place. Extension officers could encourage the use of model A at the stand to allotment scales, while many Bureau of Land Management district offices already possess sophisticated GIS systems capable of containing model D.

**Conclusions**

This chapter highlights the need for linking rangeland user/interest groups through conceptual models of rangeland degradation. The practical and theoretical demands identified in this chapter could serve as a guide for building successful exploratory and conceptual models for this purpose. The diversity of models in Table 1.1 also accentuates the need for establishing distinct objectives before the formulation of models. With a deeper knowledge of model types and the requirements of range management, it has become possible to state the objectives for a conceptual model more clearly: that is, to determine which model best serves to link vegetation dynamics, range management, and monitoring.

With specific regard to objective 2, and the identification of models subscribing to demands, it appears that none of the existing models fit all the objectives as stated above. This is because no models attempt to accommodate monitoring using remotely sensed data. In terms of linking range management to vegetation dynamics, the State-and-Transition Model (Westoby et al. 1989a, b), Clementsian Model, Friedel's
**Fig. 2.3.** Integration of the vegetation dynamics model required for range management with the larger scale (temporal and spatial) landscape/ecosystem functioning model.
Model (Friedel 1991), Milton's Model (Milton et al. 1994), and Bosch's Models (Bosch and Booysen 1991) offer suitable conceptual frameworks. These models will be examined in greater detail, and discussed further in the final chapter of this dissertation.
CHAPTER 3

A GENERAL DESCRIPTION OF SAGEBRUSH-DOMINATED VEGETATION

This synthesis of the literature will be used with information derived from the long-term trends and piospheres to determine which models of vegetation dynamics best describe observed changes in sagebrush steppe plant communities. The final assessment of model suitability is to be found in Chapter 7.

Introduction to the Sagebrush Steppe/Semi-desert Plant Communities

Sagebrush steppe has been defined as a more or less equal sharing of dominance by sagebrush (various *Artemisia*) and bunchgrasses under semi-arid, pristine conditions (West 1988, in press). More arid sites tend to be dominated by *Artemisia* and associated shrubs (Tisdale and Hironaka 1981, Blaisdell et al. 1982, Knight 1994). Thus, West (1983a, b) followed Küchler (1970) and classified sagebrush-dominated vegetation types into Western Intermountain Sagebrush Steppe (West 1983a) and the Great Basin-Colorado Plateau Sagebrush Semi-Desert (West 1983b) (Figure 3.1), the latter conforming with a slightly drier climate. The prevailing climate of both types is semiarid, temperate, and continental. Disturbance and climatic fluctuation make for a dynamic vegetation structure within both of these types. Without exact knowledge of pre-European fire/disturbance regimes, it is difficult to define the natural range of variability within sagebrush-dominated plant communities (see Wright et al. 1979). The variable nature of plant communities should be stressed to reduce the tendency to define plant communities explicitly and statically.

Some early 19th century journals describing the Intermountain West indicated a plant community visually dominated by sagebrush, with grass stands primarily confined to valley bottoms (Vale 1975). However, Hull and Hull (1974) reported that vegetation in Cache Valley of Utah and in Idaho was comprised predominantly of bunchgrasses with little sagebrush. The balance of brush versus grass can be expected to vary with topography, climate, and edaphic conditions, as well as fire and grazing history (West 1988).

The Passey et al. (1982) long-term data sets used in this dissertation (Chapter 4) and sites for the piosphere study (Chapter 6) are located on the Snake River Plains, falling within the sagebrush steppe type. The study site at Mills, Juab County (Chapter 5), in southcentral Utah, is classified as sagebrush semi-desert,
although vegetation dynamics are similar (West 1979, West and Hassan 1985).

Soils within the sagebrush steppe type range from deep loessal and alluvial deposits to skeletal on less-developed sites (West 1983a). The soils are classified as Ustolls and Xerolls to Orthids and Argids. The Passey et al. (1982) sites from the Snake River Plains are loessal, frequently underlain by basalt, or contain pumice or cinder from nearby volcanic eruptions. Soils at the Mills study site (sagebrush semi-desert) range from Durixerollic calcioorthids to Xerollic Calcioorthids (Jensen 1981).

Fig. 3.1. Mills, relict areas, and piosphere study site locations relative to the distribution of sagebrush steppe (sagebrush-grass) and sagebrush semi-desert (Great Basin sagebrush) [from Wright et al. 1979].
The major sagebrush species within the study sites used in this dissertation are *Artemisia tridentata* and *Artemisia tripartita*. *Artemisia tripartita* is usually found on more moist sites than *Artemisia tridentata* (Blaisdell et al. 1982), although some of the Passey et al. (1982) sites do exhibit mixed stands. This is particularly apparent in the higher elevation sites (1545 m at Craters of the Moon National Monument, and 1334 m at Little Crater Kipuka near American Falls) or on sites immediately adjacent to lava flows, where snowdrifts may accumulate and runoff from the rock may supplement direct precipitation.

Of the 4 subspecies of *Artemisia tridentata* [*vaseyana, tridentata, wyomingensis, and xericensis* (Rosentreter and Kelsey 1991)], the study sites used in this dissertation support only *Artemisia tridentata* ssp. *tridentata* and *wyomingensis*. *Artemisia tridentata* ssp. *wyomingensis* is usually found on slightly drier microenvironments, although examination of some of the Passey et al. sites showed mixtures of the 2 subspecies.

**Temporal Change within Sagebrush-Dominated Vegetation**

Studies of paleo-records indicated that the range of this vegetation type and the balance between sagebrush, perennial grasses, and forbs have varied over the last 10,000 years with concomitant changes in environment and fire return interval (Miller et al. 1994, Nowak et al. 1994). Harniss (1968) and French and Mitchell (1983) indicated that intra- and interdecadal fluctuation in relative abundances of sagebrush steppe plants (on the Snake River Plains in Idaho) due to climatic fluctuation are sufficient to mask secondary succession over time periods as long as 25 years. This may constitute a problem in portions of this study dealing with shorter-term vegetation changes that fall within management time frames.

**Short-Scale Temporal Dynamics**

This study emphasized not only the end result of vegetation change but is also particularly interested in the nature of that vegetation change, and its range of natural variability. All characteristics examined in this dissertation can be found across a temporal window of 25 to 50 years.

Many authors inherited (from the Clementsian model) the notion that vegetation change is continuous, an idea which has seldom been tested. A few papers, however, emphasize more discrete types of plant
community changes. The following paragraphs identify these instances.

Miller et al. (1994) identified 3 stable states within the sagebrush steppe vegetation type: a sagebrush-dominated state; a state with more or less equal dominance by sagebrush and bunchgrasses, often found under conditions of infrequent fire and light grazing by cattle; and a cheatgrass-dominated state associated with a fire interval of 3-5 years. The first state may be indicative of stagnation. The third state is associated with the introduction of Eurasian grasses since settlement by Europeans, and appears to be the predominant change presently occurring in existing sagebrush steppe areas. Hall (1993) indicated that natural seedling recruitment of woody plants does not occur once the understory has been replaced by cheatgrass. Similar problems have occurred with Medusahead (*Taeniatherum asperum*) (Young and Evans 1970, Young and Evans 1982).

West (in press) used a multiple-stable-states model incorporating multiple pathways to describe 7 different states and environmental/management criteria resulting in changes between states (Figure 1.4). The defined stable states include: a pristine condition; late seral sagebrush steppe under lightly grazed conditions; denser stands of larger sagebrush, with remnants of native perennial herbs under moderately grazed conditions; dense stands of large sagebrush, the understory dominated by introduced annuals, cheatgrass/medusahead-dominated communities following heavy grazing and burning; communities dominated by native grasses under moderate grazing conditions, and, finally, communities dominated by seeded wheatgrasses or ryegrasses. The "forces" moving communities from one stable state to another are livestock grazing, rest from livestock grazing, fire, herbicides, tillage followed by seeding, accelerated soil erosion, interseeding, restoration, and further weed invasion. In an update of this model, West and Young (in press) also considered vole, insect, and fungal damage, as well as poor soil aeration during extremely wet years.

Pechanec and Stewart (1949, page 1) recognized 4 basic communities on the spring-fall ranges of southern Idaho. These are "sagebrush with a good understory cover of perennial grasses and weeds," "sagebrush with a sparse understory of perennial grasses," "sagebrush with an understory chiefly of annual grasses and weeds," and "range with sagebrush replaced by cheatgrass or annual weeds."

West et al. (1979) indicated that certain demographic characteristics of semi-desert plant populations, namely recruitment, occurred in pulses. Cawker (1980) was able to explain 40% to 50% of the age structure
variance of *Artemisia tridentata* by climatic variables using stepwise multiple regression. Temporal dynamics appeared to be controlled by a complex variety of climatic controls. Age structures for different sites appeared cohort driven. Eckert and Spencer (1986) also noted cohorts of sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) seedlings following a sequence of dry and wet years.

Pechanec et al. (1937) identified the correspondence of heavy grazing and drought resulting in communities of consecutively lower production which is not recovered during normal years. This related well with the modern concept of stable states and thresholds.

There are several aspects of vegetation change (such as pulsed recruitments of *Artemisia* and change induced by the combination of heavy livestock grazing, vole girdling of sagebrush [Mueggler 1967, Parmenter et al. 1987], drought, flooding [Lunt et al. 1973, Ganskopp 1986], insect or microorganism attack) that do show state and transition effects. Recent papers reflect the acceptance of the state and transition paradigm for sagebrush steppe (Laycock 1992). Older literature using multiple-stable-states models identify particular plant communities showing an inability to change through loss of species propagules (stagnated stands of *Artemisia*) (Rice and Westoby 1978, West et al. 1984, Winward 1991), insulation from periodic disturbance, or changed ecosystem functioning. Scanlan and Archer (1991) explained differences in dynamics due to species longevity. For example, change from bunchgrass to woody domination is faster than the reverse process because woody plants are generally much longer lived. Hull (1976) observed that it took only 12 - 15 years after the introduction of livestock for sagebrush to become the dominant plant in the foothills around Cache Valley, Utah - Idaho.

**Sagebrush-Dominated Community Responses to Abiotic Factors**

Since these environments are moisture stressed, most of the work on community responses to abiotic gradients are directly or indirectly related to soil moisture. This literature is well-described in (Tisdale and Hironaka 1981, West 1983a, c, Blaisdell 1958, Blaisdell et al. 1982, West 1988).

Using data from the same Passey et al. (1982) sites reexamined in this dissertation, Harper and Climer (1985) showed a significant positive relationship between annual production and average precipitation,
soil nitrogen, and soil potassium. Community complexity also seemed to play a role in annual production. Species richness was found to be positively correlated to coefficients of variation.

Another important factor in determining the composition of plant communities are the effects of plant herbivores and pathogens.

**Plant-Herbivore/Pathogen Interactions**

There are many plant-herbivore/pathogen interactions that contribute to making sagebrush steppe a dynamic vegetation type. Important organisms include large hooved animals, rodents, lagomorphs, birds, insects, mites, and plant parasitic nematodes (Miller et al. 1994).

Using studies initiated by Craddock and Forsling (1938), Laycock (1967) presented evidence showing how heavy spring livestock grazing increases the sagebrush component while reducing the herbaceous component of sagebrush steppe vegetation. Young (1994) has blamed rest rotation grazing during the growing season for putting greater selective grazing pressure on remnant native grasses mixed in with cheatgrass, because native species remain green longer in the early summer. Laycock (1967, 1987) advocates the use of late fall grazing by sheep as a remedial manipulation, showing that it is more effective than rest for returning sagebrush-dominated rangelands to a higher condition. At the same research station, West et al. (1979) showed that longevity of major grasses was considerably longer under conditions of fall grazing by sheep than under ungrazed conditions. The major shrub, three-tip sagebrush, showed a reduced longevity under a fall grazing regime. The increase in bunchgrasses relative to sagebrush can be explained in terms of tipping the balance of competition and is specific to the fact that sheep browse sagebrush in the fall. These effects of seasonality of grazing are supported by clipping studies (Trlica and Cook 1971, Cook and Child 1971, Cook and Stoddart 1963). They concluded that desert ranges were best grazed during the winter and, if done so, would have twice the grazing capacity in comparison to spring and summer grazing. Furthermore, late spring grazing was shown to be more detrimental than early spring grazing. Increased plant mortality in plots with increased intensity of clipping remained true for all seasons, but was most marked in late spring and summer. Other clipping studies indicated that the recovery of some species' vigor and density require several years of rest after heavy defoliation (Trlica et al. 1977).
Generally, the effects of livestock grazing are not quite as explicit. In a description in "Canyon Grasslands and Associated Shrublands of West-Central Idaho and Adjacent Areas," Tisdale (1986) postulated the following changes under the site-specific grazing history: major declines of the predominant bunchgrasses, species-specific responses but general reduction in native perennials, and a large increase in alien plant species. Most studies focused on the effect of rest on continuously grazed rangelands and may not consider the different effects of cattle versus sheep grazing. Under rest from livestock grazing, usually all growth-forms show increased abundance. Livestock have also been shown to have a detrimental effect on seed production in the semiarid grasslands of northeastern Colorado. The effects of livestock and their interactions with fire are considered in greater detail within the case studies presented in the ensuing chapter sections.

The effects of harvester ants on sagebrush-bunchgrass vegetation are visually apparent through the formation of piospheres as a result of harvesting both leaf material and seeds. Although not intensively studied in the sagebrush steppe, they have significant impacts in grasslands (Beattie 1989) and so can be postulated to also have an impact on sagebrush-bunchgrass vegetation. Studies on a South African harvester ant indicated that physical and chemical properties of soils may change in a similar fashion, contributing to changes in the expression of vegetation (Dean and Yeaton 1993). Similar effects have been described in semiarid grasslands in northeastern Colorado (Coffin and Lauenroth 1992). Nest sites of western harvester ants (Pogonomyrmex occidentalis) showed significant differences in plant recovery and seed storage on nest mounds versus surrounding circular disks. Both annual plants and seeds occurred in greater numbers on the mounds. Occupancy of the nest sites was found to range from 29 to 58 years. Sneva (1979) examined data spanning 40 years in eastern Oregon and found a direct relation between denuded disc diameter and increased sagebrush canopy and decreased herbaceous production.

Jackrabbits are another potentially important factor influencing sagebrush steppe vegetation dynamics. Black-tailed jackrabbits (Lepus californica) have been found to fluctuate in about 10-year cycles (Anderson and Shumar 1986). The fluctuation in numbers was found to affect the total aboveground phytomass, but postulated not to change species composition because of the lack of differentiation between species (Anderson and Shumar 1986) as food sources. These results are supported by Rice and Westoby
(1978), who did not notice any effects of jackrabbit exclusion in addition to livestock exclusion in a range of vegetation types, including sagebrush-dominated vegetation.

Evidence from Chihuahuan Desert shrub communities indicated that rodents (*Dipodomys* spp.) may play a key role in maintaining certain communities (Brown and Heske 1990). This was shown to occur through seed predation and soil disturbance. Passey et al. (1982) indicated that the activities of pocket gophers are often evident as patches of disturbance. Seed predation has also been shown to occur through the actions of rodents, birds, and ants (Parmenter et al. 1984, Longland and Young in press). Voles have also been found to influence sagebrush rangelands (Mueggler 1967, Frischknecht and Baker 1972, Parmenter et al. 1987). This occurred in years with persistent winter snowpacks where an ungrazed herbaceous canopy exists, coincident with years of peak vole populations (Frischknecht and Baker 1972).

Little is known about insect predation on seeds, while some literature on the direct impact on vegetation composition through herbivory is available. There are several insects that contribute to vegetation dynamics in sagebrush steppe. Grasshoppers are recorded to have had severe impacts on sagebrush. Allred (1941) measured a 50% mortality of big sagebrush on the Little Powder River in Montana and Wyoming following grasshopper explosions. Recent studies have indicated that grasshopper infestations may be short, lasting only a few insect generations (Kemp 1992b, Kemp and Dennis 1993). Certain years could be classified as "outbreak" years, depending on grasshopper numbers (Kemp 1992b). Grasshopper communities have also been shown to vary greatly over the landscape (Kemp 1992a). Use of insecticides was found to be counterproductive by allowing rapid resurgence of pest populations (Lockwood et al. 1988).

Though Mormon crickets (*Anabrus simplex*) are frequently viewed as a pest within the Great Basin, Young (1978) and Redak et al. (1992) showed that densities simulating pest proportions did not significantly decrease understory phytomass production in the longer term.

*Aroga websteri*, known as the sagebrush defoliator moth, has been known to weaken and even kill stands of sagebrush (Knight 1987, Hsiao 1984). Hsiao (1984) found that high temperatures and low precipitation reduced numbers of the sagebrush defoliator. Out of 12 long-term plots in sagebrush steppe vegetation, Passey et al. (1982) reported 3 plots to have been impacted by *Aroga*. Snea et al. (1984) reported
reductions in sagebrush due to *Aroga* on the Squaw Butte Station of eastern Oregon during the early 1960s when this insect was prevalent throughout the Great Basin (Gates 1964).

Insects of the class Diptera are known to cause galls on *Artemisia tridentata* (Fronk et al. 1963), but little is known about their impact on rangeland forbs and grasses (Knight 1987). The major influential insect is probably the cicada (West 1983a), whose long-lived larvae eat sagebrush roots.

Allen et al. (1987) indicated that parasitic fungi sometimes detrimentally affected sagebrush production. Decreases in production down a slope in southwestern Wyoming were associated with decreases in mycorrhizal production and the increased incidence of snow mold.

Although the above list of organisms impacting sagebrush and associated species may seem extensive, their biology and particular effects on the expression of plant communities are not well known.

**The Effect of Fire**

In North America, fire is often thought to have a devastating effect on vegetation. In sagebrush steppe, however, estimates of fire frequency ranging from 17 to 41 years (Houston 1973) indicate that fire is an integral part of such systems. Extremes in fire return intervals lead to dominance by either sagebrush or cheatgrass.

The most visible effect of fire on sagebrush steppe is the removal of the sagebrush species. All subspecies of *Artemisia tridentata* are killed by fire and depend on the proximity of a seed source for reestablishment (Wright et al. 1979, Blaisdell et al. 1982). Bitterbrush (*Purshia*), an important browse species, is likewise damaged by fire (Blaisdell 1953, Blaisdell and Mueggler 1956). Other species of *Artemisia* and other members of the shrub component may resprout following fire. Recovery, whether by seed or resprouting, is dependent on the seasonality of the burn and moisture distribution following the burn event (Wright et al. 1979). Some shrubs (*Chrysothamnus* spp., *Tetradymia canescens*, and *Ephedra*) may increase in abundance within 2 to 3 years of the fire event (Blaisdell 1953, Harniss and Murray 1973, Wright et al. 1979, West and Hassan 1985). Thus, *Chrysothamnus* is enhanced, although its resprouting ability (arising from its stem) is quelled by high intensity fires. All of these factors contribute to the range of the reaction of the shrub component to fire in terms of abundance of particular taxa, as well as timing of return. In contrast to
the shrubs, the perennial bunchgrass component establishes primarily vegetatively, providing a more uniform response to fire through this growth-form (West and Hassan 1985).

The smaller-statured bunchgrasses (*Poa* and *Sitanion*) escape fire more easily and, because of their smaller fuel load, generate less heat to the belowground component (Wright and Klemmedson 1965). This allows a faster recovery following a fire event and, subsequently, relatively greater increases in phytomass. Similarly, coarser grasses (*Agropyron spicatum* and *Sitanion hystrix*) generate less heat on combustion and are thereby favored over species such as *Festuca idahoensis* and various *Stipas* (Wright 1971). The effect of repeated burning on the survival of bunchgrasses is well known and is discussed elsewhere. The most favorable periods of prescribed burning to favor bunchgrasses are early spring and late fall (Wright et al. 1979).

Forbs also are favored by late fall burning after they have dried out and disintegrated (Wright et al. 1979). Certain species remaining green longer may be more susceptible to fire (Frischknecht 1978). Pechanec et al. (1954) classified forbs into 3 classes of fire susceptibility, providing useful information for management.

**Case Studies of Long-Term Vegetation Dynamics**

Anderson and Holte (1981) reported a doubling in the cover of shrubs and perennial grasses after 25 years of rest from livestock grazing at Idaho National Engineering Laboratory. The associated 20-fold increase in grasses is thought not to be at the expense of shrubs but related to increased seed reserves with the development of the perennial grass plants. The authors described a stage of slow recovery (the initial 10 years) followed by more rapid recovery related to seed reserves. No obvious seral stages could be defined. The study also showed high variance between plots (Anderson 1986). Anderson and Inouye (1988) discussed the establishment of dense stands of *Bromus tectorum* since monitoring the initial presence of *B. tectorum* at the INEL sites in 1975. The authors noted that establishment occurred in the absence of fire and grazing and during a period of higher than average rainfall (1966-1975). A subsequent decrease during drier years implied a dependence on rainfall trends. Young (1994) noted similar trends in western Nevada.

Burning of good condition plots, which included perennial grasses, resulted in an increase in palatable grasses, in spite of an initial large increase in cheatgrass. The exclusion of cattle during the recovery period
after burning is thought to be crucial (West and Hassan 1985, Hassan and West 1986).

Yorks et al. (1992) reported on the repetition of a 63-year-old transect covering several vegetation types, including sagebrush-dominated communities in Pine Valley, Utah. Many factors, including a moderation in livestock grazing, could be responsible for the substantial increases in canopy cover observed for several perennial grasses. This trend was less noticeable with sagebrush and was attributed to a filling out of individual plants rather than increased numbers. The proportion of understory cover relative to total plant cover also showed an increase.

West et al. (1984) found that *Artemisia tridentata ssp. wyomingensis*-dominated communities (sagebrush semi-desert) in 5 large paddocks in west central Utah did not show significant increases in perennial grasses following 13 years of rest from livestock use under favorable precipitation conditions. The presence of annual grasses increased the possibility of community deflection towards cheatgrass domination. This indeed did happen after a wildfire in 1985 (Pers. comm., N.E. West 1994).

Eckert and Spencer (1986) examined changes in shrub canopy cover, basal cover of herbaceous species, and frequency of occurrence of all species at 2 sites in northern Nevada. Both sites were managed under a 3-pasture rest rotation grazing system. One site showed no long-term change in frequency of species. The other site showed increased shrub cover and deceased palatable grass (*Stipa thurberiana* and *Agropyron spicatum*) cover over the 10 years examined. At 1 of the above sites, Eckert and Spencer (1987) found heavy periodic grazing to be the major cause for restriction of basal area growth and reproduction of palatable grass species over a 9-year study period.

Long-term studies near Dubois, Idaho, indicated increased phytomass of total grasses and forbs following a fire treatment (Harniss and Murray 1973). The long-term perspective showed an increase in sagebrush (*Artemisia tridentata*) with a subsequent decrease in phytomass of the other growth-forms, apparently because of competition.

**Various Exclusion Studies**

Peters et al. (1993) commented on vegetation changes in 2 exclosures near Burley and Castleford (Idaho) over 50+ years following cropland abandonment. Using frequency of occurrence data, the authors
showed that 1 site showed change toward late seral perennial grass species (*Agropyron riparium* and *Poa secunda*) while the other site remained dominated by annuals and biennials.

Rose and Miller (1993) reported on inside versus outside differences of 13 livestock exclosures in southeastern Oregon 66 years after establishment using cover and density data. No statistically significant differences in cover between grazed pastures and exclosures were found for shrubs, although *Artemisia tridentata* showed increased density outside the exclosure. Total grass cover and density of all perennial bunchgrasses, except *Poa sandbergii*, were higher inside the exclosure. Forbs appeared to have a slightly higher cover and density within the exclosures, although these changes appeared to be species-specific.

Robertson (1971) examined an eroded and grazed tract in northeastern Nevada 30 years after the initiation of rest from livestock use. The plant community showed increased cover by all its growth-forms and reestablishment by *Agropyron spicatum*. The highest recovery was exhibited by thurber needlegrass (a 7-fold increase). The only decreases were shown by annual forbs and locoweed.

Tueller and Tower (1979) emphasized the negative aspects of exclosures—the stagnation effect arising from nonuse of plants. As an example, they presented data showing an average 70% decline in the production of bitterbrush 10 years after fencing, in central Nevada.

Pearson (1965) showed that aboveground production for sagebrush and several major bunchgrasses increased after 11 years of rest, in comparison to a site on the upper Snake River Plains of Idaho that had been grazed continuously for 70 years. An exception was *Phlox caespitosa*. This trend did not extend to belowground production. The area being rested showed only 68% of the belowground root mass of the grazed area.

Sanders and Voth (1983) found greater ground cover on grazed plots versus protected plots within sagebrush steppe in the Boise National Forest, Idaho, after 46 years of periodic data collection. No clear-cut trends could be found on a species basis.

Holecheck and Stevenson (1983) found that 22 years of rest from grazing in northwestern New Mexico had little influence on plant composition at either of 2 sagebrush semi-desert sites studied. Forbs had been eliminated by heavy sheep grazing from the study site prior to construction of the exclosures.
Potter and Krenetsky (1967) showed a decrease in ground cover by both grass and forbs in protected and grazed plots occupied by sagebrush semi-desert in northwestern New Mexico.

Daddy et al. (1988) examined 3 sites with different grazing histories in northwestern New Mexico. Major phytomass contributors at the heavily grazed site were Aristida sp. and Bromus tectorum. Bouteloua gracilis and Hilaria jamesii were more productive on grazed sites. The moderately grazed site had twice the herbaceous aboveground phytomass than the protected site.

Sneva et al. (1984) examined 10 exclosures established in eastern Oregon during the drought years of the 1930s in big and low sagebrush-dominated vegetation. Frequency estimates were evaluated in 1937, 1960, and 1974. Frequency of all native grasses (Agropyron spicatum, Festuca idahoensis, Sitanion hystrix, Stipa thurberiana, Poa sandbergii) were shown to increase or remain stable both within and outside the exclosures with one exception. Poa sandbergii frequency decreased in 1 exclosure located in low sagebrush-dominated vegetation. Several factors confounded the results: the switch from spring sheep to spring-through-fall grazing by cattle, higher precipitation following 1937, a decline in overall livestock grazing intensity, and the effects of the sagebrush defoliator moth during the early 1960s.

**Chronosequence Approaches**

Burning of 8 environmentally similar sites during different years over a period of 36 years enabled Humphrey (1984) to determine likely long-term plant compositional changes in sagebrush steppe near Pocatello, Idaho, following wildfire. Initial establishment after disturbance favored perennial grasses and forbs able to resprout following fire. Shrubs able to resprout became prevalent after 6 years, whereas shrubs establishing from seed required longer intervals. Differences between sites were ascribed to slightly different prefire species composition, signifying a time-disturbance interaction.

Brotherson and Brotherson (1981) compared relict and grazed areas in sagebrush communities bordering Utah Lake to determine plant community changes due to livestock impact. The major changes observed were the reduced cover by perennial grasses and the increased cover by annual species.

Tueller and Platou (1989) determined a successional gradient in northern Nevada by examining plant community changes moving away from a watering point. The observed pattern was determined to be different
from theoretical pathways. *Agropyron spicatum* was found to vary between plots, but was greatly reduced in the 2 plots closest to the watering points. *Bromus tectorum* cover was found to be highest closest to the watering points, while *Lupinus caudatus* and *Phlox longifolia* showed the opposite trend. *Poa secunda* generally showed a lack of trend. These cover values seem to correspond well with density data. *Sitanion hystrix* showed relatively higher densities in early and late seral stage plots. Sagebrush density appears to vary considerably, being greatest in the third and last plots, thus not yielding a clear pattern. In general, vegetation cover increased with decreasing condition, while litter cover and microphytic cover were highest in the plots furthest away from the water.

**A Summary of General Pathways of Vegetation**

**Change in Sagebrush-Dominated Vegetation**

**Cheatgrass Invasion**

Numerous papers have recorded the increasing preponderance of cheatgrass in the Intermountain Region over the past decades. This winter annual has become a member of the plant community on both livestock-impacted and undisturbed areas. Studies of undisturbed and relict areas have noted the presence and even dominance of cheatgrass (Passey et al. 1982, Lovejoy 1980, Anderson and Inouye 1988, Svejcar and Tausch 1991, Kindschy 1994). The ability of *Bromus tectorum* to initiate growth early in the growing season and subsequent mobilization of available nutrients is regarded as the most important factor of its competitive ability. The dry flammable nature of cheatgrass material and the resultant change in timing of natural fire at a stage when competing bunchgrasses are susceptible are also important factors aiding the demise of sagebrush steppe communities (Wright and Klemmedson 1965, Young and Evans 1982, Whisenant 1989, Billings 1994). The spread of cheatgrass has been associated with disturbance by livestock trampling and reduction of microphytic crusts (Mack and Thompson 1982), but some studies of relict areas indicated cheatgrass presence (and sometimes dominance) within undisturbed areas (Passey et al 1982, Anderson and Inouye 1988, Svejcar and Tausch 1991). This goes against convention, and some authors have stated the opposite quite categorically; for instance, Piemeisel (1951) stated that he knew of no instance where alien species overcame
native perennials without the intervention of humankind. Whisenant and Wagstaff (1991) showed that the timing of grazing had a significant effect on cheatgrass abundance at a salt desert shrubland site. Spring grazing showed higher abundances of cheatgrass than fall grazing. Daddy et al. (1988) showed highest cheatgrass abundance in the most heavily grazed of 3 sites in southwestern Colorado with different grazing histories. Domination by cheatgrass of former sagebrush and shadscale communities in Skull Valley, western Utah, is ascribed to the interactive forces of unrestricted grazing and wildfires (Sparks et al. 1990).

Whisenant (1989) stressed that the continuity of fine fuel is important in favoring the large early fires that are so detrimental to the natural sagebrush-dominated communities. Homogenization of rangelands, initially through grazing and, subsequently, through the changed extent of fires, could thus be seen as an early indicator of degradation. It can be assumed that both of these disturbances result in the increased abundance of cheatgrass, thus providing a fine fuel load continuous over a larger area than prior to advent of European livestock. The size and frequency of fires are linked in that larger fires imply that a particular point in space would be burnt more frequently if the rate of fire initiation remained unchanged in the presence of a continuous fine fuel load. However, the rate of fire initiation has probably increased because of higher flammability of cheatgrass (Hunter 1991, Whisenant 1989). Thus, at least 2 concerted positive feedbacks promoting increased and detrimental fire frequency exist.

Two papers indicate that perennial vegetation can predominate over cheatgrass under certain circumstances. Hosten and West (1994) showed that cheatgrass-dominated semi-desert sites near Mills in central Utah can return to perennial cover 10 years after fire and grazing disturbance events. Hironaka and Tisdale (1963) showed how plots originally dominated by cheatgrass can change to a community incorporating Sitanion hystrix and Artemisia tridentata. Though these papers emphasized the reversibility of cheatgrass domination, Caron et al. (1992) indicated the presence of a positive feedback loop in addition to that of increased fire frequency resulting in the persistence of a cheatgrass-dominated state. Their research showed that cheatgrass presence may result in soil degradation due to a weakening of the soil aggregates or enhanced wetting and drying. Using applications of sucrose to decrease the availability of soil nitrogen, McLendon and Redente (1992) indicated that cheatgrass abundance may also be linked to increased nitrogen availability.

Once cheatgrass dominates, mycorrhizal fungi decline (Wicklow-Howard 1994). The native perennials require
mycorrhizae to establish and thrive.

All these disparate facts lead one to the conclusion that the problem of cheatgrass domination is still poorly understood and affords an opportunity for continued research. An additional stable state identified in the literature is one of sagebrush domination.

**Sagebrush Domination**

Winward (1991) reported particular circumstances leading to exclosures with a high cover of sagebrush. Exclosures constructed when sagebrush canopies are already well developed do not lead to recovery of the herbaceous component. This appears to be especially so where heavy livestock grazing has depleted the understory. This is because mature sagebrush is a strong competitor against herbaceous seedlings. Shrubs are able to quickly increase their size to take up vacant sites (West et al. 1978). Reduction in livestock or rest may not allow the herbaceous vegetation to recover without management intervention (West 1979, West et al. 1984).

The concept of stagnation indicates a second mechanism by which sagebrush domination may occur. Exclosures may exhibit this phenomenon defined as "the reduction in productivity of range plants resulting from a lack of grazing" (Tueller and Tower 1979, page 258). This is thought to result from nutrients becoming bound within the woody aboveground phytomass. This would favor longer-lived plants as nutrients become too scarce for the support of herbaceous vegetation. Sagebrush plants and their litter also slow down several processes in the nitrogen cycle (West 1983c).

**Management of Sagebrush Steppe**

Perspectives of managing sagebrush steppe rangelands have changed considerably over the past decade. A general dissatisfaction with Clementsian-based management is forcing the acceptance of new paradigms (Brown 1992). The notion of multiple-stable-states in sagebrush steppe communities is becoming more popular (Miller et al. 1994, West in press, Laycock 1992). Some government agencies are switching from climax to "desired future condition" (Williamson and Schlatterer 1992) or "desired plant community" (DPC) (Willoughby 1992) as management objectives. The Soil Conservation Service is also adopting the idea
of thresholds of change (Willoughby 1992, Bormann and Pyke 1994). While these changes can be seen as progressive, many remnants of management based on Clementsian ideas still linger.

A possible example of a desired plant community is that favored by Winward (1991). The author promoted the maintenance of open mountain and big sagebrush sites with 15% to 20% shrub cover. From the range manager's perspective, there are several reasons for maintaining sagebrush steppe rangelands as open stands of sagebrush. Such communities keep snow on site, probably recycle nutrients from deeper soil horizons through root transport and litterfall (Winward 1991), and could supply moisture to grasses during crucial summer months through hydraulic lift (Caldwell and Richards 1989). All of these factors could contribute to the maintenance of a higher annual phytomass production on a site sparingly occupied by shrubs.

Little effort has been made at accommodating such concepts within models of vegetation dynamics. The final chapter of this dissertation will attempt to accommodate such notions within existing or new models of vegetation dynamics for sagebrush steppe dynamics.
CHAPTER 4

DETECTING LONG-TERM CHANGE IN SAGEBRUSH-DOMINATED RELICTS

Justification

This study will examine the long-term vegetation trends of some ecological sites within selected relict areas first studied by Passey et al. (1982) and considered to be in pristine condition (Tisdale et al. 1965). This will be accomplished at various data resolutions to examine some of the concepts and assumptions pertinent to important models of vegetation dynamics identified in Chapter 1. Some objectives can be presented as alternative hypotheses with predictions, while other exploratory objectives are left as statements.

Specific Objectives (O)

O1: To determine if relict areas subscribe to the constancy definition of stability. The assumption of stability is inherent to many models of vegetation dynamics. The Clementsian Model assumes that undisturbed areas (including relict areas) do not change over time, and that they are suitable benchmarks by which to judge grazed areas. Testing of this assumption will be achieved by observing if change has occurred within the 10 years of the Passey et al. (1982) data collection in the 1950s and 1960s and that which I collected from 1991 to 1993. Ordination supported by randomization procedures will be used to gauge change.

HA1.1: There are no differences between plant compositional data collected by Passey et al. (1982) and that collected from 1990 to 1993. (Prediction: The Passey et al. (1982) data and data from 1991 - 1993 show interspersion in ordination space, and randomization tests indicate no significant differences.)

HA1.2: There are differences between plant compositional data collected by Passey et al. (1982) and that collected from 1991 to 1993. (Prediction: The Passey et al. (1982) data and data from 1990 - 1993 show no interspersion in ordination space, and randomization tests indicate no significant differences.)

O2: To determine if change in species composition is on a continuous basis or if it occurs in discrete steps. The nature of change (discrete versus continuous) of plant communities has become an issue in semi-arid lands. Some models assume or imply discontinuous change (Egler's complete and pre-emptive...
initial floristics [Wilson et al. 1992] and the State-and-Transition Model [Westoby et al. 1989a, b]),
while other models assume continuous change (Clementsian Model).

HA2.1: The nature of change of plant communities over time is continuous (Prediction: Ordination of the ten years of Passey et al. (1982) data show continuous trends, supported by high serial correlations based on randomization tests).

HA2.2: The nature of change of plant communities over time is discontinuous (Prediction: Ordination of the ten years of Passey et al. (1982) data show a lack of continuous trends, and few serial correlations can be found within the data).

O3: To determine if stands act individualistically or on a community basis. Community versus individualistic change indicate two major classes of models (Table 1.1) with different approaches of operation. An indication of how sagebrush steppe and sagebrush semi-desert plant communities operated would facilitate the choice of an alternative to the Clementsian Model as a basis for range condition and trend analysis.

HA3.1: The relict area data sets indicate community change (Predictions: Similar sets of species (identified using randomization tests) change across all sites within the 10 years of Passey et al. (1982) data, and between the Passey et al. (1982) data and that collected from 1991 to 1993).

HA3.2: The relict area data sets indicate individualistic change (Predictions: No similar sets of species change across all sites within the 10 years of Passey et al. (1982) data, and between the Passey et al. (1982) data and that collected from 1991 to 1993 can be identified).

O4: To determine the predictability of plant species compositional changes. The requirement for predictability in a model of vegetation dynamics upon which to base range condition and trend analysis forces the identification of variables that are themselves predictive.

This will be accomplished by determining whether the same set of species consistently exhibit serial correlation within the Passey et al. (1982) data.

O5: To determine the predictability of plant species' abundance changes. This will be achieved by examining whether species showing high temporal serial correlation display the same shape of abundances across sites over the same period of time.
To understand the biology underlying any changes observed using historical and anecdotal information.

**Introduction**

Most long-term studies of plant communities consider changes in species or growth-form composition following well-discerned disturbances such as fire or the advent or rest from grazing. Few long-term studies deal with fluctuation of vegetation measures in "undisturbed areas." The Passey et al. (1982) project was originally designed to "gain a better understanding of relationships between soil, climate, and climax communities, [to] . . . identify factors important to the wise use and management of rangeland resources, [and to] . . . facilitate interpretation of soil surveys for appropriate alternative uses of rangelands" (Passey et al. 1982, p. 2).

My reexamination of some of the Passey et al. (1982) sites and their data will be chiefly concerned with determining the validity of their use as benchmarks and to investigate time trajectories of plant communities at individual range sites. For this purpose, the exact sampling techniques used during the 1950s and 1960s were repeated in 1991 through 1993.

A general description of the entire study area (including physiography, geology, soils, land use, climate, and study locations) can be found on pages 3-6 of the Passey et al. (1982) document. Of the original 17 relict vegetation sites examined, several have subsequently been lost to disturbance by cattle grazing, agricultural development, or could not be relocated. Lost sites occurred at Promontory Point, Hansel Valley, Rattlesnake Pass, and Adams Farm within Utah, and Morgan's Pasture within Idaho. This leaves 12 sites: 4 at Carey Kipuka (ID 9-59, ID 8-59, ID 18-58, ID 17-58 [pages 68, 75, 82 and 86 of Passey et al. [1982], respectively); 2 at Kettle Butte Kipuka (ID 8-60, ID 9-60 [pages 71 and 101, respectively]); and 6 at Little Crater Kipuka (ID 15-58, ID 1-59, ID 6-58, ID 12-58, ID 13-58, ID 3-58 [pages 90, 94, 108, 112, 114, and 116, respectively]), all within south central Idaho (Figure 3.1).

Cumulative precipitation data at these 3 sites (Figure 4.1) during my study period indicated that all received similar amounts of precipitation during dry years (the slightly lower precipitation at Carey Kipuka may be due to rain-gauge location). Carey Kipuka received much higher precipitation prior to the 1993 phytomass
estimation compared to other sites. This may be due to its higher elevation. Field experience indicated that this site also received greater precipitation in the form of summer thunderstorms. Long-term data indicated that the 1991 to 1993 data collection period was influenced by a period of drier than average rainfall at all 3 sites (Figure 4.2). Only 1992 precipitation is above average at American Falls. Precipitation during 1993, however, was higher than the long-term mean.

Fig. 4.1. Cumulative precipitation for the 3 Passey et al. (1982) study site locations from September 1990 to June 1993.
Fig. 4.2. Long-term precipitation (cumulative from Sept. to June) for weather stations matched to each study site location. (A represents Craters of the Moon, B represents Idaho Falls, and C represents American Falls, all on the Snake River Plains.)
Methods and Materials

Passey and Hugie (1962) summarized the procedures followed at each site, where "range site" (now known as ecological site [NAS 1994]) is defined as a term developed to express differences in the inherent productive capacity of different kinds of rangelands. A brief summary of their methods follows.

First year of study:
1. three clustered plots (0.89m² each) were located at a central point within the study area, the current season's growth was estimated, total weight for each plot was recorded;
2. plant litter was estimated;
3. the weight of individual species and litter was estimated on an additional 20 randomly selected plots (0.89m² each);
4. after all the weight estimates were made, all the herbaceous plants in the central 3 plots were clipped and weighed;
5. the current season's growth of all woody plants was also collected in the 3 central plots;
6. a transect was conducted intersecting the 3 central plots (200 by 5 feet) in which all woody species were recorded by maturity class.

Second and following years of study:
1. 20 random 0.89m² plots were selected and biomass estimated;
2. of these, three plots were selected and harvested as described above.

The shape and size of each study location were defined by its homogeneity. For example, a site at Little Crater Kipuka was determined to occupy an area of approximately 200 feet by 200 feet (Passey and Hugie 1963). I used aerial photos to help delineate such ecological sites in 1991. None of the published papers relating to the relicts give any hint as to which sampling model was used. In fact, it appears that plots were chosen subjectively at some study sites.

Sampling during the 1990s was conducted within 1 macroplot per ecological site. This macroplot was 60 m by 60 m, if the stand permitted it, smaller otherwise. Remaining evidence of the soil pits dug in the 1950s and 1960s was used to determine the location of the Passey et al. (1982) sampling sites. The first year's
25 unclipped, stratified plots were fixed and reexamined in subsequent years. A reference unit technique was used for phytomass estimation at all plots (Carpenter and West 1987), following the procedure employed by Passey et al. (1982) as closely as possible.

Most of the studies in this dissertation dealt with elucidating temporal and spatial trends or detecting differences between points in space and time at the stand and individual species level. For this reason, a single detailed account of all the analytical techniques used is presented in this chapter.

In addition to simple graphic depiction of individual variables examined, various multivariate techniques have been used to examine the concepts described in Chapter 1 and hypotheses posed at the beginning of this chapter. All of these techniques require the calculation of an association matrix.

Many choices of association measure are available. In general, some measures give equal weight to attributes (plant species, growth-forms, or soil surface components) showing different abundances, while others accentuate attributes that are the most abundant. There is no right or wrong choice of association measure. Those favoring abundant species bias against rare species, whereas the other option may place too much emphasis on ephemeral species, thus confusing trends. Authors of certain multivariate techniques recommended specific association measures; for example, Faith et al. (1987) recommended the Kulczynski and Bray-Curtis association measures for ecological applications. The choice of association measure does affect the end result of an analysis. My approach was to try several association measures (including those recommended) on a subset of the data and then to select a single measure resulting in the easiest interpretable distribution of points. This association measure was then used for the remainder of the analyses. Analysis of several sagebrush steppe data sets suggested that the continuous form of the Kulczynski association measure was adequate for this project. The computer package PATN (Belbin 1992) was used for the multivariate ordination and network analysis performed on the sagebrush steppe vegetation data sets.

**Ordination**

Ordination methods are commonly referred to as "dimension reduction" techniques (Kent and Coker 1992). Such algorithms summarize data from numerous dimensions to just 2 or 3. The proximity of objects within ordination space (defined by 1 to 3 axes) is a representation of similarity. Patterns between sets of
objects in ordination space are said to represent patterns in multidimensional space. Herein lies one of the problems with ordination techniques. Since summarization implies loss of information, and ordination detects relationships at the level of the data set, relationships between individual points are frequently represented incorrectly. For this reason, such techniques are commonly designated as "exploratory" (Kent and Coker 1992). The ordination algorithm used in this dissertation (SSH = Semi-Strong Hybrid Multi-Dimensional Scaling [Faith et al. 1987]) does have a measure of adequacy of fit of the scattergram to the association matrix, termed "stress." The estimated value of stress ranges from 0 to 1.0, representing an acceptable fit, whereas 0.2 is considered poor.

In this dissertation, the size of some of the data sets and the range of temporal and spatial scales examined enhanced variability between objects, often resulting in high stress values. For this reason, network analysis was also performed so as to validate the ordination scattergrams.

**Network Analysis**

Network analysis focuses on object-to-object relationships, a very different perspective compared to the "data-wide" patterns detected by ordination techniques. The algorithm creates minimum spanning trees (MST), relating objects monotonically and using association values from the association matrix for the data set being examined. I superimposed the MST on the ordination scattergrams as a form of validation of the ordination derived patterns. A good configuration of points is represented in the situation where the closest objects are joined by the MST. MST was used as a technique for investigating the relationship between relict areas and piospheres (Chapter 6).

The combination of ordination and network analysis thus represents a powerful graphical tool for interpreting spatial or temporal relations between objects. However, the constraints of representing multivariate data in 1 or 2 dimensions still persists. In addition, it is difficult to determine what attributes are responsible for the relationships observed in ordination space. Experience has shown that a single attribute out of 30 or more can be largely responsible for an observed trend. This makes the detection of community trends within ordination space dubious. For this reason, alternative methods for detecting trend and linking trend of individual attributes to community trends were sought out.
Serial Correlation

Randomization techniques have been used to detect stability in stochastic systems. Crowley (1992) advocated random walk techniques for univariate data and randomization techniques for multivariate data. Various correlation techniques could be used for trend detection, where determination of direction of change is important. However, 10 consecutive data points (the minimum number of spatial and temporal points allowed by the algorithms) are usually not sufficient to adequately calculate trend considering noise within the data set arising from sampling error and year-to-year climatic fluctuation. For this reason, a "common denominator" approach for detecting change was used. Serial correlation was determined to detect consecutive change for community matrices and individual species. Data exploration indicated that significance at the 5% level (5% implying relative frequency of randomized data showing higher serial correlation than the nonrandomized data, expressed as a percentage) was sufficient to identify attributes showing continuous change when examined graphically. Suitable algorithms for serial correlation were found in Manly (1991). Serial correlation at the matrix (community level) was determined by performing a correlation between the association table (derived from PATN) for the data matrix in question and a distance matrix representing expected distances (spatial or temporal) between object points. The nature of the second distance matrix determines the kind of correlation detected. For example, consider the following data matrices: matrix A (Table 4.1) represents the association values between all 2-way combinations of objects; matrix B (Table 4.2) shows the distances of a hypothesized linear relationship between all objects--all objects are considered in the correlation; matrix C (Table 4.3) represents a distance matrix defining a hypothesized serial correlation between 10 objects.

Serial correlations of individual attributes were determined using a different algorithm also from Manly (1991). The subroutine "SERIAL" (p. 197) calculated serial correlations and the von Neumann ratio, which is used as the test statistic for determining significance of the unrandomized sequence relative to the randomized sequences. For the determination of serial correlation, only the "strength" of the correlation was considered important; thus, a one-tailed test was performed. The observed "p" value represented the percentage of randomized correlations greater than that for the unrandomized data.
Table 4.1. Matrix A: Hypothetical association values representing the strength of relationship between objects.

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Table 4.2. Matrix B: A distance table representing a purported linear relationship between objects, with all objects contributing to the overall relationship.

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Table 4.3. Matrix C: A distance table representing a purported serial relationship between objects, with adjacent objects contributing to the overall relationship.

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3 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
4 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 \\
5 & 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\
6 & 0 & 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 \\
7 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 1 & 0 \\
8 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 1 \\
9 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
10 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\end{array}
\]

Similar randomization techniques were used to detect attributes (species) showing strong differences between the Passey et al. (1982) data sets and the data collected from 1991 to 1993. The algorithm for conducting a 2-sample randomization test (Manly 1991, p. 61) calculated significance based on the mean difference and variance ratio statistics. In all the data sets considered in this dissertation, the 2-tailed test based on mean differences was used.

It is important to note that for the serial correlations and difference testing of individual attributes, the significance level is taken as a representation of the strength of that relationship and not as a test of statistical significance at a larger scale.

Measuring Stability, Equilibrium, and Similarity in Attribute and Composition Data

Ordination has recently become a popular multivariate tool for depicting spatial and temporal community trends. Several authors have advocated the use of ordination to discern long-term treatment effects as an aid to range condition assessment (Friedel et al. 1988, Friedel 1991, Bosch and Gauch 1991, Laycock
1991, Whisenant and Wagstaff 1991). Stafford Smith and Pickup (1990) suggested ordination as a method for detecting pathways and stable states. Other authors simply used the percentage similarity between plots to determine if change has occurred. In this case, a certain threshold value could be deemed to indicate change.

**Results**

See the section "A Discussion of the Underlying Biology" for a general review of these data and to achieve an understanding of the contribution of the different data components. Figures 4.3 and 4.4 are included as graphical verification of the results presented as serial correlations and t-tests. Since these results define the interesting properties of the ordinations, the latter are not shown exhaustively.

**Change Within the Passey et al. (1982) Data Set**

**Ordinations**

Ordination of the 13 selected Passey et al. (1982) data sets indicated a high degree of serial correlation at some of the long-term sites. This is indicated by the presence of a pattern of the arrangement of spatial data within ordination space (see Figure 4.3 as an example). Nine out of 12 stands examined (data not shown) showed trends in ordination space at the individual, and 2 out of 12 stands showed trends at the growth-form resolutions, respectively. In many cases, interpretation of the ordinations was problematical and had the potential of being highly subjective. For this reason, matrix correlations and serial correlations at the individual species and growth-form data resolutions were used to validate results and to better define the major contributors to the observed trends.

**Serial Correlations**

Serial correlations for plant community dynamics (calculated for all 17 long-term Passey et al. [1982] sites) indicated that nonrandom changes in community structure (based on individual species) do commonly occur (11 out of 17 data sets) at the 5% level of statistical significance (Tables 4.4 and 4.5). Only 2 out of 17 data sets showed matrix serial correlation at the growth-form resolution, indicating that species fluxes within growth-forms may be antagonistic.
Fig. 4.3. An ordination at the individual species resolution for the Passey et al. (1982) stand identified as ID 3-58. SSH1/2 refer to Semi-Strong Hybrid Multi-Dimensional Scaling components 1 and 2.
Serial correlations using the von Neumann index were conducted to determine if total phytomass, particularly growth-forms, or individual species showed serial correlations (Tables 4.4 and 4.5). At the 5% level of statistical significance, there were no serial correlations for total phytomass, 5 significant correlations for total shrubs (TWO), 3 for total forbs (TFO), and 1 for total bunchgrasses (TGR).

Seventeen species (1 annual, 4 perennial grasses, 5 woody plants, 7 forbs [Tables 4.4 and 4.5]) contributed to 32 cases of serial correlation amongst species only. *Artemisia tridentata* (ARTRD) was the most consistent species showing serial correlation (5 cases out of 17), indicating that a diversity of species contribute to serial correlation within plant communities. Fourteen out of 18 species showing serial correlation do so only once or twice, indicating that the collection of species contributing to community serial correlation varies from stand to stand.

While serial correlation may be indicative of the nature of change within plant communities, the following paragraphs attempt to define changes that have occurred between the times of data collection by Passey et al. (1982) and more recently.

**Change Between the Passey et al. (1982) Data Set and Similar Data Collected from 1991 to 1993**

Since the method used for phytomass estimation may be subjective, alternative methods (photo retakes and anecdotal data) for determining gross change were investigated to corroborate phytomass estimations and to understand the underlying biology of the plant communities. Direct observation of the ordinations (using both species and growth-form resolutions), as well as randomization t-tests, were used to elucidate change. As with the previous section, emphasis is placed on the randomization tests.

**Ordinations**

Within ordination space, major change was indicated by a separation of the Passey et al. (1982) data and that collected in the early 1990s (see Figure 4.3 as an example). Ordinations at the data resolution of species indicate major change in community composition in 12 of 13 stands examined. Eleven out of 13 stands also showed change at the growth-form level of data resolution (see Figure 4.4 for an example of lack of change at the growth-form data resolution). As with trend detection (previous section), differences between the
Table 4.4. Table of serial correlations for individual species in Passey et al. (1982) sites reexamined from 1991 to 1993.

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Note: Values are relative frequency of randomized data showing higher serial correlation than the non-randomized data, expressed as a percentage. Blank spaces indicate insufficient data for analysis. See Appendix B for a full list of species acronyms and their explanations. Column labels represent Passey et al. (1982) notation for long-term stands examined.
Table 4.5. Serial correlations of individual species within the remaining Passey et al. (1982) plots not examined from 1991 to 1993.

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Note: The final column is a summation of the number of instances a particular species shows a serial correlation significant at the 5% level for all Passey et al. (1982) long-term sets. Remaining values are relative frequency of randomized data showing higher serial correlation than nonrandomized data, expressed as a percentage. Blank spaces indicate insufficient data for analysis. See Appendix B for a full list of species acronyms and their explanations. Column labels represent Passey et al. (1982) notation for long-term stands examined.
Passey et al. (1982) data and that collected in the 1990s are validated using a suitable index and randomization statistics. These results are presented in lieu of the full complement of ordination diagrams.

**t-Tests**

Two sample t-tests (using randomization techniques) were used to identify statistically significant differences in species and growth-forms, as well as total phytomass between data collected in the 1950s and 1960s versus 1991 to 1993.

Only 1 stand (Table 4.6) showed significant differences in total phytomass between the Passey et al. (1982) data and data collected in the 1990s (TOT, Table 4.6). Total annuals (TAN) and total forbs (TFO) showed no significant results at the 5% level of statistical significance. Grasses (TGR) and woody plants (TWO) show 3 and 9 (counts of percentage significance < 5% for taxa), respectively, out of 11 possible significant differences at the 5% level (Table 4.6).

Twenty different species (1 annual, 7 bunchgrasses, 8 forbs, and 4 woody plants) accounted for the 60 cases of significant differences among all stands. The most consistent species showing significant differences are *Artemisia tridentata* (ARTRD, 7 out of 11 stands), *Artemisia tripartita* (ARTRP, 5 out of 11 stands) and *Agropyron* species (AG, 4 out of 11 stands). Total forbs showed significant differences ranging from 1 to 3 cases out of 11, making it difficult to reach generalizations. Therefore, a few species most commonly contribute to the differences at the community level, while the bulk of species do so sporadically.

The direction of change is also of interest. The single site showing a significant difference in total phytomass is one of increase. Of the 2 growth-forms showing significant differences, woody plants consistently show an increase, while grasses show 1 case of increase, and 2 of decrease. Of the woody species, *Artemisia tridentata* (ARTRD, the dominant shrub in all cases) always shows an increase in phytomass, while others show a mixed response. *Agropyron* spp (AG) shows 3 cases of decrease and 1 of increase, while *Sitanion hystrix* (SIHY) shows 3 cases of increase. Other bunchgrasses show too few significant differences to comment on. Forbs also show too few differences to enable comment.
Fig. 4.4. An ordination at the growth-form data resolution for the Passey et al. (1982) stand identified as ID 1-59. SSH1/2 refer to Semi-Strong Hybrid. Multi-Dimensional Scaling components 1 and 2.
Table 4.6. Probability of differences of abundance between the Passey et al. (1982) data and data collected from 1991 to 1993 for individual species.

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Note: Values are relative frequency of randomized data showing larger differences than non-randomized data, expressed as a percentage. Blank spaces indicate insufficient data for analysis. See Appendix B for a full list of species acronyms and their explanations. Column labels represent Passey et al. (1982) notation for long-term stands examined. d = decrease, i = increase. SUM = summarization of number and direction of significant changes.

Repeatability of Species Response Curves

Most abundance curves over time within the relict areas are nonlinear, implying that even if serial correlation is detected, no definite trend can be identified (Tables 4.7 and 4.8). The shape of abundance histograms varies between species, as well as within species for those showing serial correlations at several sites (Table 4.9).

Population Parameters

From the scant information available on shrub demography (Table 4.10), it appears that both sites in Kettle Butte Kipuka (ID 8-60 and ID 9-60) experienced a recent increase in the number of seedlings.
(expressed as a proportion of the total individuals of a species for a particular site) and immature plants of *Artemisia tridentata*. *Chrysothamnus viscidiflorus* at ID 9-60 also showed an increase in immature, mature, and partly dead age-state classes. Three plots on Carey Kipuka showed changes in shrub demography. ID 17-58 showed a clear increase in *Artemisia tridentata* of the mature class and of *Artemisia tripartita* of the mature and partly dead classes. ID 18-58 showed an increase in *Artemisia tripartita* of the mature and partly dead classes. ID 8-59, previously devoid of shrubs, showed the increased presence of *Artemisia tridentata* and *Chrysothamnus viscidiflorus*. From available information on average height and range of heights of shrubs within the stands examined (Table 4.11), it appears that several changes in plant stature have occurred. ID 6-58, ID 12-58, and ID 1-59 all showed increases in plant height.

**Photo-Interpretation**

Three parameters relating to phytomass were assessed from photo retakes (Table 4.12). The three parameters, stature, number, and foliage density of shrubs, were all assessed visually by projecting photos adjacent to each other using two slide projectors. Two to three sets of photos (usually different perspectives) were examined per site. Change was considered valid only if it was easily observed in more than one photo set. Stature, number of shrubs, and foliage density all appeared to vary between years examined and may contribute to changes in phytomass.

### Table 4.7. The number of linear and nonlinear species changes in the Passey et al. (1982) data sets reexamined from 1991 to 1993.

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Note: Column labels represent Passey et al. (1982) notation for long-term stands examined. X = not enough data
Table 4.8. The number of linear and nonlinear species changes in the Passey et al. data sets not reexamined from 1991 to 1993.

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Note: Column labels represent Passey et al. (1982) notation for long-term stands examined.

Table 4.9. The nature of species fluxes for all long-term Passey et al. (1982) data sets.

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Note: See Appendix B for an explanation of the species acronyms. Unimodal = single maxima, bimodal = 2 maxima, increaser = general increase over time period examined, decreaser = general decrease over time period examined.
Table 4.10. Proportion of seedlings, immature, mature, partly dead, and completely dead shrubs within the Passey et al. (1982) data sets.

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<td>0.3(0.1)a</td>
<td>0.3(0.1)a</td>
<td>0.2(0.1)a</td>
<td>0.4(0.1)a</td>
<td>0.3(0.1)a</td>
<td>0.3(0.1)a</td>
<td>0.3(0.1)b</td>
</tr>
</tbody>
</table>

Note: Unbracketed numbers are from the initial data collection, while bracketed numbers were collected in 1992. Column labels represent Passey et al. (1982) notation for long-term stands examined. * = a few large sagebrush reported, ** = collected in 1994. a = Artemisia tridentata; b = Artemisia tripartita; c = Chrysothamnus viscidiflora.
Table 4.11. A few comparisons of present shrub height with incidental data derived from archived field notes.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Average height (cm)</td>
<td>56(60)a</td>
<td>51(67)a</td>
<td>56(93)a</td>
<td>71(75)a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range (cm)</td>
<td>45.7-91.4</td>
<td>25-31</td>
<td>51-91</td>
<td>46-60</td>
<td>41-92</td>
<td>61-76</td>
<td>20-25</td>
<td>76-127</td>
<td>16-26b</td>
</tr>
<tr>
<td>Occasional (cm)</td>
<td>61(1 of 76.2(4 of 12)a</td>
<td>76.2(4 of 12)a</td>
<td>45.7</td>
<td>112</td>
<td>60</td>
<td>*(2 of 15)b</td>
<td>*(9 of 15)b</td>
<td>*(2 of 15)b</td>
<td>*(2 of 15)b</td>
</tr>
</tbody>
</table>

Note: Column labels represent Passey et al. (1982) notation for long-term stands examined. Unbracketed numbers are from the initial data collection, while bracketed numbers were collected in 1992. None indicates no match between Passey et al. (1982) data and recent data. *(x of y) indicates number of individuals subscribing to "occasional" (exceptional) height. a = Artemisia tridentata; b = Artemisia tripartita; c = Chrysothamnus viscidiflora.

Table 4.12. Photo-derived comparisons of stature, number, and foliage density of dominant shrubs on Passey et al. (1982) sites.

<table>
<thead>
<tr>
<th>ID3</th>
<th>ID6</th>
<th>ID1</th>
<th>ID13</th>
<th>ID15</th>
<th>ID1</th>
<th>ID8</th>
<th>ID9</th>
<th>ID17</th>
<th>ID18</th>
<th>ID8</th>
<th>ID9</th>
<th>ID6</th>
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<tr>
<td>Stature</td>
<td>--</td>
<td>--</td>
<td>i</td>
<td>--</td>
<td>i</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>*</td>
<td>--</td>
<td>--</td>
<td>i</td>
</tr>
<tr>
<td>Density</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>i</td>
<td>--</td>
<td>--</td>
<td>i</td>
</tr>
<tr>
<td>Foliage density</td>
<td>i</td>
<td>--</td>
<td>--</td>
<td>i</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>i</td>
<td>i</td>
<td>i</td>
<td>i</td>
<td>i</td>
</tr>
</tbody>
</table>

Note: (i signifies increase, -- signifies no detectable change). Column labels represent Passey et al. (1982) notation for long-term stands examined. * = photos not repeatable.

Three stands (ID 12-58, ID 15-58, ID 6-60) showed clear increases in shrub stature. Only 1 stand (ID 8-59) showed an increase in the density of shrubs. Five stands (ID 3-58, ID 15-58, ID 8-59, ID 9-59, ID 6-60) all showed an increase in foliage density.

A Discussion of the Underlying Biology

Although my first aim was to present data in general terms so as to allow validation of research hypotheses, it is also necessary to try to understand some of the anomalies discovered. This section will also relate different sources of information to strengthen results and provide a better ecological understanding of the
general interpretations.

The matrix, growth-form, and individual species serial correlation show mutual support. High matrix serial correlation is generally a good indication that species fluxes are occurring in a non-random manner on a year-to-year basis. Serial correlation of growth-forms may not always reflect species fluxes because of antagonistic species changes. Species were thus deemed to be the most important level of data resolution for examining plant community change.

The only case (ID 9-60) of significant difference in total phytomass between the Passey et al. (1982) data and the present is supported by a large increase in seedling and immature shrubs. Sagebrush are known to establish as cohorts (West et al. 1979, Cawker 1980, Eckert and Spencer 1986), and the combination of a more mature stand together with newly established plants could result in a temporarily greater phytomass. The nature of such increases could be short term only, since the lag effects of competition between individuals of the same or different species may moderate phytomass in the longer term. The woody growth-form shows a close relationship to the results obtained for *Artemisia tridentata* as a result of the dominance of this shrub. Since *Artemisia tridentata* is often the largest contributor of phytomass in the stands examined, it is expected that the fortunes of this species may, at least partially, drive phytomass fluctuations of other species and growth-forms. An effort was therefore made to validate some of the observed increases in sagebrush phytomass using other sources of information.

From anecdotal information and data presented in Tables 4.9 through 4.11, it appears that several factors may be responsible for observed fluxes in *Artemisia tridentata*. Among these are variation in and history of precipitation, demographic patterns, webworm infestation, past episodes of snow mold, vole girdling, and increased stature and net growth of shrubs. These factors merely represent possible explanations for the manifestation of increased sagebrush and cannot be reliably interpreted as causal in nature. The retroductive nature of this project does not allow the determination of causality, although speculation is warranted.

Several major causal factors vie for the explanation of the increased phytomass of *Artemisia tridentata*. Examination of the histories of the different stands investigated shows that the study sites have not been burnt for many decades. Although the fire cycle in the relatively small and isolated kipukas may be
lengthened relative to areas outside of the protective lava, there can be no doubt that such long cycles would occur in any area of sagebrush steppe not dominated by cheatgrass. Increased phytomass of *Artemisia tridentata* may thus be a natural long-term increase of a fire-sensitive species able to utilize deeper-lying water resources.

Passey et al. (1982) have suggested that the process of stagnation may be occurring within stands examined. Sequestration of nutrients within the tissues of woody plants has often been hypothesized (Passey et al. 1982, Tueller and Tower 1979) but never validated because of the long-term nature of this process. If this was occurring within the stands examined, simultaneous decreases in the phytomass of shorter-lived species and total live phytomass of the plant community could be expected. This was not generally the case in the stands examined (Table 4.6).

Field notes taken by Passey and his coauthors (deposited in Utah State University archives) indicate that infestations by webworm were a common occurrence in the early 1960s. Any increase in phytomass during the 1960s and differences between the 1960s and early 1990s may thus be a recovery phenomenon. This applies also to the occurrence of snow mold (Allen et al. 1987), vole girdling (Mueggler 1967, Parmenter et al. 1987), or poor soil aeration during unusually wet periods (Ganskopp 1986).

A fourth possible causal mechanism that cannot be separated from the above mechanisms is the effect of elevated atmospheric carbon dioxide (CO₂) concentrations. Elevated CO₂ favors C₃ metabolism (most woody plants and bunchgrasses of this region), though not equally. Changes in the competitive balance between species are thus possible (Mayeux et al. 1991). Greenhouse studies have shown that *Bromus tectorum* (C₃) is strongly favored by increased CO₂ levels relative to bunchgrasses (Billings 1990). The relict area data examined, however, do not indicate a strong increase in cheatgrass phytomass. Mayeux et al. (1991) suggested that several whole plant measures may change as a result of increased CO₂ levels. Thus, phytomass, leaf area, size, and growth rates of sagebrush and bunchgrasses could increase.

Sagebrush develops a set of perennial, as well as a set of ephemeral, leaves (Miller and Shultz 1987). The colder and wetter than average growing season of 1993 resulted in the late retention of the ephemeral leaves, resulting in a greater shrub phytomass. Although this is an occasional event, the analyses in this chapter...
indicate that differences apply to all 3 individual years of data collection within the 1990s.

It is likely that other causal mechanisms could be advanced in the future. It is also very likely that fluxes of species within the communities examined are due to a combination of the above and other, yet undiscovered, causal mechanisms.

**Discussion and Conclusions**

A more extensive consideration of objectives encompassing data from all the field studies and literature is to be found in the final chapter of this dissertation.

**Stability/Equilibrium**

It is quite apparent from the results obtained that relict areas do not exhibit to the constancy theme of stability. The literature and long-term data indicate a trend of increased woodiness occasionally reversed by fire, insect/pathogen outbreaks, or supersaturated soils. This may result in a cycling of plant community changes in such relict areas, and other communities with sagebrush as an integral member. Such a phenomenon could still exhibit a boundedness aspect of stability pertinent to the State-and-Transition Model.

**Continual versus Discrete Change**

Data for individual species and communities indicate that change within undisturbed relict areas is generally in a continuous form, as evidenced by the serial correlation. This may not be the case in relicts impacted by fire or flooding, considering autecological traits such as the differential ability to resprout following fire, or tolerate poor soil aeration. Evidence from other studies (Lovejoy 1980) shows disjunct change where cheatgrass assumes dominace.

**Individualistic versus Community Change**

The relict areas do seem to exhibit some concerted species changes that could be interpreted as community changes. Most cases are associated with an increase in the shrub component (specifically *Artemisia tridentata*) and a decrease in *Agropyron spicatum*, the major grass. The balance between these two species suggests an antagonistic relationship, either in terms of induced physical environment or competition.
for resources. Caldwell and Richards (1989) indicated that *Artemisia tridentata* is a stronger competitor for phosphorus against *Agropyron spicatum* than *Agropyron desertorum*. Similarly, bunchgrass species not showing consistent decreases concomitant with an increase in sagebrush may be less susceptible to competition for resources. Plant species other that *Agropyron spicatum* and *Artemisia* do not show consistent change, implying that change on a landscape is site specific and individualistic. The interpretation of results in terms of individualistic versus community change is thus ambiguous.

**Repeatability of Serial Correlations, t-Tests and Species Response Curves**

Few species exhibit consistent temporal serial correlation. Neither do species show consistent shapes of abundance curves over the time period examined. An exception is the increased woodiness of plant communities, particularly of *Artemisia* species. Although this has happened in the absence of livestock, this phenomenon could also be expected on grazed rangelands, especially where grazing pressure favors woody species. Long-term increase in woody species in the absence of fire is thus identified as a predictive element of vegetation dynamics of sagebrush steppe vegetation, because of its repeatability at the sites examined.
CHAPTER 5
VEGETATION DYNAMICS FOLLOWING A WILDFIRE AND THE
ADVENT OF LIVESTOCK GRAZING AT A SAGEBRUSH
SEMI-DESERT SITE IN CENTRAL UTAH

Justification

This data set affords one of the few recent opportunities to examine vegetation dynamics following
fire and the advent of grazing within "high" condition sagebrush semi-desert. An even rarer opportunity is that
of examining a possible interaction between the two disturbance types. Specific objectives follow from Table
1.2. Some objectives can be presented as alternative hypotheses with predictions, while other exploratory
objectives are left as statements.

Specific Objectives (0)

O1: To determine if the plant communities near Mills follow the resilience model of stability following
fire. Since this is a community concept, this objective will be achieved by examining long-term trends
within ordination space.

HA1.1: The resilience model of stability does not hold (Prediction: No temporal trends are apparent in the
Mills data, or if trends are apparent, the plant communities do not return to predisturbance
compositions).

HA1.2: The resilience model of stability does hold (Prediction: Temporal trends are apparent in the Mills
data, and plant community data collected in the 1990s' is more similar to data collected in 1981 than
intervening years).

O2: To determine if changes in these plant communities are discrete or continuous following wildfire and
the advent of grazing. The nature of change will be examined at the individual species and
growth-form resolutions using graphical techniques, serial correlation, and ordination.

HA2.1: Change over time appears discontinuous (Prediction: Graphs and ordinations appear discontinuous,
and low values of serial correlation are apparent).
HA2.2: Change over time appears continuous (Prediction: Graphs and ordinations appear continuous, and high values of serial correlation are apparent).

O3: To determine if changes within plots indicate individualistic or community change.

HA3.1 Vegetation dynamics appear individualistic (Prediction: Trends for individual plots tend to diverge).

HA3.2 Vegetation dynamics appear to conform to community principles (Prediction: Ordination trends for individual plots mirror each other).

O4: To determine if plant communities show hysteresis following disturbance or not. This will also be examined within ordination space. Hysteresis will be considered to have occurred if the return pathway after disturbance follows the same pathway of vegetation change with the advent of disturbance.

HA4.1: The Mills data shows hysteresis (Prediction: Ordination based trajectories show a close affinity between the advent and relinquishment of disturbance).

HA4.2: The Mills data does not show hysteresis (Prediction: Ordination based trajectories do not show a close affinity between the advent and relinquishment of disturbance).

O5: To determine the predictability of plant species compositional changes.

The requirement for predictability in a model of vegetation dynamics upon which to base rangeland condition and trend analysis forces the identification of variables that are themselves predictive. This will be accomplished by examining if the same suite of species consistently exhibit serial correlation within the Mills data.

O6: To determine the predictability of plant species' abundance changes. This will be achieved by examining whether species showing high temporal serial correlation display the same shape of abundances across sites over the same period of time.

Introduction

In this chapter, ordination, serial correlation, and graphical representation of individual species and growth-forms will be used to determine long-term vegetation changes within a 13-year data set (1981-1993). The study site is located near Mills in central Utah (section 30, R2W, T15S, Salt Lake Meridian, Juab County)
on a pediment remnant. Slopes are 1-2% east-facing, and the elevation ranges between 1,617 and 1,622 meters (5,305-5,320 ft). For further details, see West and Hassan (1985).

Previous work at the site examined seed pool dynamics in burnt and unburnt patches (Hassan and West 1986) and shorter-term vegetation dynamics following a wildfire event (West and Hassan 1985). Hosten and West (1994) described individual species fluxes for the initial 11 years of this study.

The history of the site is summarized by Figure 5.1. Pretreatment data were collected on 4 plots in 1981 prior to a wildfire event. Since burning was patchy and a watering point about 2 km distant was only established during the second year following the fire, an ad hoc experiment allowing the investigation of vegetation dynamics in burnt and unburnt patches under grazed and ungrazed conditions was possible. The 4 original plots were fenced off and paired with nearby burnt patches following the 1981 wildfire. Although the study site probably had been lightly grazed in winter by sheep several decades before the wildfire event, little grazing by cattle during the growing season had occurred because of distance to water. The range was consequently considered to be in very good (late seral) condition (Hassan 1983) in July of 1981. Several years after the initiation of the study, unfenced portions of the area were chained to remove juniper snags and remaining live trees. One of the unburnt and grazed replicates was lost during this procedure. A second wildfire occurred before the 1987 data collection. However, because of the ensuing drought and lack of continuous fuel, the fire was very patchy. From photos and site notes, it appears that two of the burnt and ungrazed exclosures were partially impacted, while one was completely reburnt. It was impossible to discern between burnt and unburnt patches 1 year later. The possible implications of this are discussed within the "Results" section.

Methods and Materials

The ordination and randomization techniques used are summarized in Chapter 4. Cover data were collected during the third week of July every year using the gimballed point cover technique (Winkworth and Goodall 1962). Understory as well as ground cover was observed under the uppermost vegetation layer. One hundred stations were examined per macroplot and interpreted as percentage cover by stratum. Twenty-five stations were located along each of 4 transects located randomly within macroplots. From Figure 5.1, it is
Fig. 5.1. Graphical representation of the experimental design for plots near Mills, Utah.
apparent that all treatments show some replication, though not on an equal basis. There are 4 burnt and ungrazed plots, while other treatments initially had 3 replications. Ordination of plots within treatments allowed discerning within treatment differences for long-term vegetation dynamics. Ordination at the level of the entire data set focussed on between-treatment differences. As with the previous chapter, different data resolutions and serial correlation were used to elucidate the dynamics observed in ordination space. Sampling adequacy was determined in 1993 with results presented in Appendix B. A second wildfire occurred prior to the 1987 field season. Exclosures 2 and 3 were partially reburnt, while exclosure 1 was not impacted at all, and exclosure 4 was completely reburnt. The fact that exclosures 2 and 3 show the extreme in community response at the overall trajectory level (Figure 5.2), and that no definite discontinuity in the ordination is apparent other than the initial perturbation associated with the first wildfire event, implies that the second wildfire did not have a strong impact on the community dynamics.

Results

Examining the Resilience Model of Stability
Within Ordination Space

Burnt and Ungrazed Plots

Figure 5.2 indicates that within a treatment, the various exclosures can show a range of trajectories. Exclosures 1 and 2 show pathways returning to predisturbance plant communities in a circular mode, while exclosures 3 and 4 do so in a more linear fashion. All exclosures (original plots) show a tendency to return to predisturbance plant composition, though this is more marked in exclosures 3 and 4.

Burnt and Grazed Plots

Figure 5.3 shows a much greater similarity of pathways (indicated by overlap with the background) than the burnt and ungrazed exclosures. Plots 1 and 3 appears to move back towards predisturbance plant composition (indicated by squares) until 1989. Following 1989, any indication of trend appears to be one of increasing difference from predisturbance plant composition so that plant communities appears increasingly different from predisturbance communities in the 1990s than in the late 1980s. The trend for plot 2 appears to
skirt predisturbance composition. Cattle grazing has appeared to intensify since 1989 (Pers. comm., N.E. West 1994).

**Unburnt and Grazed Plots**

Figure 5.4 indicates that the unburnt and grazed "additional" plots show trend, but not towards predisturbance plant composition. As with the burnt and grazed plots, trends appear to skirt predisturbance plant composition.

**Determining the Nature of Change at the Community Level**

Within- and between-treatment plant community changes have already been examined in previous sections. This section is merely to draw attention to the dependence of the nature of change of plant communities to the perspective adopted. For this reason, only 1 treatment, involving the burnt and ungrazed exclosures, is examined.

In this section, ordinations are shown on the background of the entire data set. The shapes of trajectories are not always the same as for the same plots of previous figures. This is because of the increased difficulty of arranging an increased number of objects within ordination space. The increased stress associated with doing so is reflected by a decreased accuracy of the spatial arrangements of objects in ordination space.

**Mill's Data Including Bromus tectorum**

All 4 plots of Figure 5.5 show continuous change (or trend, identified as a visible patterning of connected points), as opposed to a lack of change (identified as a cluster of points).

**Mills Data Excluding Bromus tectorum**

Exclusion of Bromus tectorum from the data set (Figure 5.6) appears to change the nature of the trajectories of many of the plots analyzed. Two plots (exclosures 3 and 4) show a complete lack of trend (identified by a cluster of points). Exclosures 1 and 2 show combinations of trends and stable states (within which no trends can be identified). This inconsistency of interpretation following the exclusion of a single species from the community matrix ordination space forces closer scrutiny on individual species.
Fig. 5.2. Ordinations of plant community change near Mills at the data resolution of individual species for the burnt and ungrazed treatment. (The 4 sets of axes represent different plots against the same background [stippled lines], allowing comparison between exclosures. SSH1/2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.)
Fig. 5.3. Ordinations of community change at the data resolution of individual species for the burnt and grazed treatments near Mills, Utah, 1981-1993. (The 3 sets of axes represent different plots against the same background [stippled lines], allowing comparison between plots. SSH1/2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.)
Fig. 5.4. Ordinations of community change at the data resolution of individual species for the unburnt and grazed treatments near Mills, Utah, 1981-1993. (The 3 sets of axes represent different plots against the same background [stippled lines], allowing comparison between plots. SSH1/2 refers to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.)
Determining the Nature of Change at the Individual Species Level

Only 1 species (*Artemisia tridentata* [ARTRD, Table 5.1], Figure 5.7b) showed a discrete change in cover abundance, while several species showed continuous change (*Agropyron spicatum* [Figure 5.7c], *Poa* spp., *Stipa comata*, *Bromus tectorum* [Figure 5.7a] and *Ephedra nevadensis* [Table 5.1]). The only other species showing consistency in nature of change was *Bromus tectorum* (9 times out of 9, Table 5.1), which varied in a unimodal pattern exclusively (Table 5.1).

Only treatments encompassing a burn (BF and BG) showed a discrete change in cover abundance for any particular species (Table 5.2). Only *Artemisia tridentata* shows continuous linear changes in abundance, while many species show continuous nonlinear trends (Table 5.2). Of the continuous nonlinear trends, all are unimodal.

The shapes of the cover histograms for *Bromus tectorum* (Figure 5.7a) indicate that there may be an interaction with precipitation (Figure 5.8) as well as treatment. Cover for the above categories all appear to vary somewhat with precipitation (Figure 5.8).

Serial Correlations for Determining Suites of Species Change

Serial correlation at the matrix level indicates very significant temporal dynamics for all treatments at the 5% level of significance (Table 5.3). The only species showing consistent serial correlation across all plots and treatments is *Bromus tectorum*. No other species or growth-form shows repeated serial correlation across the entire data set or even within a single treatment combination. Four out of 9 plots (across all 3 treatment combinations) showed serial correlation of total cover over time. This may be an indication that an extrinsic factor was important in determining temporal dynamics. This is most likely to be drought (Figure 5.8).
Fig. 5.5. Ordinations of community (all species included) change at the data resolution of individual species for the burnt and ungrazed treatments near Mills, Utah, 1981-1993. (The 4 sets of axes represent different plots against the background [dots] of the entire Mills data set, allowing comparison between panels. SSH1/2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.)
Fig. 5.6. Ordinations of community (without cheatgrass) change at the data resolution of individual species for the burnt and ungrazed treatment. (The 4 sets of axes represent different plots against the background of the entire Mills data set, allowing comparison between panels. SSH1/2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.)
Fig. 5.7. Examples of the individual species abundances (percentage cover on ordinate axes) for *Bromus tectorum* (A), *Artemisia tridentata* (B), *Agropyron spicatum* (C), and total bunchgrass (D) in the burnt and grazed treatment, near Mills, Utah, 1981-1993.
Table 5.1. The nature of change on an individual species basis at Mills, Utah, 1981-1993.

<table>
<thead>
<tr>
<th></th>
<th>AGSP</th>
<th>POA</th>
<th>STCO4</th>
<th>BRTE</th>
<th>ARTRD</th>
<th>EPNE</th>
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<tbody>
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<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Increaser</td>
<td>0</td>
<td>?</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>?</td>
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<tr>
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<tr>
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<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Note: numbers represent instances of occurrence, blanks indicate a lack of data to make a decision, ? = no definite shape, see Appendix B for species acronyms. Discrete = disjunct change, increaser = general increase in cover over time period examined, decreaser = general decrease in cover over time examined, unimodal = a single cover maxima, bimodal = two cover maxima.

Table 5.2. The nature of change of species within plots of the burnt and ungrazed (BF1-4), burnt and grazed (BG1-3), and unburnt and grazed (UG1-2) treatments at Mills, 1981-1993.

<table>
<thead>
<tr>
<th>Change class</th>
<th>BF1</th>
<th>BF2</th>
<th>BF3</th>
<th>BF4</th>
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<tr>
<td>Increaser</td>
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<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Unimodal</td>
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<td>2</td>
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<td>1</td>
<td>1</td>
<td>1</td>
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<tr>
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<td>0</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Note: Continuous change includes linear and nonlinear change subdivided into increaser and decreaser versus uni- and bimodal change, respectively. See Figure 5.1 for definition of change classes.
Fig. 5.8. Crop-year (1 Sept. of previous year-30 June of year indicated) precipitation at the Mills data site for the duration of the study. (Missing values are approximated using regression against the nearest weather station [Scipio, Utah].)
Table 5.3. Serial correlations for entire data matrices, growth-forms, and individual species at Mills, Utah, examined from 1991-1993.

<table>
<thead>
<tr>
<th></th>
<th>BF1</th>
<th>BF2</th>
<th>BF3</th>
<th>BF4</th>
<th>BG1</th>
<th>BG2</th>
<th>BG3</th>
<th>UG1</th>
<th>UG2</th>
<th>&lt;5%</th>
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</thead>
<tbody>
<tr>
<td>MATRIX</td>
<td>0.02</td>
<td>0.08</td>
<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
<td>0.02</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>AGSP</td>
<td>1.5</td>
<td>0.1</td>
<td>9.6</td>
<td>0.08</td>
<td>0.08</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ORHY</td>
<td>7.8</td>
<td>9.1</td>
<td>4.24</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>POSE</td>
<td>9.1</td>
<td>0.8</td>
<td>0.8</td>
<td>0.04</td>
<td>0.14</td>
<td>0.5</td>
<td>0.1</td>
<td>0.1</td>
<td>0.04</td>
<td>9</td>
</tr>
<tr>
<td>STCO4</td>
<td>6.6</td>
<td>7.9</td>
<td>40</td>
<td>47.7</td>
<td>6.5</td>
<td>13</td>
<td>6.6</td>
<td>3.7</td>
<td>16</td>
<td>1</td>
</tr>
<tr>
<td>TOTAL</td>
<td>90</td>
<td>36</td>
<td>1.4</td>
<td>2.2</td>
<td>6.5</td>
<td>7.7</td>
<td>3.1</td>
<td>7.7</td>
<td>0.2</td>
<td>4</td>
</tr>
</tbody>
</table>

Note: Values are percentage significance (probability of randomized data showing higher serial correlation than the nonrandomized data), and blank spaces indicate insufficient data for analysis. See Appendix B for a full list of species acronyms and their explanations.

Understanding the Underlying Biology

Vegetation dynamics at the Mills site is most easily understood in terms of the autecology of the species involved and not in terms of models of vegetation change involving species replacement. The acute disturbance, the fire during 1981, resulted in sudden changes within the plant community. Most notable was the domination by cheatgrass (Figure 5.7a) during the three years following the fire event, and the disappearance of *Artemisia tridentata* (Figure 5.7b). Since its initial appearance and dominance, cheatgrass abundance has declined to a marginal presence only (across all treatments and all plots--see Figure 5.7 as a representative of all plots and Appendix C for the remainder). This is characteristic of an annual plant associated with a particular disturbance type. Since no major wildfire has occurred since the initiation of the project, cheatgrass abundance has declined. The second wildfire immediately prior to the 1987 data collection does not seem to have had a great impact on the vegetation dynamics of the study site. It is possible, though data supporting this do not exist, that the drought and consequent low fuel load did not allow for a burn with the same ecological consequences as the fire of 1981. This implies that the destructive fire cycle (see Chapter 3) resulting in the elimination of native perennials occurs primarily during wet years.

Of interest is the presence of cheatgrass within the unburnt and grazed treatment combination, albeit
at a reduced cover abundance. Presence within the latter treatment may be ascribed to a mass effect (Hatton and Carpenter 1986). A confounding factor is the general retreat of cheatgrass over the Great Basin ascribed to the 6-year drought of 1987-1992 (Figure 5.8, and Longland and Young [in press]).

*Artemisia tridentata* does not resprout following fire, relying on seed dispersal for reestablishment. Since it is a woody perennial, growth and attainment of maturity is slow, implying that its reestablishment as community dominant is a long-term process. All plots of all treatment combinations encompassing a burn, show a reduced cover of sagebrush (see Figure 5.7b as a typical example, and Appendix C), while the unburnt and grazed plots have maintained their woody plant cover (Figure 5.9 and Appendix C).

Bunchgrasses are relatively unaffected by isolated fire events and so have reattained their cover abundance since the wildfire event and subsequent domination by cheatgrass in the absence of grazing (see Figure 5.9 and Appendix C). This may be aided by the likely decrease in competition for resources following the decline of sagebrush and cheatgrass.

Results for treatments encompassing grazing are more difficult to interpret. Graphs of both burnt and grazed, as well as unburnt and grazed, treatments may show either a decline or an increase in bunchgrass cover (usually reflecting *Agropyron spicatum* cover) through the years of data examined (Appendix C). During the most recent years, bunchgrass cover within both treatments incorporating grazing is comparable. Both unburnt and grazed and burnt and grazed treatment combinations usually show less than the prefire abundances collected for the 4 initial plots examined in 1981. Cattle grazing has intensified in years closer to the present (N.E. West, personal communication). However, this latter observation may also be connected to subtle differences in soils (Jensen 1981).

Since grazing is a chronic disturbance, the reaction of the vegetation is expected to be slower and less dramatic than for fire. This is reflected by the slow decline of total bunchgrass cover in treatment combinations encompassing grazing during the latter years (Appendix C). The heavy grazing of the past few years may also have mediated the increase in *Salsola* (Figure 5.10).
Fig. 5.9. Cover data for total bunchgrass (A) and total woody (B) vegetation for the unburnt and grazed treatment combination, near Mills, Utah, 1981-1993. (Note: Data collection started in 1982 for this treatment.)

Discussion and Conclusions

Determination of Stability Status

The burnt and ungrazed treatment is the only treatment combination that allows the testing of the resilience model of stability, since the grazing influence is still ongoing. It appears that, in this instance, the model does apply since ordinations show a return towards predisturbance plant composition. It is envisaged that this trend will continue with the eventual return of shrubs within the grazing exclosures.

Continual versus Discrete Change

In the case of the Mills data set, it is very difficult to interpret plant community trajectories as continuous or discrete. This is because different species may exhibit either continuous or discrete change under the circumstances examined, and the appearance of community trends is dependent on the relative emphasis of analytical techniques on the different species of the plant community. For example, cheatgrass is the only species showing high serial correlation, and therefore the only species considered to show
Fig. 5.10. Cover by *Salsola kali* for all treatments in the data set collected at Mills, Utah, 1981-1993. (Bars indicate one standard error of the mean.)
continuous change over the time period examined. Consequently, ordinations with cheatgrass included show continuous change, while those without cheatgrass show less well defined trends, or even a complete lack of trend (associated with discontinuous change). Once the influence of cheatgrass was removed, ordinations indicated that the remainder of the plant community moved towards a new point of equilibrium removed from the predisturbance composition (Figure 5.6). This can be considered as a discontinuous change at the community level. The determination of nature of change for communities is therefore ambiguous, while the nature of change for individual species reflects their mode of persistence across disturbance events.

**Individualistic versus Community Change**

The divergence of plots within treatments indicates that (according to the hypotheses and predictions at the start of this chapter) an individualistic mode is favored. However, there are certain community characteristics (such as the resilience concept) that have also been validated. This may also be ascribed to the low plant species richness at this site. It appears likely that different plots may tend towards the same plant composition because of the few options (species) available.

**Hysteresis**

After careful thought, it was decided that the Mills data set does not allow an opportunity to test hysteresis. In the case of fire disturbance (an acute disturbance), there is no opportunity to measure a retrogressive pathway, since the effects of the disturbance are instantaneous. Chronic disturbances (such as livestock grazing) afford an opportunity for examining hysteresis, but cattle grazing is still ongoing outside the exclosures at the Mills site.

**Repeatability of Serial Correlations**

The only species showing clear and repeatable serial correlation is *Bromus tectorum*. This repeatability indicates that this species would make a good predictive variable in a model of vegetation dynamics.
Repeatability of Species Response Curves

Most plant species for which there are enough data show clear repeatability of a response to a particular disturbance type. For example, cheatgrass, sagebrush, and bunchgrasses all show a characteristic change in their abundance relative to fire disturbance. Results are less definite for the chronic disturbance, grazing, but can also be related to their mode of persistence at the study site. This implies that the relation of the above-mentioned species to fire disturbance could form a valuable component of a predictive model of vegetation dynamics at this study site.
CHAPTER 6
PIOSPHERE STUDIES OF GRAZED SAGEBRUSH STEPPE
IN SOUTH CENTRAL IDAHO

Justification

Piospheres (gradients of livestock impact usually radiating out from a watering point) have been useful for discriminating between livestock-induced range degradation and natural fluctuation largely due to climatic variation (Pickup 1989, Bastin et al. 1993a, b, Pickup and Chewings 1994). This chapter constitutes a test to determine if relict areas should be used as benchmarks in range condition assessment of sagebrush steppe. The method of data collection (using a piosphere approach) allows the detection of continua of change versus discrete change along gradients of cattle disturbance. Similarity of stands along the gradient of livestock impact to the Passey et al. (1982) long-term sites was determined. The nature of vegetation change relative to cattle disturbance is of importance in understanding spatial dynamics of vegetation change for the judicious choice of a model of vegetation dynamics and placement of benchmarks within livestock-impacted areas.

Specific Objectives (O) and Hypotheses (H)

O1: To determine the similarity of relict and grazed areas. This objective serves to test the present use of relict areas as pristine sites representative of climax within the Clementsian context.

HA1.1: Relict and disturbed areas are similar within ordination space (Prediction: relict and non-relict sites show interspersion within ordination space).

HA1.2: Relict and disturbed areas are not similar within ordination space (Prediction: there is no interspersion of relict and non-relict sites within ordination space).

O2: To determine if livestock disturbance results in a gradient of vegetation change, disjunct changes associated with thresholds of disturbance, or no discernable pattern. This objective determines the relative utility of two major classes of vegetation models--those that incorporate thresholds versus those that postulate continua of vegetation change.

HA2.1: No pattern in plant community due to livestock impacts are evident (Prediction: the two-dimensional
ordination scattergrams represent a cluster of points with no discernable order based on the hypothesized spatial pattern).

HA2.2: Livestock impact is evident as thresholds of change of the plant communities along the piospheres (Prediction: disjunctions separate data points into 2 or more clouds of stands within ordination space).

HA2.3: Livestock impact is evident as a continuum of change in the plant community along the piospheres (Prediction: trends supporting the hypothesized gradient in livestock impact are evident within ordination space). Trends (identified using serial correlation) in individual soil surface components and most abundant plant species will be used to corroborate trends identified in ordination space.

O3: To determine if piosphere endpoints are most similar to relict areas. This objective is a further test of the notion that a gradient of livestock disturbance radiating out from a watering point will result in a gradient of vegetation change with piosphere endpoints the least disturbed and, therefore, the most similar to relict areas. If this is the case and if the assumption that relict areas are representative of livestock-disturbed areas could be correct, then relict areas should resemble the endpoints of piospheres the most.

HA3.1: Relict areas are equally similar to all sections of the piospheres.

HA3.2: Relict areas are most similar to piosphere endpoints.

O4: To determine the predictability of spatial trends for individual plant species.

HA4.1: There is no predictability in individual species trends (Prediction: no consistent trends for individual species can be discerned).

HA4.2: Individual species trends are predictable (Prediction 1: the same species show trends within different piospheres; Prediction 2: individual species show similarly shaped abundance curves in different piospheres).

O5: To understand the underlying biology of the changes observed. This will be achieved by drawing together all the data collected, while considering past site history and autecology of the dominant plant species.
Introduction

Traditional North American range condition analysis is based on a Clementsian successional model (Smith 1989). Range condition is thought to be inversely related to livestock disturbance, and relict areas are commonly sought to represent rangeland in its best condition. Such an approach would be validated if clearly defined trends could be found from data collected along gradients of livestock impact. Such gradients are to be found around watering points and have been termed piospheres (Lange 1969, Andrew 1988). An additional test of the applicability of the Clementsian Model is the determination of similarity to the relict areas of sampling points furthest from the piosphere hub (watering point). A high similarity would indicate that relict areas would be a good choice of benchmark and management objectives. There is evidence, however, that this traditional perspective of relict areas may not be true. Passey et al. (1982) observed many differences between relict and non-relict sites. These included soil surface parameters (cover by litter, cover by soil microphytes, evidence of erosion) as well as vegetation parameters (e.g., plant vigor). Passey et al. (1982) noted that changes in vegetation often occurred prior to changes in soil trend indicators. Moreover, soil trend indicators were found to be misleading since natural erosion and stagnation cycles occur on micro-scales within relict areas. Using these criteria, moderately grazed areas were frequently found to be in better condition than relict areas.

The use of the piosphere approach involves several assumptions that need to be discussed. The most important assumption is that all sampling points along the livestock impact gradient represent the same ecological site. In this study, 12 of the Passey et al. (1982) relict sites used for detailed plant community analysis were used for comparison to disturbed areas in the same region. Since the relict areas were selected to represent diverse ecological sites and the set of piospheres covered diverse ecological sites, it was reasoned that for each piosphere at least 1 of the relict areas would constitute a suitable benchmark. Furthermore, it is likely that similar changes in plant communities due to livestock impact occur on dissimilar but related ecological sites. Species such as Chrysothamnus, Artemisia tridentata, and various bunchgrasses are thought to react to disturbance in a similar manner (within species) throughout the sagebrush steppe and sagebrush semidesert systems (Blaisdell et al. 1982). Such changes in abundant individual species may result in
community changes overriding more subtle differences in ecological site. A second assumption is that the
gradients in livestock disturbance radiating from the watering points are real. A heterogenous landscape may
result in deviations from the expected distribution of cattle. In spite of these assumptions, piosphere
approaches have been used successfully in chenopod shrublands grazed by sheep (Andrew and Lange 1986a)
and cattle in the central Australian savanna (Pickup and Chewings 1994).

Andrew and Lange (1986a) found distinct soil surface-related patterns in dung deposition, sheep track
development, and lichen cover. Similar patterns were found for vegetation components. Mortality of the main
forage shrub, density of short-lived forbs, and growth of short-lived grasses were all found to increase towards
the watering point. Factors such as grass phytomass, shrub phytomass, and percentage of individuals of a
major shrub in flower decreased towards the watering point (Andrew and Lange 1986b). The general shape of
measured soil and vegetation parameters is a sigmoidal logistic curve (Graetz and Ludwig 1978), although
animal activity patterns, forage distribution, topography, water quality, and climatic factors may cause
deviations (Andrew 1988). Tueller and Platou (1991) found similar patterns in sagebrush steppe vegetation
grazed by cattle in Nevada (see Chapter 3).

Several studies have recently examined piosphere effects using remotely sensed data (Bastin et al.
1993a, b, Chewings et al. in press, Pickup and Chewings 1994). Bastin et al. (1993a, b) proposed the use of
piosphere models to examine landscape degradation in terms of plant recovery in wet years. Since the
degradation is apparent through reduced plant cover closer to watering points, lack of recovery during wet
years (years when livestock grazing has little impact) signifies degradation. Predictability following this model
is marred by the possible increase in phytomass around watering points by unpalatable species (Pers. comm.,
G. Pickup 1994) and frustrated by an inability to separate different growth-forms using techniques tested so far.

Several management criteria within the Laidlaw Park Allotment (the area chosen for this piosphere
study, Figure 6.1) may reduce the feasibility of piosphere studies locally. Foremost is the past and present
impact of sheep overlying that of cattle. Since herded sheep are less dependant on water, they are able to
impact vegetation further away from the watering point, thus confounding the piosphere effect of cattle.
Numerous areas considered to have been severely degraded have been reseeded. Management within Laidlaw
Park also calls for a dispersion of salt licks (and mobile watering points used during the past drought) to
minimize localized resource degradation (BLM 1991). These potential confoundments could also be enlightening, since they are representative of the real world.

Fig. 6.1. The location of Laidlaw Park relative to Craters of the Moon National Monument and Carey Kipuka, Idaho, site of some of the long-term relict stands.
Study Site Location and Description

Laidlaw Park represents a large kipuka that has been penetrated by roads. Figure 6.2 shows the area to be large enough to have been subdivided into three allotments currently managed on a rest rotation basis (BLM 1991). Areas of the different allotments are large and uniform enough to enable the determination of piosphere effects around watering points due to livestock grazing.

Methods and Materials

Ten watering points were selected within areas designated as containing extensive areas of the same ecological site (Figure 6.2). Point cover data using a gimballed point technique (Winkworth and Goodall 1962) were collected along mini-transects dispersed along the piospheric gradient. Data were collected at 4 possible levels (canopy, subcanopy, basal, and soil surface). One hundred points (stations) were collected per mini-transect, perpendicular to the piospheric gradient (Figure 6.3) at the end of the 1992 growing season.

The mini-transects were located closer to each other in the vicinity of the associated watering point where changes in the plant communities were expected to be greatest. The mini-transects within a single piospheric gradient were all located within similar ecological sites. Additional gimballed-point cover data were also collected within the Passey et al. (1982) long-term sites to enable comparison to the above transects as a whole or to homogenous sections of the transect. Soil samples for texture analysis were collected at all sites examined to enable the detection of confounding soil gradients.¹

Since pattern-seeking approaches were used to evaluate the data, conventional statistical validation was not possible. The following rules were thus used to determine if hypotheses were validated. Replication was generally considered to be at the level of the piosphere. Particular hypotheses were supported if a majority of piospheres showed the characteristic used as a predictor. A more detailed description of procedures is provided for each of the objectives:

¹No serial correlations significant at the 5% level were found.
Fig. 6.2. Individual piosphere locations within Little Park and Laidlaw Park, southern Idaho, U.S.A.

(Grid designates square miles.)
Objective 1: To determine the general similarity of relict and grazed areas.

This objective was examined at the level of the entire data set (all piospheres and relict area data) and for individual piospheres. At the larger scale (all the data combined), both soil surface data as well as plant community data at the species and growth-form data resolutions were examined. At the smaller scale (individual piospheres), minimum spanning trees (MST, see Chapter 4 for an explanation of the method) were overlayed on the ordination scattergrams as a validation of the general trends. Interspersion within ordination space was assessed visually and deemed to occur if any of the relict sites occurred within the cloud of points representing disturbed sites. Such visual assessment would lead to more stringent analysis in comparison to randomization tests, because interspersion of only one relict stand amongst livestock-impacted stands within ordination space would necessitate comment.

Objective 2: To determine if livestock disturbance results in a gradient of vegetation change versus disjunct changes associated with thresholds of disturbance.

Ordination scattergrams of individual piosphere data were visually judged to determine whether data within piospheres are interspersed, showed evidence of thresholds of change, or indicated the presence of trends (consecutive ordering of piosphere sampling points). In addition, separate graphical representation of individual species and growth-forms was considered. Both ordination and graphical techniques were supported by serial correlations.

Fig. 6.3. A schematic description of data collection along piospheres in Laidlaw Park, Idaho.
O3: To determine if piosphere endpoints are most similar to relict areas.

This analysis was conducted at the individual piosphere level, and then tabulated for all piospheres to enable a global summary. Association matrices incorporating all mini-transects for a particular piosphere and all relict areas were examined to determine the most similar mini-transect to each relict area. Each of the 10 mini-transects of a piosphere had 13 chances (the number of relict areas studied) of being the mini-transect most similar to a relict area. Similarity of piosphere to relict area was judged by the relative number of closest similarities for mini-transects 1 to 5, and 6 to 10. The piosphere section with the highest number of closest similarities was judged to be most similar to the relict areas. Since the 10 piospheres represent a finite sample, overall statistical validation was based on the hypergeometric distribution (Sokal and Rohlf 1981).

O4: To determine the predictability of spatial trends as suites of species showing change, and the shape of abundance curves for individual plant species.

Changes in abundance for individual species were visually assessed and classed as nonlinear, linear, or no observable trend. In addition, nonlinear trends were broadly classed as unimodal or bimodal versus increasing or decreasing for the linear species responses. Assessments were tabulated to allow comparison between piospheres.

O5: To understand the underlying biology of the changes observed by considering past land use history and species autecology.

Results

Ordinations

Ordinations at various data resolutions and spatial scales were performed to gain an overall understanding of vegetation change within piospheres relative to relict areas.

Ordination of All Piospheres and Relict Areas Simultaneously

Ordinations based on soil surface components (bare soil, rock, litter, and microphytic cover [Figure 6.4]) indicated that there was interspersion of relict and livestock-impacted stands. However, many of the
relict areas, as well as mini-transects closest to the watering points, act as outliers, implying lack of similarity in terms of soil surface components. This description also fits the ordinations based on individual species (Figure 6.5).

Ordination based on growth-forms (Figure 6.6) showed much clearer interspersion of most of the relict areas. The only outliers were those mini-transects closest to the watering points. More relict areas were similar to livestock-impacted areas at this scale of resolution in comparison to individual species.

Ordination of Individual Piospheres

Instead of showing similar figures for individual piospheres, overall interspersion and trend characteristics (important to objective 2) are summarized in Table 6.1. At the individual piosphere level, only 5 out of 10 piospheres showed interspersion with relict areas. Within these, the first mini-transect of the piosphere was markedly different from other mini-transects and relict areas.

![Figure 6.4. Ordination of relict and livestock-impacted areas based on soil surface components in Laidlaw Park, Idaho. SSH1, SSH2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.](image)
Fig. 6.5. Ordination of relict and livestock-impacted areas based on individual species in Laidlaw Park, Idaho. SSH1, SSH2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.

**Determination of Nature of Change**

Table 6.1 indicates that the only discrete kind of changes in vegetation are associated with the high impact zones closest to the watering points. The disparity between relict areas and all piosphere mini-transects may be an indication of further change due to livestock impacts, although this is more likely due to differences in ecological site and/or changes in vegetation composition due to other influences such as fire frequency.
Fig. 6.6. Ordination of relict and livestock-impacted areas based on growth-forms in Laidlaw Park, Idaho. SSH1, SSH2 refer to Semi-Strong Hybrid MultiDimensional Scaling components 1 and 2.
Table 6.1. Summary of the trend characteristics of piospheres within ordination space.

<table>
<thead>
<tr>
<th></th>
<th>Interspersion</th>
<th>Threshold</th>
<th>Trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>All piospheres:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil surface components</td>
<td>Y</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>Growth-forms</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>Species</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>Individual piospheres (based on species):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 (A)</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>2 (BLOW)</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>3 (TWIN)</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>4 (AIRSTR)</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>5 (B)</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>6 (MORAN)</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>7 (LINDA)</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>8 (10)</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>9 (TOP)</td>
<td>Y(excl.1)</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>10 (LITTLE)</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
</tbody>
</table>

Note: Y = yes, N = no, excl.1 = exclusion of mini-transect 1.

Serial Correlation at the Individual Piosphere Level

Six out of 10 piospheres showed serial correlation at the matrix (community) level (Table 6.2). Few species showed consistent serial correlation across all piospheres (Table 6.2). Only 2 species [Agropyron spicatum (AGSP) and Festuca spp. (FEST)] showed serial correlation significant at the 5% level or less on more than 1 occasion. Of the growth-forms, bunchgrasses (TGRS) showed 4 out of 10 serial correlations, while shrubs (WOODY) showed 3 out of 10 serial correlations. Total cover (T.COVER) also appeared to show consistent serial correlation in 5 instances out of 10. Bare ground showed only 1 instance of serial correlation, while basal cover and litter showed no instances of serial correlation.

Similarity of Piosphere Endpoints to Relict Areas

Table 6.3 indicates that 7 out of 10 piospheres have a greater number of mini-transects farthest from the watering point similar to relict areas than mini-transects closest to the hub of the piosphere. This is
significant at a probability of 0.15 based on the hypergeometric distribution.

**Shapes of Abundance Curves of Species Showing High Serial Correlation**

Tables 6.4 and 6.5 indicate a diversity of abundance shapes within and between piospheres for individual species. No discrete changes occurred within any of the piospheres for any species. Since *Bromus tectorum* has played a key role in changes in plant vegetation of the Intermountain West (Billings 1990), it merits closer examination. *Bromus tectorum* showed little tendency for serial correlation (only 1 instance out of 12) along livestock impact gradients, and yet cover within the piospheres was generally higher than within relict areas (compare Tables 6.6 and 6.7). Only 1 out of 12 relict areas showed cover by cheatgrass higher than 5%, while column indicates the number of instances of serial correlation <= 5% relative frequency.

**Table 6.2. Within piosphere serial correlations of piosphere data matrices, individual species, growth-forms, total plant cover, and various soil surface components.**

<table>
<thead>
<tr>
<th>TAXON</th>
<th>A</th>
<th>BLOW</th>
<th>TWIN</th>
<th>AIRSTR</th>
<th>B</th>
<th>MORAN</th>
<th>P1LI</th>
<th>PIO10</th>
<th>PTOP</th>
<th>P2LI</th>
<th>&lt;5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>MATRIX</td>
<td>0.44</td>
<td>1.04</td>
<td>0.06</td>
<td>2.14</td>
<td>75.40</td>
<td>0.08</td>
<td>34.87</td>
<td>8.82</td>
<td>4.30</td>
<td>0.98</td>
<td>6</td>
</tr>
<tr>
<td>AGIN</td>
<td>3.74</td>
<td>29.09</td>
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<td>19.62</td>
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</tbody>
</table>

Note: Values are relative frequency of randomized data showing higher serial correlation than the non-randomized data, expressed as a percentage. Blanks indicate insufficient data for calculation of serial correlations. BASAL = Total percent plant basal cover. BARE GR. = Total percent bare ground. The final
Table 6.3. Summary of closest relict to mini-transect similarity on an individual piosphere basis.

<table>
<thead>
<tr>
<th>Piosphere</th>
<th>1 (A)</th>
<th>2 (BLOW)</th>
<th>3 (TWIN)</th>
<th>4 (AIRSTR)</th>
<th>5 (B)</th>
<th>6 (MORAN)</th>
<th>7 (LINDA)</th>
<th>8 (10)</th>
<th>9 (TOP)</th>
<th>10 (LITTLE)</th>
<th>Sum &lt;=5</th>
<th>Sum &gt;=6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (A)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
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<tr>
<td>2 (BLOW)</td>
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<td>0</td>
<td>0</td>
<td>2</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>3 (TWIN)</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>11</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>4 (AIRSTR)</td>
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<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>5 (B)</td>
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<td>0</td>
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<td>0</td>
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<td>1</td>
<td>0</td>
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<td>9</td>
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</tr>
<tr>
<td>6 (MORAN)</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>13</td>
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<td>0</td>
</tr>
<tr>
<td>7 (LINDA)</td>
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<td>7.5</td>
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<tr>
<td>8 (10)</td>
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<td>1</td>
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<td>0</td>
<td>1</td>
<td>10</td>
<td>2</td>
<td>11</td>
<td>13</td>
</tr>
<tr>
<td>9 (TOP)</td>
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<td>0</td>
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<td>1.5</td>
<td>3</td>
<td>4</td>
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<td>0</td>
<td>3.5</td>
<td>9.5</td>
<td>3.5</td>
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<tr>
<td>10 (LITTLE)</td>
<td>0</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>1</td>
<td>7</td>
<td>3</td>
<td>10</td>
<td>4</td>
</tr>
</tbody>
</table>

Note: <= 5 refers to instances of mini-transects 1 - 5 being most similar to relict areas, >=6 refers to instances of mini-transects 6 - 10 being most similar to relict areas.

Table 6.4. The nature of change of cover abundance for species within individual piospheres.

<table>
<thead>
<tr>
<th>Piosphere</th>
<th>Discrete</th>
<th>Continuous</th>
<th>Nonlinear</th>
<th>Woody Plant Dominance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Decreaser</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unimodal</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bimodal</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| 1 (A)     | 0        | 1         | 0         | p/d                   |
| 2 (BLOW)  | 0        | 0         | 0         | p                     |
| 3 (TWIN)  | 0        | 0         | 1         | d                     |
| 4 (AIRSTR)| 0        | 0         | 2         | p                     |
| 5 (B)     | 0        | 0         | 0         | d                     |
| 6 (MORAN) | 0        | 0         | 1         | a                     |
| 7 (LINDA) | 0        | 0         | 0         | d                     |
| 8 (10)    | 0        | 0         | 0         | p                     |
| 9 (TOP)   | 0        | 0         | 0         | a/d/p                 |
| 10 (LITTLE)| 0    | 1         | 0         | p                     |

Note: Numbers indicate number of occurrences. "a", "p," and "d" indicate dominance by Artemisia arbuscula, Artemisia tripartita, and Artemisia tridentata, respectively.

33 out of 100 mini-transects showed cover greater than 5%. Lack of serial correlation may indicate that cheatgrass cover does not react as strongly to livestock impact as to some other factor. The majority of these instances, however, occurred in particular piospheres dominated by Artemisia tridentata (BB and Linda, Table 6.6). This contrast follows popularly held notions, although such views may be generated from the acceptance of the machinations of the Clementsian Model, and the definition of a sagebrush-bunchgrass mixture as climax.
It should also be noted that 2 piospheres (TWIN and AIRS, dominated by *Artemisia tripartita* and *Artemisia tridentata* respectively) showed no instances of cover by cheatgrass greater than 5%. A further 2 piospheres (BLOW, LITTLE), dominated by *Artemisia tripartita*, have only 1 mini-transect with cheatgrass cover greater than 5%. Fire frequency is also a confounding factor. BLM records indicated that the areas in which the piospheres were studied have burnt more frequently in the near past than the relict areas examined.

Table 6.5. The nature of change of cover abundance for individual species across all piospheres.

<table>
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<th>Nonlinear</th>
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<tr>
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</tr>
<tr>
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<td>Increaser</td>
<td>Decreaser</td>
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<tr>
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</tr>
<tr>
<td>POSE</td>
<td>0</td>
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<tr>
<td>CAREX</td>
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</tr>
<tr>
<td>BRTE</td>
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<td>1</td>
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<tr>
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<tr>
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</table>

Note: Numbers indicate number of occurrences.

Table 6.6. Summary of *Bromus tectorum* cover data within piospheres.

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<th>5</th>
<th>6</th>
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<th>8</th>
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<th>DOM</th>
<th>&gt;=5</th>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>p</td>
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</tr>
</tbody>
</table>

Note: Dominance by *Artemisia arbuscula* (a), *Artemisia tripartita* (p), and *Artemisia tridentata* (d) is indicated in the column labeled "DOM", numbers of mini-transects showing percentage cover equal to, or greater 5% is indicated in the ">=5" column.
Table 6.7. A summary of mean *Bromus tectorum* cover (percentage) within the Passey et al. (1982) long-term sites.

<table>
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<th>ID1</th>
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<td>KC</td>
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<td>CN</td>
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<td>d</td>
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</tr>
</tbody>
</table>

Note: "p" and "d" indicate dominance by *Artemisia tripartita* and *Artemisia tridentata*, respectively.

A Few Generalizations Gained from the Piospheres

Several piospheres (4 out of 10) showed an increase in total plant cover with a decrease of livestock impact. Others did not show much change, other than the high impact zone around the watering point. Such "sacrifice zones" showed either higher or lower plant cover than the remainder of the piosphere. This was dependent on past grazing history and precipitation. High impact zones within allotments then at rest from grazing showed high cover due to a proliferation of annuals which would otherwise be trampled. Low precipitation years may elicit the same response. During such years, water is provided within watering troughs situated away from the reservoirs, thus allowing the growth of annuals.

Litter frequently increased sharply outside the sacrifice zone (8 out of 10 cases), thereafter decreasing towards the end of the piosphere. This may be due to the trampling effect as well as increased dung depositions. This response, together with change in species composition, resulted in a general increase in bare ground along the piosphere gradient in spite of general increases in total plant cover.

Trends for individual species are more problematic. Figure 6.7 depicts what theory would have predicted. The initial increase in sagebrush closest to the watering point could be attributed to a shift in the competitive balance between woody plants and grasses as a result of heavier cattle grazing. The second increase, farther from the watering point, probably indicates the stagnation process. The supposed balance between growth-forms could result in the mirror-like reaction of the bunchgrasses. Research in central Australia (Bastin et al. 1993a, b) indicated that different patterns are found depending on the palatability of species. If dominant species are palatable, then a local depletion in total phytomass occurs closer to the
Figure 6.7. The theoretical distribution of sagebrush and bunchgrasses along the piosphere gradient.

If unpalatable species have invaded this area, then phytomass increases closer to the watering point (Bastin et al. 1993a, b).

Some piospheres reflected the trends of Figure 6.7; for example, 4 out of 10 piospheres showed intermediate increases in bunchgrasses, while 5 cases of Artemisia followed the above definition (although the latter interpretation was often subjective). Chrysothamnus was not restricted to high impact areas as its species autecology would indicate. Poa spp. were expected to show a higher abundance closer to the watering points than other bunchgrasses. Although this was found to be the case in 4 occasions out of 10, the converse was sometimes true for other piospheres.

In conclusion, it is difficult to derive generalizations from piospheres in the context studied. While explanations of fluxes for individual piospheres are easy to conjure up, landscape heterogeneity and varied past history make larger scale generalizations difficult.

Discussion and Conclusions

Similarity of Relict and Grazed Areas

Results indicate that similarity of relict and piospheres is dependent on the data resolution at which plant community information is viewed. Regardless of data resolution (species and growth-form), the initial...
mini-transect of all piospheres (corresponding to the sacrifice zone) is always different from the remainder of the mini-transects, as well as the relict areas. The remainder of the mini-transects are similar to relict areas (show interspersion) at the growth-form data resolution, but not at the species resolution. This may be due to different past histories (fire and grazing) of the grazed areas, or may be due to environmental/site differences.

**Continuous versus Discontinuous Change**

Since half of the piospheres show distinct gradients of vegetation response (in spite of difficulties in locating piospheres, collecting data on the same ecological site across a single piosphere, and landscape heterogeneity), it can be safely concluded that differential livestock impact can result in a differential plant response. The nature of this response, however, is strongly dependent on the data resolution used, being apparent at the species level only.

**Similarity of Piosphere Endpoints to Relict Areas**

Though not statistically significant at the 5% level, the majority of piospheres did show a tendency for mini-transects closest to the end of the livestock impact gradient to be most similar to relict areas. Some piospheres showing high overall serial correlation did not show this relationship, indicating that change with increasing livestock impact did not always reduce similarity to the relict areas.

**Predictability of Spatial Trends for Individual Plant Species**

Spatial trends were not predictable for individual species. If the repeatability of serial correlation is any indication of predictability, then total plant cover followed by that of growth-forms was the most predictable of the attributes examined. However, abundance histograms indicated that there is no hope of predictability based on the distribution of cover along piospheric gradients.

**Understanding the Underlying Biology**

Cover abundance by *Bromus tectorum* did not show significant serial correlation with livestock impact. The higher cover by this species within grazed areas may be a confoundment with fire frequency, since the isolated nature of kipukas resulted in less frequent burning than those areas studied for piospheres. Some
kipukas farther out into the Great Rift lava fields not included in this study, but more recently burnt, showed cheatgrass dominance (Lovejoy 1980).

Few general trends were found along the piospheres for individual species. More clearly defined serial correlations occurred for growth-forms and total plant cover. This indicated that the nature of changes observed at the species level is site-specific (often because dominant species change for different piospheres) and extrapolation beyond an individual piosphere should not be hazarded. Growth-forms and total plant cover or individual species present across the landscape appeared to be a more consistent indicator of vegetation change at larger spatial scales.
CHAPTER 7
FINAL CONCLUSIONS

This chapter will synthesize information from my individual studies and literature to gain an overall understanding of the concepts and assumptions discussed in Chapters 1 and 2. These assumptions and concepts are discussed as positive and negative aspects of the models examined, and may be particular to sagebrush steppe and sagebrush semi-desert plant communities, constituted of vegetation other than that defined by the models.

The Clementsian Model

An important positive aspect is the relatively simplistic and, therefore, heuristic nature of the model. The inclusion of both vegetation dynamics and degradation in this model further contributed to its acceptance by range managers. Since the model incorporates remedial action (reduction or rest from livestock grazing) for the degradation process, it also serves as an expert system. A better (and therefore more complex) knowledge of vegetation dynamics in sagebrush-dominated rangelands may prevent accomplishing the above combination of "positive aspects" in future conceptual models used as a basis for range condition assessment.

The negative aspects of the Clementsian Models are generally the underlying assumptions and concepts that scientists feel are no longer valid and acceptable. These include the acceptance of the concepts of stability and equilibrium, and the definition of a single endpoint to vegetation dynamics. Furthermore, the relationship between range condition and seral stage is being questioned, so the endpoint (represented by relicts) is no longer acceptable as a benchmark for excellent range condition.

Since these negative aspects have fueled the search for an alternative model, it is no surprise that the converse falls within the popular notion of "positive aspects" for the major alternative model to the Clementsian Model.

The Multiple-Stable-States Model

The perceived positive aspects of the Multiple-Stable-States Model are the definition of multiple states (cf. a single endpoint), multiple pathways, and the "more realistic" representation of community dynamics
characteristic of semiarid lands. The latter conforms to the dynamics defined by the Westoby et al.'s (1989a, b) State-and-Transition Model, namely, rapid change between defined states. These assumptions still need to be validated.

So far, the literature has focussed only on positive aspects of the State-and-Transition Model, neglecting the possible negative characteristics. A critical evaluation of the model follows the section "An Overall Synthesis and Evaluation of Concepts and Assumptions Examined."

The terms Multiple-Stable-States Model, and State-and-Transition Model are often viewed as synonyms. There is thus a need to examine these terms more closely to determine if this is indeed the case.

**Multiple-Stable-States versus State-and-Transition Models**

The major difference between Multiple-Stable-States Models and State-and-Transition Models is one of user orientation. Multiple-Stable-States Models have been used to indicate alternate endpoints of succession, or alternate species compositions at a site without implying a particular mode of species dynamics. Westoby et al. (1989a, b) stipulated rapid change between states (Friedel [1991] and NAS [1994] made use of the concept of thresholds of change), where states are defined according to the maintenance of soil resources. Westoby et al. (1989a, b) also mentioned rapid transition mediated by fire and slow transition attributed to the gradual dominance of a cohort of woody plants. The authors added to this ambiguity by stating that criteria pertaining to management be used rather than those derived from theoretical models of vegetation dynamics in recognition of states. Furthermore, their terminology (Westoby et al. 1989a, page 268) includes persistent versus transient states and the observation that states are necessarily an "abstraction encompassing a certain amount of variation in space and time." Ultimately, the states, as defined for the two model types, are distinguished in their applicability to management.

Any drawbacks to the use of State-and-Transition Models are of a philosophic nature, perhaps due to the broadness of definition. The model allows for both continuous and discrete change and, ultimately, would accommodate any of the alternative concepts/assumptions to be examined.
An Overall Synthesis and Evaluation of Concepts and Assumptions Examined

The assumptions and concepts underlying various models of vegetation dynamics were examined to discern the relative utility of models used to describe the vegetation dynamics of sagebrush-dominated rangelands.

**Stability and Equilibrium**

From Chapter 1 it is apparent that two models of stability are implicated by the Clementsian Model—that of constancy within the undisturbed pristine vegetation, and one of resilience following disturbance. The Stat-and-Transition Model allows for change within certain limits but emphasizes communities that are different from each other in terms of gross species abundances and ecosystem functioning. This allows fluctuation within a state, but no directional changes, conforming to a boundedness definition of stability. Examination of these concepts is therefore important as a test of the validity of these models.

The literature indicated that there are separate instances where the resilience model of stability may hold (Peters et al. 1993, Humphrey 1984, Sneva et al. 1984, Anderson and Holte 1981, Robertson 1971, Pearson 1965) and other instances where it is not supported (Holechek and Stephenson 1983, Tueller and Tower 1979, Rose and Miller 1993, West et al. 1984). The Mills data (Chapter 5) validated the resilience model (the burnt and ungrazed treatment—Figure 5.2), since all four exclosures show a tendency to return to a predisturbance community. The range of ordination trajectories obtained, however, indicates considerable variation in plant community response to the disturbance.

My study of relict areas (Chapter 4) invalidated the notion of constancy and, therefore, the single equilibrium model for undisturbed plant communities (Table 4.6). The literature supports at least 3 equilibria (stable states) associated with changes in fire frequency (Miller et al. 1994, West in press, Tueller and Tower 1979, Whisenant 1989, Winward 1991).

It thus appears that plant communities can be resilient within certain bounds (a characteristic of the Clementsian Model), although continued disturbance may result in gross changes of plant communities (intuited by the State-and-Transition Model). Evidence from my reexamination and extension of the Passey et
al. (1982) data sets indicates that movement of plant communities within these bounds may occur without the intervention of humankind. Furthermore, other examinations of relict areas indicate that change across defined bounds (states) may similarly occur without human-mediated disturbance (Svejcar and Tausch 1991, Kindschy 1994). While stability and equilibrium have implications about vegetation dynamics, they do not fully address the nature of plant community change.

**Continual versus Discrete Change**

The Clementsian Model suggests continuous change from the disturbed community back to the community representative of pristine conditions, while the State-and-Transition Model implies long periods of lack of change interspersed with shorter periods of rapid change. As with the stability concept, examination of the nature of change of plant communities also constitutes a test of the relative utility of the Clementsian Model and State-and-Transition Models.

The literature and long-term data sets examined indicated the importance of several parameters regarding classification of the nature of vegetation change. These included data resolution, spatial resolution, temporal resolution, type of disturbance (chronic versus acute), individual species response to disturbance, and their modes of reproduction.

Data resolution is important because not all species within a growth-form or growth-form group may react in the same way to a disturbance. For example, different species of *Artemisia* react differently to fire or may show different palatabilities and tolerances to browsing impact. In the relict areas, individual species fluxes appeared to be antagonistic to each other so that growth-form dynamics are different from species fluxes. The Mills data (Chapter 5) implied that individual species fluxes of bunchgrasses are complementary, and that growth-form fluxes are therefore a gross approximation of individual species fluxes. This may reflect growth-form response largely to grazing, rather than climatic variation.

Spatial resolution must be considered when interpreting spatial data. This became apparent in the piosphere study (Chapter 6), where biological interpretation of observed species change relative to livestock impact was possible at the level of an individual piosphere, but not over the entire collection of piospheres. This is probably because lack of homogeneity between areas occupied by piospheres prevented the replication
of the exact same plant communities. Changes in plant communities may thus seem continuous at finer spatial resolutions, but discontinuous at larger spatial resolutions. Friedel et al. (1993) made similar observations.

Temporal resolution presents an interesting problem. Short periods of rapid community change could be viewed as continuous over the time period within which they occur. However, when they are viewed within a larger temporal window, which includes slower vegetation dynamics, the outcome appears as discrete change. Within the relict areas, data suggest that long term change is often continuous, but that short term climatic fluctuation could hamper the detection of long-term trends.

Different disturbances may elicit different responses from the same plant species. Furthermore, the severity and timing of a particular disturbance may also yield different outcomes of plant community change. Generally, acute disturbances have the potential of resulting in a more discrete change in plant communities than chronic disturbances. This is due to the direct impact of the disturbance on the plants—acute disturbances remove all foliage, while chronic disturbances only partially remove foliage and disseminules. This is discussed in further detail under "Repeatability of Abundance Curves." As with spatial change, temporal change becomes an enigma.

**Individualistic Versus Community Change**

*(= Deterministic Change)*

The building blocks of models, individualistic versus community criteria, identify two important groups of models (Table 1.1). Clear identification of the favored criteria on which to base a model of vegetation dynamics would thus greatly aid model choice for a particular situation.

Previous authors examining this concept did so using a variety of indicators. Indicators of individualistic dynamics include a divergence among plots with similar past history (West and Van Pelt 1987), an increase in 1 species without a visible effect on others (Bastow and Allen 1990, Glenn-Lewin 1980), and the persistence of communities other than the acclaimed climax (Glenn-Lewin 1980). I will consider all of these indicators in addition to detecting suites of species common to plots/stands with the same past history (identified using serial correlation) as an indicator of community change.

Replicates of treatments within the Mills data set showed divergence (Figure 5.2). This has also been reported within some of the long-term studies reviewed in Chapter 3, thus favoring the notion of individualistic
change.

Only a few instances of consistent change in individual species abundance occurred within the data sets examined in Chapters 4 and 5, and never for suites of species. First, consistently increased sagebrush phytomass was observed within the relict areas examined (Table 4.6). This was associated with a less consistent decrease in *Agropyron spicatum*. The Mills data emphasize the observation of individual species response to fire, again validating the individualistic perspective.

The range of plant communities on relict areas (including domination by sagebrush, bunchgrasses, or cheatgrass) defy the definition of a single climax species assemblage. This assumption of the Clementsian Model is thus invalidated.

The data presented here thus generally support the importance of individualistic change over that of community change. The only contentious data is that of balance between sagebrush and *Agropyron spicatum* within the relict areas. This suggests that the individualistic nature of vegetation dynamics holds within communities showing a more or less equal sharing of species/growth-forms.

**Hysteresis**

The hysteresis concept, as used by ecologists, differs from the source of derivation-- the field of physics. Westman (1978, page 705) defined hysteresis as the "degree to which the pattern of recovery is not simply a reversal of the pattern of initial alteration." The McGraw-Hill Dictionary of Physics and Mathematics (McGraw-Hill 1978, page 469) defined it as "the dependence of the state of a system on its previous history," a different perspective to Westman's (1978) definition. Conceptually it is closely related to the Clementsian Model of vegetation dynamics and the resilience model of stability, where return to a previously defined state is critical. Closer reflection on the concept revealed that none of the data sets used here allowed an opportunity for investigation. Further consideration of this concept is therefore not possible.

**Repeatability of Abundance Curves and Serial Correlations**

The repeatability of abundance curves and serial correlations for individual species was examined to identify species which could lend predictability to a model of vegetation dynamics. The only species that
showed repeatability of abundance curves were those that reacted to disturbance in a characteristic way. Thus, in the Mills data (Chapter 5) the increased abundance of cheatgrass and the loss of sagebrush following fire was very predictable (Figure 5.7), conforming to a vital attributes model. Cheatgrass represented a group classified as annuals dependent on seed for dispersal. The sagebrushes (excluding *A. tripartita*, which can resprout following fire) typified long-lived woody plants relying on seed dispersal for reestablishment (Figure 5.7). The longer term data of the relict areas confirmed this (Table 4.6). The behavior of the bunchgrasses conformed to a group of plants characterized as unresponsive to fire, and propagating vegetatively. Within the Mills data (Chapter 5), bunchgrass reaction to grazing pressure was much slower. Ungrazed treatments showed a gradual increase in cover, while grazed treatments showed a slow decline. This is characteristic of chronic disturbances, or disturbance types through which a particular species can persist.

Data collected along the piospheres and within the kipukas indicated that species abundance curves (across time or space) can be Gaussian, although lack of control over the spatial and temporal domains usually made them otherwise (Appendix D). This negates the use of models and statistical procedures that assume the Gaussian nature of species abundance change. Austin (1987) found similar results.

The circumstances identifying species with characteristic abundance curves also resulted in species showing consistent serial correlation over time. Thus, repeatability of both serial correlation and abundance curves identify cheatgrass and sagebrush to be particularly important as predictive variables of vegetation change. Bunchgrasses appear more persistent under most circumstances (other than prolonged grazing and repeated fire).

**Similarity of Relicts to Livestock-Impacted Areas**

Examination of this characteristic constitutes one of the most important tests of the Clementsian Model, and also serves to validate the use of relict areas as benchmarks in range condition and trend analysis. Similarity of relicts to livestock-impacted areas can be viewed in several ways. If thresholds of disturbances are responsible for changes in vegetation or other parameters, we would expect relict areas to be different from the piospheres as a whole. There was little difference between relict areas and livestock-impacted areas based on growth-forms. The largest differences between relict and livestock-impacted areas occurred within
ordinations based on individual species. Such differences probably reflect spatial heterogeneity due to environmental variability, past history, and autogenic vegetation dynamics.

Within the piospheres, the Clementsian Model predicts that the piosphere endpoints would be most similar to the relict areas. Table 6.3 indicates that this is so for 7 cases out of 10. This is significant at the probability of 0.15. However, the piospheres were selected on areas where these relations were most likely to occur (in terms of landscape homogeneity). It is therefore unlikely that areas farthest from watering points will always be most similar to relict areas. This, and the variable nature of relict area communities, discounts their use as benchmarks by which to judge range condition and trend.

**General Summary**

Both the literature and the spatial and temporal data of this dissertation attest to the dynamic nature of sagebrush-dominated plant communities. The reasons for these dynamics were various, and included insect/pathogen outbreaks, fire/livestock disturbance, and climatic variability. While the dynamic nature of vegetation was apparent, the static nature of some rangeland communities falling within the vegetation types considered also needs to be acknowledged. Several papers expound the static nature of certain communities (Laycock [1991] and many of the individual exclosure studies examined in Chapter 3). These are usually communities dominated by cheatgrass or sagebrush, with few other species. This frequently occurs following heavy livestock impact, especially grazing by sheep. This long-term disturbance removes many of the forbs and bunchgrasses and eventually depletes the seed pool, leading to permanent species loss. If this occurs over a large area, there is little hope for the introduction of new propagules, hence the lack of change in such communities. The higher fire frequency within cheatgrass-dominated rangelands acts in much the same manner. Studies of such sites in exclusion of others may well yield a notion of lack of change. Indeed, such sites at Curlew Valley (Rice and Westoby 1978) were the experiences that led to the formulation of the State-and-Transition Model by Westoby et al. (1989a, b). From the perspective of maintaining biodiversity, these communities should be avoided at all costs and not used as benchmarks for management.

One way of accommodating both the Clementsian and State-and-Transition Models is to recognize that they describe different phenomena. The State-and-Transition Model is able to describe gross changes in a
plant communities associated with exogenous factors. The Clementsian Model describes species replacement within a community, usually on the basis of autogenic factors. The two models are thus not alternatives, but describe different phenomena. For a full understanding of vegetation dynamics relative to management, both phenomena need to be recognized (Figure 7.1).

Few community characteristics of vegetation change showed potential for prediction over the longer term. The strongest hope for predictability came from the reaction of individual species to different disturbance types (an individualistic approach). Furthermore, the resilience concept shown to occur in the case of the Mills data would likely be predicted on an individualistic basis. Thus, the model to be adopted as a basis for range condition and trend analysis ought to be individualistic, and placed within a framework of disturbance.

Of the other models examined in Chapter 1, only Friedel's (1991) model clearly indicated both the static and dynamic aspects of vegetation change relative to management, while Milton et al.'s (1994) conceptual model remained the sole example of incorporation of multiple criteria. It appeared that general models were too abstract to impart useful information about the dynamics of a particular system, while models specific to particular circumstances were not transferable. New models incorporating the biology of individual species therefore need to be formulated with objectives firmly in mind.

Fig. 7.1. The different focus of the Clementsian Model versus the State-and-Transition model contrasted with the (my) desired perspective.
A New Conceptual Model

To build a new conceptual model, the predictive aspects of vegetation dynamics need to be accentuated. These include the existence of attractor plant communities, the dynamic nature of the sagebrush-bunchgrass-forb relationship, the effect of fire frequency, and the individualistic nature of vegetation change. Objectives for model application also need to be defined. Henceforth, the objectives will be to identify a model linking range management, vegetation dynamics, and monitoring using remote sensing.

Important Characteristics to Be Incorporated

Chapter 2 indicated that there were several theoretical and practical requirements of any model to be adopted by the range management profession. Briefly summarized these include: incorporating multiple temporal and spatial scales; incorporating multiple criteria; reflecting current ecological theory; being heuristic; being predictive; being flexible to changing management objectives; and being closely associated with a methodology for data collection. Other important characteristics were identified by the literature and data sets used within this dissertation.

First, the literature indicated that there were particular plant compositions that act as stable states or "attractors." Second, both the literature reviewed and data presented within this dissertation asserted to the dynamic nature of change outside of the "attractor" communities. Accepting this dynamic nature of plant communities implies management of trends rather than specific communities (Pers. comm., D. Roberts 1994). Third, of the concepts and assumptions examined in this dissertation, that of individualistic change versus community change was most strongly supported. Fourth, the piosphere studies (Chapter 6) also emphasized the variable nature of plant communities in the spatial domain such that the effects of grazing at the landscape scale were difficult to discern. Thus, common denominator species that can act as indicators of change for the remainder of the community need to be identified. These need to be visible within the remotely sensed data to be used, if larger landscape scale vegetation monitoring is to be incorporated in the new conceptual model. Fifth, noise within all of the data sets examined and pathways within the Mills data set (Chapter 5), in particular, indicated that subtle differences in plant communities/environment can result in deviations between observed "pathways" of change for different plots/stands examined even at small spatial scales. This implies
that change at larger scales should be seen as swaths of change rather than distinctive pathways. The larger the spatial scale considered, the broader the swath of change observed.

A Multiple-Stable-States Model by West (in press) (Figure 1.4) can be used as a basis for further inspiration. West (1995) defined 10 states that conformed to the State-and-Transition Model. Most of these are important from a management perspective and incorporate the states that identified lack of further change from a vegetation dynamics perspective. If the conceptual model is to reflect real vegetation dynamics, then the latter ought to be recognizable from those defined simply as of importance to management. Taking the above into account, the West (in press) model can be redrawn as Figure 7.2.

Figures such as 1.4 and 7.2 are very important from an historical perspective because they summarize how forces have acted upon our rangelands in the past. However, from a practical management perspective, it would be impossible to map all such communities on a landscape scale because of the labor that would be required. In addition, landscape heterogeneity does not allow the effects of livestock impact to be gauged as indicated by the definition of the above states. Finally, the fact that relict areas can occupy all of the states as defined in Figure 1.4 indicates that other factors and combinations of forces also play important roles. The communities within the stippled borders of Figure 7.2 could be considered to define the bounds of possible species combinations—a single large dynamic state. Within this range of plant communities, largely due to the positive feedbacks associated with fire frequency, two attractor plant communities (sagebrush- and cheatgrass-dominated) can be identified (Chapter 3). In conclusion, a new conceptual model with emphasis on abundant or "driver" (Walker 1989) species of the community that appear to govern community dynamics is needed to complement existing models.

A Graphic Representation of the New Conceptual Model

Two species fulfilling the foregoing requirements to serve as a basis for a new model are *Artemisia tridentata* and *Bromus tectorum*. The former was found under conditions of low fire frequency, while the latter was fostered by high fire frequency. Because of the deleterious effects of the communities dominated by these two species, management objectives should be aimed at staying away from critical species abundances associated with the "danger zones" of Figure 7.3. Such danger zones might be associated with critical states of
Fig. 7.2. A Stable States Model for vegetation dynamics in sagebrush steppe, modified from West (1995).

Fig. 7.3. A graphical representation of predicted plant communities relative to sagebrush and cheatgrass abundance.
the seed bank, minimum number of plants to maintain a population, or represent a realistic amount of time to community recovery. The mechanisms leading to these plant communities were reviewed in Chapter 3.

Bunchgrasses appear more persistent, and since this growth-form is the major portion of dependable forage for the cattle industry, management has focussed on these species. An additional perspective that would be useful to the management of our rangelands is the focus on the undesired species whose abundance has consequences for the major forage base and as wildlife habitat. A start to building such a model might be to graph abundances of cheatgrass and sagebrush as in Figure 7.3.

Both of these species are easily quantified in the field and likely also from remotely sensed data (at least in areas of high relative abundance [Tueller 1994]). The use of remote sensing would serve to link management to the landscape (see the discussion under monitoring) in the manner depicted by Figure 2.2. The relationship depicted by Figure 7.3 was somewhat validated by data from Passey et al. (1982) (Figure 7.4).

Consider Figure 7.4 for *Artemisia tridentata* and *A. tridentata*, respectively. Both sets of axes indicated that there was a strong tendency for communities dominated by *Bromus tectorum* to have very little sagebrush. The opposite holds true also. Considering that the authors were investigating the relationship between soils and plant communities and ignored communities not representative of "climax," evidence of the relationship between cheatgrass and sagebrush within this data set as described above can be seen as validation.

Scattergrams of other species are shown as contrast. Similar axes could be drawn for other species, although for the purposes of this chapter, I will continue building a model based on the important species identified.

Figure 7.5 is an extension of Figure 7.3, using the Milton et al. (1994) model for inspiration. Loss of species richness and soil resources can be associated with the identified attractor communities. This applies to both plant and animal communities (Longland and Young in press). In the case of the sagebrush-dominated community, loss of soil resources may be in the form of soil erosion, while for the cheatgrass-dominated community, it is more likely to be in the form of loss of soil structure and altered soil chemistry. Loss of species richness follows those mechanisms identified in Chapter 2.

A good management objective would be, therefore, to maintain a plant community closer to the origin of the two axes rather than at the endpoints. This might be achieved by defining the present plant community in the manner depicted by Figure 7.4. In this case, the community was considered to be dynamic and its future
Fig. 7.4. A validation of the tentative model described by Figure 7.2. [axes are phytomass (kg/ha) relativised by total phytomass]
Fig. 7.5. A model of vegetation dynamics for sagebrush steppe and semidesert on the basis of sagebrush and cheatgrass abundance.

appearance moldable by the forces indicated (derived from West in press). Figure 7.6 is a graphic depiction of how different forces known to be important in sagebrush-dominated vegetation could be utilized to determine sagebrush and cheatgrass abundances in a plant community.

The Underlying Theoretical Framework

Since the vegetation dynamics described in this dissertation can usually be explained in terms of species autecology, this ought to form the theoretical framework for vegetation dynamics. Thus, models based on life history strategy or vital attributes ought to be particularly suitable for describing vegetation dynamics within the sagebrush-dominated rangelands. Various species could be classified according to their reaction to the various disturbance types predominating on these rangelands. The nature of the long-term trends observed indicated that the vegetation was in constant change mediated by disturbance and a fluctuating environment. The vital attributes thus ought to be related to disturbance within kinetic theory (Burrows 1990) or dynamical systems theory (Roberts 1987) or models such as those prescribed by Pickett et al. (1987) rather than autogenic change.
The necessity to consider individual species characteristics is important. However, this still needs to be considered relative to the community as a whole. The effects of a particular disturbance or management option need to be considered for all of the species within the community being managed. For this purpose, only the Vital Attributes Model seems well suited. Expert systems need to present information on all species in such a manner that decisions regarding the community as a whole can be implemented. Management aids such as Table 2.2 and Figure 2.1 serve as examples.

The Effect of Model Choice on Monitoring

I see 4 major inputs of information needed for monitoring. They are the theoretical basis (model) chosen for the "condition and trend" analysis, statistics, remote sensing and GIS, and ground sampling (Figure 7.7).

Remotely sensed data are essential for quick, inexpensive, and extensive (over the landscape) monitoring. Careful choice of variables collected on the ground should meet management objectives as well as
Fig. 7.7. Contributing components to the monitoring process.

serve ground truthing for remotely sensed data.

Statistics are still required to ensure adequate sampling and significance of results collected at the ground level. Synoptic coverage by remotely sensed data ensure sampling adequacy only. Replication and validation are still required if an attempt is made to generalize about a particular information class spread out over a dissected landscape.

An important by-product of the remote-sensing procedure outlined above would be the formation of a GIS layer of landscape classification based on abundance of cheatgrass and sagebrush over the landscape. This could be achieved using straightforward classification procedures or superior alternatives such as mixed pixel modelling (Settle and Drake 1993, Foody and Cox 1994, Cetin et al. 1993). This procedure would identify areas requiring the particular attention of the land manager. For example, an area dominated by sagebrush may be put to rest (from grazing) to allow an accumulation of fine fuels so that a prescribed or wildfire could reduce the abundance of this species. Adjacent areas, on the other hand, could be heavily grazed to provide some protection against the possibility of the fire spreading beyond its intended realm. Although this may be difficult to achieve in practice, the judicious placement of watering points and salt licks could be a partial remedy. The net result of this is management based on the requirements of the vegetation relative to management objectives. The use of remote sensing and GIS as outlined above removes the constriction of property/allotment lines from
management and provides a format that makes more ecological sense. Other variables (for example, indicators of possible soil erosion) could be examined over the landscape and also incorporated as layers of the GIS. Once this has been achieved for all of the perceived problems within a management area, a management plan taking into account all of the above in relation to physical features could be formulated on a 2-dimensional map. A subsequent collection of remotely sensed data could be used to evaluate and modify the management plan. A general procedure for this process is envisaged as follows:

1. The determination of management objectives relative to the undesirable dominant species. Careful choice of an abundance measure reflecting these undesirable species is required for achieving a landscape perspective using remotely sensed data.

2. The construction of a conceptual model of vegetation dynamics. This requires definition of the vegetation type, the utilization of all of the available literature, and a knowledge of the management objectives. This should include the identification of undesirable communities, and the dominant species associated with these.

3. The classification of the landscape relative to undesirable species abundance. These species (representative of undesirable, non-dynamic communities) and any other variables of particular interest (for example, an index taking into account bare ground and slope as an indicator of erosion potential) are used to create 2-dimensional maps identifying areas requiring particular management attention.

4. The enactment of the management plan. Action on the ground is through enactment of the management plan using all of the available forces (as depicted in Figure 2.1) for a particular management area.

5. The assessment and reevaluation of the procedure. This should be followed by an assessment of the success of the management plan using remotely sensed data. The original model should be validated and reconstructed if necessary. The cycle should be continued through the formulation of a new management plan taking into account the successes and failures of the previous management plan.

Conclusions

This dissertation goes against several commonly held notions of vegetation dynamics and range management. This is primarily because convention is still based on the Clementsian Model of vegetation
dynamics, a model designed for reasons other than the assessment of range condition and trend. Some of the important outcomes of this dissertation are summarized below.

Both static and dynamic aspects of vegetation change exist in sagebrush-dominated vegetation. Static communities are defined as those that are composed almost exclusively of cheatgrass or sagebrush. The prevailing fire frequency, competition regime, and/or lack of propagules prevent such communities from changing back to a balance of growth-forms without intense management input. Dynamic communities are those that still retain a balance of growth-forms and have the potential of varied plant community composition in response to various forces.

The long-term data and literature examined suggested that an alternative to focussing on "Desired Plant Communities" is to examine the abundance of undesired species. In the case of sagebrush-dominated vegetation, attention ought to be focussed on cheatgrass and sagebrush, since these species are instrumental on inducing conditions that do not support a balance of growth-forms and high species diversity. The use of remotely sensed data and modelling techniques for estimating relative abundance of these species allow for the definition of management units requiring the application of particular forces for manipulating plant composition. This procedure would allow management on a more ecologically sound basis than that imposed by allotment or property lines. Such a protocol would also allow for the identification of management units in peril of becoming static communities. This results in a practical plan for the application of management over the landscape, synonymous with adaptive management (Walters 1986).

The examination of existing models suggests that most models (including the Clementsian and Multiple-Stable-States Models) could be validated using a set of plant community data. This is because of the multivariate nature of such data sets and the varied perspectives that are thus possible. Rather than adopting theoretical and conceptual models or expert systems that may bear little relevance to management or to the area being managed, attention should be focussed on meeting particular objectives. This requires more imagination and an understanding of the underlying ecology of the system being examined.


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APPENDICES
Point cover data were collected at Mills, Utah, to determine sample adequacy using the gimbelled-point (Winkworth and Goodall 1962) sighting tube technique. Data collection at Mills has been in the form of 4 minitranssects of 25 stations each for each plot examined since the inception of the long-term data set (see chapter 5 for more detail). For the validation of sample adequacy, 8 minitranssects were collected at each of 4 "original" exclosures. Graphical techniques were used to determine sample adequacy from an individual species (the abundance dominant for the particular exclosure examined) and community perspective. This was achieved by plotting running means and average similarity against the cumulative number of minitranssects considered. In the case of the community data, dependent axes were based on the Kulczinsky (Belbin 1992) distance measure (see chapter 4 for more detail).

Figures A1.1 and A1.2 indicate that, for the test of sample adequacy of the stand dominant, 4 appears to be the absolute minimum number of minitranssects required (the point at which the graphs level off). Similarly, Figures A1.3 and A1.4 indicate that the minimum number of minitranssects required from a community perspective is also 4. The above figures indicate some variation between plots, with some plots showing sample adequacy prior to achieving 4 minitranssects, while others only reach equilibrium after 4 minitranssects have been examined. This implies that 4 minitranssects are adequate, but barely so!
Fig. A.1. Using the running mean for total cover to determine sampling adequacy (number of minitranssects) for major species in the 4 "original" exclosures. Symbols represent different exclosures.
Fig. A.2. Using the running mean for the major species to determine sampling adequacy (number of minitranssects) at the 4 original exclosures. Symbols represent different exclosures.
Fig. A.3. Using the percentage similarity of the first sample to the running mean to determine sampling adequacy (number of minitranssects) at the community level at 4 different sites exclosures. Symbols represent different sites.
Fig. A.4. Using the percentage similarity of the running mean to the overall mean to determine sampling adequacy (number of minitranssects) at the community level for 4 different sites. Symbols represent different sites.
## Appendix B: List of Species and Growth-Form Acronyms

Table B.1. List of species and growth-form acronyms used in this dissertation.

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Scientific Name</th>
<th>Plant List</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>AG</td>
<td><em>Agoseris</em> spp</td>
<td>agoseris</td>
<td></td>
</tr>
<tr>
<td>FEID</td>
<td><em>Festuca idahoensis</em> Elmer</td>
<td>Idaho fescue</td>
<td></td>
</tr>
<tr>
<td>POA</td>
<td><em>Poa</em> spp</td>
<td>bluegrass</td>
<td></td>
</tr>
<tr>
<td>SIHY</td>
<td><em>Sitanion hystrix</em> (Nutt.) J.G. Smith</td>
<td>bottlebrush squirreltail</td>
<td></td>
</tr>
<tr>
<td>ST</td>
<td><em>Stipa</em> spp</td>
<td>needle and thread</td>
<td></td>
</tr>
<tr>
<td>ALAC</td>
<td><em>Allium acuminatum</em> Hook</td>
<td>tapertip onion</td>
<td></td>
</tr>
<tr>
<td>BASA</td>
<td><em>Balsamorhiza sagittata</em> (Pursh) Nutt.</td>
<td>arrowleaf balsamroot</td>
<td></td>
</tr>
<tr>
<td>CRAC</td>
<td><em>Crepis acuminata</em> Nutt.</td>
<td>tapertip hawksbeard</td>
<td></td>
</tr>
<tr>
<td>DENU2</td>
<td><em>Delphinium nuttallianum</em> Pritzel ex Walpers</td>
<td>Nuttall larkspur</td>
<td></td>
</tr>
<tr>
<td>LASE</td>
<td><em>Lactuca serriola</em> L.</td>
<td>prickly lettuce</td>
<td></td>
</tr>
<tr>
<td>LEPU</td>
<td><em>Leptodactylon pungens</em> (Torr.) Nutt.</td>
<td>rock gilia</td>
<td></td>
</tr>
<tr>
<td>LOMA2</td>
<td><em>Lomatium macdougalii</em> Coul &amp; Rose</td>
<td>MacDougal lomatium</td>
<td></td>
</tr>
<tr>
<td>LOTR</td>
<td><em>Lomatium triternatum</em> (Pursh) Coul &amp; Rose</td>
<td>nineleaf lomatium</td>
<td></td>
</tr>
<tr>
<td>PHLOX</td>
<td><em>Phlox hoodii</em> Rich</td>
<td>Hoods phlox</td>
<td></td>
</tr>
<tr>
<td>PHLO2</td>
<td><em>Phlox longifolia</em> Nutt.</td>
<td>longleaf phlox</td>
<td></td>
</tr>
<tr>
<td>BRTE</td>
<td><em>Bromus tectorum</em> L.</td>
<td>cheatgrass</td>
<td></td>
</tr>
<tr>
<td>ARTD</td>
<td><em>Artemisia tridentata</em></td>
<td>big sagebrush</td>
<td></td>
</tr>
<tr>
<td>ARTP</td>
<td><em>Artemisia tripartita</em></td>
<td>threetip sagebrush</td>
<td></td>
</tr>
<tr>
<td>ARTA.</td>
<td><em>Artemisia arbuscula</em></td>
<td>low sagebrush</td>
<td></td>
</tr>
<tr>
<td>CHVI8</td>
<td><em>Chrysothamnus viscidiflorus</em> (Hook) Nutt.</td>
<td>Douglas rabbitbrush</td>
<td></td>
</tr>
<tr>
<td>GUSA</td>
<td><em>Gutierrezia sarothrae</em> (Pursh.) Britton &amp; Rusby</td>
<td>broom snakeweed</td>
<td></td>
</tr>
<tr>
<td>JUOS</td>
<td><em>Juniperus osteosperma</em> (Torr.) Little</td>
<td>Utah juniper</td>
<td></td>
</tr>
<tr>
<td>TAN</td>
<td>Total annuals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TFO</td>
<td>Total forbs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TGR</td>
<td>Total bunchgrasses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOT</td>
<td>All vegetation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TWO</td>
<td>Total woody plants</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix C: Abundances of Major Species and Growth-Forms Within the Mills Data Set (Chapter 5)

In all cases, Y-axes refer to cover abundance, while the X-axes refer to consecutive years of data collection. 1 corresponds to 1981, the first year of data collection for the burnt and fenced exclosures. Data collections started in 1982 for the other treatments.
Fig. C.1. Cover for species and collective categories for the burnt and ungrazed exclosure at Mills, central Utah, plot 1.
Fig. C.2. Cover for species and collective categories for the burnt and ungrazed exclosure at Mills, central Utah, plot 2.
Fig. C.3. Cover for species and collective categories for the burnt and ungrazed exclosure at Mills, central Utah, plot 3.
Consecutive year

Fig. C.4. Cover for species and collective categories for the burnt and ungrazed exclosure at Mills, central Utah, plot 4.
Fig. C.5. Cover for species and collective categories for the burnt and grazed exclosure at Mills, central Utah, plot 1.
Fig. C.6. Cover for species and collective categories for the burnt and grazed exclosure at Mills, central Utah, plot 2.
Fig. C.7. Cover for species and collective categories for the burnt and grazed exclosure at Mills, central Utah, plot 3.
Fig. C.8. Cover for species and collective categories for the unburnt and grazed exclosure at Mills, central Utah, plot 1.
Fig. C.9. Cover for species and collective categories for the unburnt and grazed exclosure at Mills, central Utah, plot 2.
Appendix D: Cover Abundances for Species and Growth-Forms Encountered Along the Piospheres (Chapter 6)

In all cases, Y-axes refer to cover abundance, while the X-axes refer to consecutive minitranssects along which data were collected, moving away from the watering point. Identification codes consist of a piosphere identification and a species/growth-form identification separated by a hyphen.
Fig. D.1. Cover abundance curves for species and growth-forms showing high serial correlations the piosphere 'MORAN'. See appendix B for species and growth-forms acronyms.
Fig. D.2. Cover abundance curves for species and growth-forms showing high serial correlations for piospheres 'A' and 'TWIN'. See appendix B for species and growth-forms acronyms.
Fig. D.3. Cover abundance curves for species and growth-forms showing high serial correlations for the piospheres 'P1LI' and 'P2LI'. See appendix B for species and growth-forms acronyms.
Fig. D.4. Cover abundance curves for species and growth-forms showing high serial correlations for the pionsphere 'AIRSTR'. See appendix B for species and growth-forms acronyms.
CURRICULUM VITAE

Personal Details

Full name: Paul Eric Hosten
Date of Birth: 5 April 1963
Citizenship: Belgian

Education and Qualifications

1980 - 1984 B.Sc. (University of Port Elizabeth, South Africa)
1985 B.Sc.Hons. (Rhodes University, South Africa)
1986 - 1988 M.Sc. (University of Natal, South Africa)
1989 Traineeship (University of Ben Gurion, Israel)
1990 - 1995 Ph.D. (Utah State University, U.S.A.)

Summaries of Research Interests

B.Sc.(Hons.) Research: Some aspects on the intertidal ecology of Gelidium pristoides.
Tagging experiments were conducted to determine the seasonality of growth of Gelidium pristoides.
Translocation experiments and studies involving substrate preference & availability yielded information
regards plant distribution within the intertidal zone. The agar content relative to height above spring low tide
was also investigated. Possible management implications of this information were considered.

Computer modeling techniques were used to determine the importance of phosphorus uptake by
Phragmites australis relative to other uptake mechanisms. The behavior and persistence of phosphorus
retention mechanisms were studied under simulated vegetated and non-vegetated conditions to determine
management and design criteria of artificial reedbeds.
**Traineeship:** The ecology of arid-land plant communities.

This traineeship was under the supervision of Dr. L.S. Olsvig-Whittaker, and involved practice in the use of the Cornell Ecology Program series. The project undertaken entailed determining the effect of sheep and goat grazing on the local sand-field vegetation.

**Current Ph.D. research:** Determining the relative suitability of different models of vegetation dynamics as a basis for range condition and trend analysis in sagebrush-dominated rangelands.

Current models of vegetation dynamics were assessed relative to the needs of range managers, and validated for sagebrush-dominated vegetation using long-term plant community data sets and piosphere effects around watering points. A knowledge of vegetation dynamics, field experience, and remote sensing technology allowed the development of an alternative strategy of rangeland management and monitoring based on undesirable species.

**Membership of Societies**

Ecological Society of America (ESA)
Grassland Science Society of Southern Africa (GSSA)
Society for Range Management (SRM)

**Additional Work Experience**

1981-1984: Information officer at Tsitsikamma National Park (vacation work over four years).

1988: Temporary Research Assistant (University of Port Elizabeth) research topic: dune stabilization and revegetation.

**Awards**

1991: Sigma Xi research award for supporting research on detecting small scale changes in microphytic crust composition and distribution.
Publications


Book Reviews