

SAGEBRUSH–GRASS VEGETATION DYNAMICS: COMPARING CLASSICAL AND STATE-TRANSITION MODELS

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Abstract. The State-Transition (ST) model has been proposed as a replacement for the widely used Classical linear succession model and its derivative Range Condition (RC) model for describing and predicting rangeland community dynamics in response to management. Although the ST model offers significant advantages because it accommodates nonlinear and nonequilibrium theory and is more amenable to quantitative testing of hypotheses about community change, to date its applications have not fully utilized those advantages using empirical data. We compare the utility of the Classical, RC, and ST models in the *Artemisia tridentata*/*Pseudoroegneria spicata* vegetation type, utilizing a long-term data set from southeastern Oregon. First we develop and examine the Classical and RC models for their ability to describe and predict observed vegetation changes; second we develop an ST model by classifying and quantitatively identifying states and transitions that were observed over a period of 20 yr. The Classical and RC models adequately describe most of the observed changes in vegetation through use and application of broad descriptive categories on extensive range sites. This greatly reduces the utility and predictive value of the Classical and RC approaches as guides to management and restoration. The states and transitions developed quantitatively for the ST model offer considerably more precision and predictive value than the Classical/RC models but require large, long-term, site-specific data sets, which are usually not available for rangeland systems. The specific seral stages developed for the Classical model and commonly described in the literature differ significantly from the states and transitions derived quantitatively from the empirical data. States in the ST model exhibit a significant time dependency and could not have been adequately developed without long-term observations.

Key words: rangeland management; sagebrush–grass ecosystem; state-transition model; succession; vegetation dynamics.

INTRODUCTION

Classical succession theory (Clements 1916), which is still widely applied, suggests that rangeland systems are best described as predictable linear sequences of plant communities, sequentially changing in orderly response to control variables like grazing, fire, precipitation, and competition. A growing body of theoretical and empirical evidence suggests that classical succession theory is a weak predictive model (Jenny 1961, Noble and Slatyer 1980, Grime et al. 1988). The State-Transition (ST) model has been proposed to account better for widely observed nonlinear, nonequilibrium plant community dynamics (Westoby et al. 1989). The ST model, which simply defines stable types (states) and catalogues transitions between states, can provide a more unifying framework than the Classical Clementsian-based model (Dyksterhuis 1949) because ST models are more general and easily adaptable to explain nonlinear and nonequilibrium processes of vegetation change. State stability and transition probabilities can be quantified and used to evaluate realistically hypotheses about vegetation processes, and could lead to im-

proved predictability of system response to management controls (Taylor et al. 1994, Whalley 1994).

Range managers use the Range Condition (RC) model (Dyksterhuis 1949) to evaluate rangelands and guide grazing management. This system identifies range sites, then links successional stages to degree of grazing impact (Bartolome and Heady 1988). Currently, range sites and ecological sites are considered synonymous and defined as “a kind of land with a specific potential natural community, specific physical site characteristics, and response to management” (Committee on Rangeland Classification 1994). The approach has not always proven effective because of flaws in the linear successional model, a lack of clearer links between grazing and vegetation change, and difficulties in objectively identifying and delineating range sites (Bartolome 1993). Predicted range condition changes on sagebrush–grass rangelands have nevertheless been used to justify the spraying and seeding of millions of hectares in the western United States (Heady 1988), and dramatic changes in livestock grazing practices (Blaisdell et al. 1982).

To date, published applications of the ST model have used its adaptability to describe processes of vegetation change and response to management controls that are

disappointingly similar to those described by the Classic succession and RC models (Westoby et al. 1989, Laycock 1991, George et al. 1992, Huntsinger and Bartolome 1992, Jones 1992). Despite their potential, ST models have not been used to test rigorously hypotheses about the structure of rangeland communities or the processes of nonequilibrium dynamics. Some researchers (e.g., Foran et al. 1986, Friedel et al. 1988, Brown 1994) have used a multivariate approach to the identification of vegetation states in an ST model and have classified states and then used ordination to arrange them so that similar sites are near each other (Gauch 1982). However, in each case, the states to be classified were identified first as known or presumed community types, which may be either states or transitions. These states and transitions were mostly derived from observations that assumed reversible changes and used community types developed under the older Classical model framework and then adapted to ST.

Secondary succession has long been studied in the sagebrush–grass type (Piemeisel 1938), and traditionally is viewed as a good match to the linear Clementsian model when linked to specific habitat types (Daubenmire 1970). The relative mix of perennial grasses and shrubs is thought to be related to fire occurrence, with recent fire favoring grass (Blaisdell et al. 1982). Much of the region has been subject to heavy livestock use since the late 1800s, which leads to loss of *Pseudoroegneria spicata* and increases in *Artemisia tridentata* (Frischknecht and Harris 1968). Exotic annuals like *Bromus tectorum* are common where past grazing and frequent fire have reduced perennials. This stage has been observed to persist for many years (Piemeisel 1951).

In this paper, we develop the ST model less subjectively than other authors to compare its descriptive and predictive power to the Classical succession model and its derivative RC model. We identify states and the relationships between states in the sagebrush–grass region of the western United States using data-driven model development. In doing so, we move the ST model from “considered opinion,” and thus subjective boxes and arrows and “single-point-in-time” comparisons (Filet 1994), to a quantitative identification of vegetation states and probable transitions based on repeated measures of the same sites over a 20-yr time frame. This alone should provide for greatly improved descriptions and better prediction of system behavior. In this analysis using actual site data, we clarify states and transitions in the sagebrush–grass system and show why prior attempts to predict management response were unreliable.

Background of the data set

The data used in this analysis were collected during monitoring of the Vale Rangeland Rehabilitation Program in southeastern Oregon and described in detail in

Heady (1988). Briefly, the Vale Program area encompasses $\sim 2.6 \times 10^6$ ha and has been described as sagebrush–grass characterized by complex, intergraded mixtures of several dominant plant species depending on prior use, fire history, and microsite. During the study time period (1955–1986), precipitation averaged 255 mm/yr, but varied from 152 to 406 mm/yr. During the Vale Program vegetation manipulation period (1962–1972), 6 yr received above-average annual precipitation, and only 1 yr (1966) was exceptionally dry, at 167 mm (Heady 1988).

When the Vale Program began, the vegetation was described as dominated by *Artemisia tridentata*, annuals, and few palatable perennial grasses (Heady 1988). In some locations, a perennial grass understory was almost absent, with annuals or bare soil occurring between the shrubs. In 1962, Congress passed a special appropriations bill to fund a $\$10 \times 10^6$ 10-yr program to rehabilitate the deteriorated rangelands of the Vale District of the Bureau of Land Management (Heady 1988).

The locations selected for this study were on *A. tridentata*-dominated range sites selected for range improvement treatments between 1964 and 1967. Locations were either: (1) plowed with a rangeland disk and seeded to *Agropyron cristatum*, (2) aerially sprayed with the herbicide 2,4D and not seeded, or (3) burned in wildfires and seeded to *A. cristatum* before 1972. All locations had been traditionally grazed in the spring since the late 1800s, and permitted use by cattle has remained generally stable since accurate records were first kept in the 1930s (Bartolome and Heady 1988). However, grazing capacity changed dramatically over time, initially declining considerably following several decades of heavy grazing in the early 1900s. Later, after Vale Program vegetation manipulation treatments and physical improvements in the 1960s, grazing capacity increased well beyond permitted levels of use by the 1980s (Bartolome and Heady 1988). Bartolome et al. (1988) reported that of the vegetation treatments, seedings sustained significantly increased grazing capacity in the long term. Sprayed areas supported higher livestock numbers immediately following treatment, but rapidly declined as *A. tridentata* reinvaded, such that after 10 yr, they were similar in productivity to native range. Untreated range increased in productivity throughout the program area, probably because of improved grazing management practices, water developments, fencing, and precipitation patterns.

METHODS

Twenty-four locations were selected for this study based on the following two criteria: (1) species cover data were collected and available for each location planned for treatments between 1962 and 1965, treated and untreated areas in 1975, and treated and untreated areas in 1986; and (2) each location included an area that was actually plowed and seeded, sprayed and not

TABLE 1. Classical model seral stages and transitions between seral stages.

Location	Untreated			Plow/seed		Spray		Burn/seed	
	1965	1975	1986	1975	1986	1975	1986	1975	1986
128	III	III	III	V	V
116	IV	IV	IV	IV	IV
97	IV	IV	IV	V	V
86	IV	IV	IV	V	V
79	IV	III	IV	IV	IV
75	V	IV	V	V	III	...	V
72	IV	III	III	V	V
67	IV	IV	III	IV	IV
65	IV	III	III	V	V
63	V	IV	IV	V	V
61	IV	IV	III	IV	II
55	III	II	III	IV	IV
54	III	II	IV	IV	V
52	IV	IV	IV	V	V
51	V	IV	IV	V	V
46	IV	IV	IV	V	V
45	IV	IV	IV	V	V
3	IV	IV	III	V	I
24	IV	IV	IV	IV	III
26	IV	IV	IV	V	III
41	IV	IV	IV	V	IV
2	III	IV	III	V	IV
27	IV	IV	IV	IV	IV
44	IV	V	IV	IV	IV

Notes: I, annual spp. dominant, perennials absent; II, *Artemisia tridentata* dominant, perennial grasses absent; III, *Artemisia tridentata* and/or *Bromus tectorum*/*Poa secunda* dominant, *Pseudoroegneria spicata* absent; IV, *Artemisia tridentata* dominant, *Pseudoroegneria spicata* present; V, *Pseudoroegneria spicata* cover > *Artemisia tridentata* cover.

seeded, or burned in a wildfire and seeded before 1972. In only one location, one area was sprayed and another burned. This resulted in a data set of 24 original untreated locations. In the 1975 data set, each location included areas that were still untreated, while parts of the originally untreated areas were plowed and seeded (10 areas), sprayed (10 areas), and burned (4 areas). In 1986, the same locations were resampled, with the addition of a burned area at Location 75 (Table 1). The treatment combinations produced a total of 25 treatment areas for analysis. Application of these criteria eliminated many of the >150 locations studied in the original Vale Program evaluation, but we wanted to ensure repeated measurement over time and space.

Data collection was designed to describe vegetation quickly to determine suitability for treatment, forage values, wildlife value, and response to treatment. Relative species cover was estimated using 100-point, paced transects for the period 1962 through 1965. In 1975 and 1986, the areas were sampled by ocular estimation of average relative cover on 5, 1 × 100 m belt transects. Although the 1965 and 1975/1986 methods differed, locations and areas were accurately relocated, and transect results for changes in dominant species were comparable. All data were incorporated into a publication (Heady 1988) summarizing the 20-yr outcome of the Vale Rehabilitation Program.

We identified seral stages using the Classical linear succession model, which has appeared in the literature for decades in various forms (Piemeisel 1951, Dau-

benmire 1970, Blaisdell et al. 1982, Hironaka et al. 1983, Bartolome and Heady 1988, Laycock 1991). Five stages were identified, and changes in vegetation between 1965 and 1975/1986 tracked for each sample area. The linear arrangement of vegetation seral stages was also divided into range condition classes with the *excellent* class corresponding to the highest seral stage (Dyksterhuis 1949).

TWINSPAN (two-way indication species analysis) classification analysis (Hill 1979) was used to determine sagebrush–grass states for each area based on species composition data from transects. TWINSPAN is a polythetic, divisive classification approach, which allows the simultaneous evaluation of species and plots, uses the original vegetation data, and is both robust and effective (Gauch 1982). Data from 1965 were classified first, then transect data from 1965 and 1975 were classified together, and finally the entire data set (1965, 1975, and 1986 transects) was combined and subjected to classification. The same community groups were determined by TWINSPAN, whether decadal data sets were classified separately or in the combined fashion described above. In each of the classifications, the same species cut levels (0, 2, 5, 10, 20, and 50) were used to define the ranges of cover classes (Hill 1979). Rare species were not omitted, and dominant species tended to drive the classification of communities. A minimum eigenvalue of 0.20 was used as the cutoff point in classification levels. The eigenvalue is a measure of the dispersion of species along a one-

dimensional ordination axis. Higher eigenvalues indicate that two groups are well separated along the axis, while smaller eigenvalues indicate that two groups are closer together. Both step points and belt transects are robust for detection of dominant species (Brown 1954). Unlike the previously considered Classical succession model, no prior model organization was assumed.

Mean species cover was calculated (Norusis 1993) for each TWINSPLAN-classified vegetation group, and used to compare individual species cover within each vegetation group classified for each of the three data sets (1965 alone, 1965 and 1975 combined, and 1965, 1975, and 1986 combined). This allowed us to determine if some states remained stable through time and whether new states appeared. A box and arrow diagram (ST model) was constructed based on the quantitative identification of vegetation states. Our knowledge of management treatment of individual areas, and their change in state over time, allowed for the identification of transitions.

RESULTS

Identifying seral stages: Classical model approach

The accepted successional pattern (Fig. 1) in the sagebrush–grass region following cultivation or damage from overgrazing includes seral Stage I: thistles or other annual weeds on bare soil, perennials absent; Stage II: mustards and other annual forbs and grasses, *Artemisia* present; Stage III: *Bromus tectorum* and *Poa secunda* dominant, which could last for years especially with fire; Stage IV: <50% cover of *Pseudoroegneria spicata*, ≥50% cover of *Artemisia tridentata*, and variable amounts of *Bromus tectorum* cover; and finally, Stage V: >50% cover of *Pseudoroegneria spicata* and other perennial bunchgrasses with ~25% cover of *Artemisia tridentata* when the community was at or near climax (Piemeisel 1938, Daubenmire 1970, Blaisdell et al. 1982). With the introduction of heavy grazing, palatable climax grasses decline and *A. tridentata* increases until, with combinations of time-dependent mortality of *A. tridentata* and/or fire, *B. tectorum* and other lower seral-stage species appear (Laycock 1991, Young et al. 1976, Branson 1985). The Classical model predicts that with improved control of grazing, *A. tridentata* would decline to levels near 25% total cover, and perennial bunchgrasses would increase, thereby improving range condition.

In 1965, most of the areas (8 of 10) selected for plowing and seeding were in seral Stage IV (Table 1). Stage IV also included most of the areas selected for spraying (7 of 10). All of the areas classified as Stage V were also selected for spraying treatments. The Classical model, designed to explain succession following cultivation, defines a very broad category IV, which is not very useful for planning land treatments; an area would have been classified as Stage IV if even a trace of *P. spicata* was present.

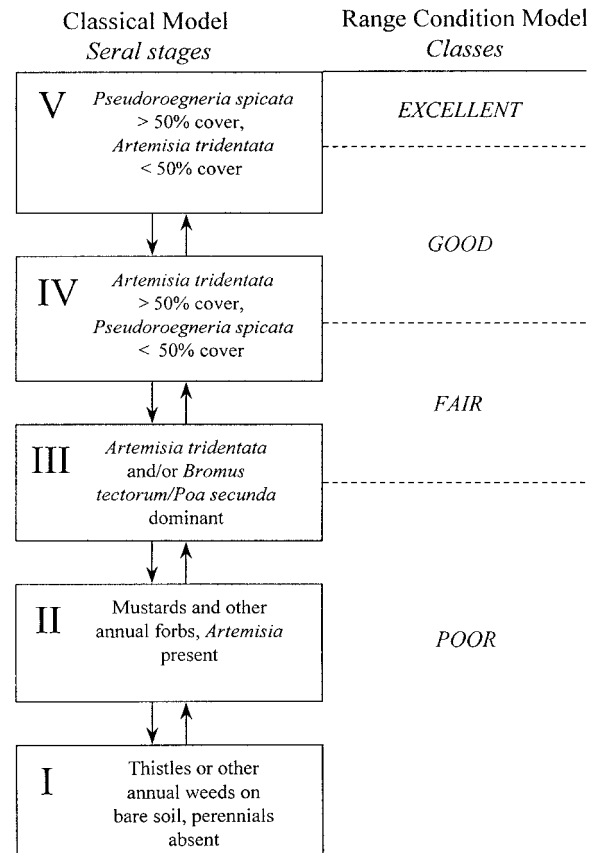


FIG. 1. Seral stages and transitions for the Classical linear succession and Range Condition models in the sagebrush–grass type of southeastern Oregon. Seral stages IV and V have equivalent State-Transition model states in *Agropyron cristatum* and *Agropyron cristatum*–*Bromus tectorum*, respectively, where seeded *A. cristatum* substitutes for *P. spicata*. Stage I: Annual species dominant, perennials absent; corresponds to poor range condition class. Stage II: *A. tridentata* dominant, perennial grasses absent; corresponds to poor range condition class. Stage III: *A. tridentata* and/or *B. tectorum*/*P. secunda* dominant (*A. tridentata* absent with frequent fire); corresponds to fair–poor range condition classes. Stage IV: *A. tridentata* dominant, *P. spicata* present; corresponds to good–fair range condition classes. Stage V: *P. spicata* cover > *A. tridentata* cover; corresponds to excellent–good range condition classes.

For sagebrush–grass vegetation, range condition classes are defined by categorizing the major species into increasers, decreasers, and invaders, depending on their response to grazing and the proportion of the hypothetical climax community present (Dyksterhuis 1949). We applied this model to assign range condition classes (the higher the percentage of decreasers, the better the condition and also the closer to the supposed climax) where excellent condition contains 50–75% cover of decreasers, 0–25% increasers and no invaders. Good condition is defined as sites containing 25–50% decreasers, 25–50% increasers, and 0–25% invaders. The fair condition class contains 0–25% decreasers, 25–50% increasers, and 25–50% invader species, and

TABLE 2. State-Transition model states and the transitions between states.

Location	Untreated			Plow/seed		Spray		Burn/seed	
	1965	1975	1986	1975	1986	1975	1986	1975	1986
128	2	2	2	2	5
116	3	3	3	4	1
97	1	3	1	5	5
86	1	1	1	5	5
79	3	1	1	6	6
75	3	1	4	1	4	...	6
72	1	3	1	5	5
67	1	3	1	6	5
65	1	3	1	5	5
63	1	3	1	4	1
61	1	3	1	4	1
55	1	1	1	6	6
54	1	2	1	6	5
52	1	3	1	5	5
51	4	4	1	4	4
46	1	1	4	5	5
45	1	1	2	5	5
3	1	3	1	1	1
24	1	4	1	4	1
26	1	3	1	3	1
41	3	3	3	4	3
2	1	3	1	5	6
27	1	4	1	6	6
44	3	3	3	3	3

Notes: 1, *Bromus tectorum*; 2, *Artemisia tridentata*–*Chrysothamnus*; 3, *Pseudoroegneria spicata*–*Artemisia tridentata*; 4, *Pseudoroegneria spicata*–*Bromus tectorum*; 5, *Agropyron cristatum*; 6, *Agropyron cristatum*–*Bromus tectorum*.

the *poor* condition class is defined as containing no decreaser species, 0–25% increasers, and 50–100% invaders.

As defined in range-site descriptions (Lovell 1980), common decreasers include *P. spicata*, *Stipa lettermannii*, *Elymus* spp., and *A. cristatum*, which is a special case, since it is an introduced species. Common increasers include *A. tridentata*, *P. secunda*, *Sitanion hystrix*, and *Chrysothamnus* spp. Invader species include *B. tectorum* and other annuals. In 1963, only 1% of the Vale Program areas were rated in *good* to *excellent* condition (Stages IV and V, Fig. 1); all the other sites selected for treatment were rated in *fair* to *poor* condition (Stages IV and III, Fig. 1) (Heady 1988).

Identifying states: state-transition model approach

The 1960s Vale Program locations selected for later treatment were classified by TWINSpan into four separate vegetation types or states: *Bromus tectorum*, *Artemisia tridentata*–*Chrysothamnus*, *Pseudoroegneria spicata*–*Artemisia tridentata*, *Pseudoroegneria spicata*–*Bromus tectorum* (Table 2). All four states contained different amounts of the native perennial grass *P. spicata* and introduced annual grass *B. tectorum*, but no differences in remaining dominant species cover (Table 3a). The *B. tectorum* state was characterized by high *B. tectorum* cover (52%) and low (3%) *P. spicata* cover. Conversely, state *Pseudoroegneria spicata*–*Artemisia tridentata* was characterized by low (<1%) *B. tectorum* cover and high (29%) *P. spicata* cover. State *Pseudoroegneria spicata*–*Bromus tectorum* contained mod-

erate amounts of both *B. tectorum* and *P. spicata* (Table 3a). *A. tridentata* and *P. secunda* cover values were not different among the four states. One area was classified into state *Artemisia tridentata*–*Chrysothamnus* because >30% *Chrysothamnus* spp. cover was estimated for this area.

All areas selected for spraying (Table 2) were in state *Bromus tectorum* ($n = 5$), *Pseudoroegneria spicata*–*Artemisia tridentata* ($n = 4$), or *Pseudoroegneria spicata*–*Bromus tectorum* ($n = 1$). All areas selected for plow and seed were in state *Bromus tectorum* in 1965. Burned and seeded areas were in various states in 1965.

Combined 1965 and 1975 data-set analysis showed six separate states. Four states remained from the 1965 data-set analysis; the *Chrysothamnus* plot from 1965 was joined by additional plots with *Chrysothamnus* cover, as *Artemisia tridentata*–*Chrysothamnus*. Two new states (*Agropyron cristatum* and *Agropyron cristatum*–*Bromus tectorum*) appeared to originate as the direct outcome of seeding management activities during the 10-yr period (Table 3b).

States *Pseudoroegneria spicata*–*Artemisia tridentata* and *Pseudoroegneria spicata*–*Bromus tectorum* contained more *P. spicata* cover than the other states and were separated from each other based on greater *A. tridentata* cover for state *Pseudoroegneria spicata*–*Artemisia tridentata* and greater *B. tectorum* cover for state *Pseudoroegneria spicata*–*Bromus tectorum* (Table 3b). States *Agropyron cristatum* and *Agropyron cristatum*–*Bromus tectorum* were distinguished from all the other states by higher *A. cristatum* cover, and

TABLE 3. Percentage cover by species and number of plots (*n*) used in the state description for: (a) 1965 states; (b) 1965 + 1975 states; and (c) 1965 + 1975 + 1986 states.

a)						
	1965 states					
Species	1 (<i>n</i> = 15)	2 (<i>n</i> = 1)	3 (<i>n</i> = 5)	4 (<i>n</i> = 3)		
<i>Pseudoroegneria spicata</i>	3	0	29	19		
<i>Bromus tectorum</i>	52	0	0.4	30		
<i>Poa secunda</i>	17	3	24	21		
<i>Sitanion hystrix</i>	1	0	5	1		
<i>Artemisia tridentata</i>	19	40	28	20		
<i>Chrysothamnus</i> spp.	0	34	0	0		
<i>Agropyron cristatum</i>	0	0	0	0		
b)						
	1965 + 1975 states					
Species	1 (<i>n</i> = 25)	2 (<i>n</i> = 5)	3 (<i>n</i> = 22)	4 (<i>n</i> = 7)	5 (<i>n</i> = 8)	6 (<i>n</i> = 5)
<i>Pseudoroegneria spicata</i>	7	0	24	31	0	8
<i>Bromus tectorum</i>	40	39	1	27	6	5
<i>Poa secunda</i>	18	0	12	8	7	14
<i>Sitanion hystrix</i>	2	2	7	17	0	0
<i>Artemisia tridentata</i>	28	39	48	16	8	1
<i>Chrysothamnus</i> spp.	0	11	0	0	0	0
<i>Agropyron cristatum</i>	0	0	0	0	65	37
c)						
	1965 + 1975 + 1986 states					
Species	1 (<i>n</i> = 50)	2 (<i>n</i> = 6)	3 (<i>n</i> = 25)	4 (<i>n</i> = 13)	5 (<i>n</i> = 18)	6 (<i>n</i> = 9)
<i>Pseudoroegneria spicata</i>	7	0	22	31	0	5
<i>Bromus tectorum</i>	30	15	0.5	16	5	26
<i>Poa secunda</i>	18	0.5	15	12	9	23
<i>Sitanion hystrix</i>	1	3	5	15	0.5	0.6
<i>Artemisia tridentata</i>	36	47	51	21	14	0.7
<i>Chrysothamnus</i> spp.	0.7	11	0	0	0.8	0
<i>Agropyron cristatum</i>	0.3	0.2	0	0	58	38

Notes: States are 1, *Bromus tectorum*; 2, *Artemisia tridentata*; 3, *Pseudoroegneria spicata*–*Artemisia tridentata*; 4, *Pseudoroegneria spicata*–*Bromus tectorum*; 5, *Agropyron cristatum*; 6, *Agropyron cristatum*–*Bromus tectorum*.

from each other by higher *B. tectorum* and *P. secunda* cover for state *Agropyron cristatum*–*Bromus tectorum*.

In classification of the entire data set, no more new states appeared in 1986 (Table 3c), and relationships between dominant species remained similar. The six states are listed below in no particular order and diagrammed in Fig. 2.

1) *Bromus tectorum*: (*A. tridentata* with very little *P. spicata*)

2) *Artemisia tridentata*–*Chrysothamnus*

3) *Pseudoroegneria spicata*–*Artemisia tridentata*: (with low/no *B.*)

4) *Pseudoroegneria spicata*–*Bromus tectorum*

5) *Agropyron cristatum*

6) *Agropyron cristatum*–*Bromus tectorum*

Identifying transitions: Classical and Range Condition models

Untreated areas usually remained in the same seral stage or switched between adjacent seral stages as expected under the Classical model (Table 1). Only one untreated area exhibited a nonlinear temporal response, changing from seral Stage III to II between 1965 and 1975, then jumping to Stage IV by 1986, reflecting a

reestablishment of *Pseudoroegneria spicata* from an “annual only” stage. This jump could, of course, have passed through Stage III as an unsampled intermediate stage between 1975 and 1986.

Plowing and seeding to *Agropyron cristatum* is a drastic treatment, which prevents recovery of the native bunchgrass, *P. spicata*. This change was adequately described by the Classical model, which classified seeded areas as special cases of seral Stages V and IV. This description is extremely general, however, and of little value in characterizing the success or longevity of a seeded area.

Spraying alters the relative proportion of *P. spicata* and *Artemisia tridentata*. The Classical model was not adequate to describe frequent, treatment-induced, nonlinear temporal transitions in sprayed areas (Table 1). Of the nine sprayed areas, four exhibited nonlinear transitions between 1975 and 1986, and four areas did not show change in seral stage after treatment. Areas that burned changed in linear successional ways predicted by the Classical model.

The RC model offers more resolution of the late seral stages, which are the focus for range management (Fig. 1). Range condition generally showed little change be-

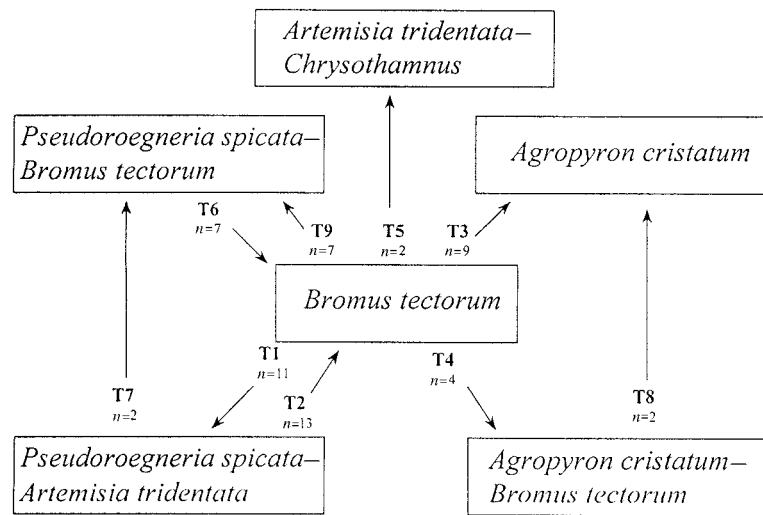


FIG. 2. State-Transition model for sagebrush–grass rangeland in southeastern Oregon. Boxes represent states (see Table 3 for state descriptions). Arrows represent transitions observed between states occurring at least twice. Catalogue of transitions: (T1) Do nothing; transition appears related to time and weather over a 10-yr period ($n = 11$). (T2) Do nothing; transition to *B. tectorum* with no change in management activities over 10-yr period ($n = 13$). (T3) Plowing (or burn, only 1 example) ($n = 9$). (T4) Plowing (or burning, only 2 examples) ($n = 4$). (T5) Do nothing; transition appears related to time and weather over a 10-yr period ($n = 2$). (T6) Do nothing following spray application ~15–20 yr earlier ($n = 7$). (T7) Spraying ($n = 2$). (T8) Do nothing; transition appears related to time and weather ($n = 2$). (T9) Spraying ($n = 7$).

tween 1965 and 1986 on untreated areas; areas that changed between seral Stages III and IV were still classified in *fair* condition by the RC model (Table 1). Eight of 10 areas selected for spraying in 1965 were in *fair* condition; the other 2 were in *good* condition. Sprayed areas improved in range condition after treatment (5 of 10) or stayed the same, but between 1975 and 1986 returned to their initial condition class or were rated *poor*. The RC model would predict that all areas would improve in range condition class with spraying. Of the 10 areas selected for plowing, 8 were in *fair* condition and 2 were in *poor* range condition initially. As expected, all plowed and seeded areas improved in range condition class, because the perennial *A. cristatum*, although not native, is categorized as a decreaser and an indicator of *good* to *excellent* range condition.

Identifying transitions: state-transition model

The ST model (Fig. 2) was developed using identified states and tracking any transition in state for a particular area over time. Although change in management activities (treatments) often resulted in vegetation changing to a new state, many areas that were not treated also shifted to a new vegetation state (Table 2). Management activities were known for each area so that transitions could be catalogued by type, as suggested in Westoby et al. (1989). Precipitation records show that the first decade (1962–1972) was a drier-than-normal period, while the second decade was slightly wetter than average (Heady 1988).

Thirteen transition types were observed between 1965 and 1986. Nine that occurred at least twice are plotted in Fig. 2. Some transitions associated with man-

agement actions were similar to those predicted by the Classical model. For example, T7 and T9 were the typical responses to spraying, with reduction of *A. tridentata* and an increase in *P. spicata* (Fig. 2). Transition T1 (*Bromus tectorum* to *Pseudoroegneria spicata*–*Artemisia tridentata*) was expected to be rare under the Classical and RC models and was a major rationale for spray treatments. T1 was observed once in response to a spray treatment but, notably, was extremely common even without treatment (Fig. 2). Under proper grazing management, T2 would not be expected to occur. However, this transition was very common on untreated areas, even with proper grazing management. T5, rabbit brush invasion, normally follows disturbance that removes *A. tridentata* or grass cover, but on Vale District lands the two examples of T5 occurred without treatment or other apparent disturbance.

Plowed and seeded areas all changed, so far permanently, through T3 or T4 to states *Agropyron cristatum* or *Agropyron cristatum*–*Bromus tectorum*. T3 and T4 are unidirectional transitions. T8 was observed twice, reflecting a decrease in *B. tectorum* on two seedings between 1975 and 1986.

Several possible transitions did not occur. No seeded areas shifted from states *Agropyron cristatum* or *Agropyron cristatum*–*Bromus tectorum*. Only two examples of T8 and a single undiagrammed change from *Artemisia tridentata*–*Chrysothamnus* to *Bromus tectorum*, with reestablishment of *P. spicata*, were observed. Examples of burned states *Bromus tectorum*, *Artemisia tridentata*–*Chrysothamnus*, and *Pseudoroegneria spicata*–*Artemisia tridentata* occurred with successful seeding changing states to *Agropyron cristatum* or

Agropyron cristatum–*Bromus tectorum* in 4 out of 5 instances. Two unique transitions, from *Artemisia tridentata*–*Chrysothamnus* to *Agropyron cristatum* and *Pseudoroegneria spicata*–*Artemisia tridentata* to *Agropyron cristatum*–*Bromus tectorum*, are not described in the model (Fig. 2), and both were associated with wildfire reseedsings.

DISCUSSION

Alternate models of rangeland-ecosystem functioning (e.g., multiple stable states and ST models) were developed because they assume that the future may contain an array of possible states, influenced by a set of events and a mixture of opportunities and hazards (Westoby et al. 1989, Friedel 1991, Laycock 1991). These models assume that a movement from one steady state to another only occurs when a threshold is crossed, and that once a threshold is crossed, a different stable plant community can exist (Schacht 1993).

Our data show that if managers plow and seed or seed after a wildfire, a threshold is crossed, new states appear, and these seem to be stable over time. When compared with a plow and seed treatment, burning and the response of burned areas to seeding appear to possess more unpredictable properties (for example, cover of *Bromus tectorum*) than other types of treatments.

Appearance of the states *Agropyron cristatum* and *Agropyron cristatum*–*Bromus tectorum* was the result of management action. When areas were plowed, five changed from *Bromus tectorum* to *Agropyron cristatum* (T3), and three changed from *Bromus tectorum* to *Agropyron cristatum*–*Bromus tectorum* (T4). When areas burned, the *Chrysothamnus* spp. plot moved to *Pseudoroegneria spicata*–*Artemisia tridentata*, and *Bromus tectorum* moved to *Agropyron cristatum* or *Agropyron cristatum*–*Bromus tectorum* (T3, T4).

If no treatment is done and grazing continues at relatively low rates, plant communities can change between states in an unpredictable manner. By revisiting locations in 1986, combining the entire data set, and tracing changes of treated and untreated areas, we found that most untreated areas which were in one state in 1965 changed to some other state in 1975, and then returned to their former state in 1985. A few areas remained in the same state the entire time period (Table 2). In any time period, our data show states that stay in *Bromus tectorum* or *Pseudoroegneria spicata*–*Artemisia tridentata* for the entire three sampling cycles or move between *Bromus tectorum* and *Pseudoroegneria spicata*–*Artemisia tridentata*, presumably dependent on environmental control variables. The new state, *Artemisia tridentata*–*Chrysothamnus*, appeared (T5) with no management input; that is, *Chrysothamnus* spp. cover increased significantly without treatment application.

The sprayed areas responded similarly to untreated areas between 1975 and 1985, suggesting that spraying had little lasting effect. They moved between *Bromus*

tectorum and *Pseudoroegneria spicata*–*Bromus tectorum* (T1 or T2), or remained in their original *Bromus tectorum* or *Pseudoroegneria spicata*–*Artemisia tridentata* states. Once in state *Pseudoroegneria spicata*–*Bromus tectorum*, subsequent changes in state were almost always to state *Bromus tectorum* through T6. Since T6 and T1 were common to untreated areas, it appears that managers could have not sprayed and gotten the same results. This is not true with plow/seed or burn/seed treatments. Most of the plowed and burned areas were still in their 1975 state in 1985. There was some fluctuation (two sites) only between states *Agropyron cristatum* and *Agropyron cristatum*–*Bromus tectorum*.

The Classical and ST models describe very different processes for vegetation change and different community-level organization. States *Bromus tectorum*, *Artemisia tridentata*–*Chrysothamnus*, *Pseudoroegneria spicata*–*Artemisia tridentata*, and *Pseudoroegneria spicata*–*Bromus tectorum* do not closely correspond to seral stages described by the Classical model (Table 4) because the definition of seral stages are broad. For example, many of the Classical model seral stages are included in the *Bromus tectorum* state. This is because the Classical model allows for the designation of seral Stages IV and V if any *P. spicata* is present, while the presence or absence of *B. tectorum* is not specifically mentioned until Stage III in the Classical model descriptions.

For range management, the inadequacies of the Classical model are partially addressed by discriminating among range condition classes at higher seral stages. However, the RC model is still limited by the built-in generality of approach and the need to define accurately and identify range sites. The model is also limited in that it failed to predict some common species' responses to management; species that responded in ways that do not fit well into the RC model of increaser, decreaser, and invader include *A. tridentata*, *P. secunda*, and *B. tectorum*, three of the most abundant species in southeastern Oregon.

The nonlinear, data-derived ST model is more effective at predicting changes than the Classical or RC models, but presents a different set of problems. The ST model appears better to predict suitability for land treatment, especially spraying, since T1 and T2 can occur without spraying. This should encourage greater efforts in determining underlying controls on community change between *Bromus tectorum* and *Pseudoroegneria spicata*–*Artemisia tridentata* community types. The ST model more specifically describes treatment response than the Classical model, in which categories are too broad, and also describes more of the short-term temporal variations in vegetation-community composition than does the Classical model. Problems with the ST model are mainly the result of errors in identification of states through classification, and the occurrence of unusual transitions. The ST model did

TABLE 4. Classification of states from State-Transition model, Classical linear succession model, and Range Condition model.

State-transition states	Classical model seral stages					<i>n</i>
	V	IV	III	II	I	
<i>Bromus tectorum</i>	4	28	16	0	1	49
<i>Artemisia tridentata</i> – <i>Chrysothamnus</i>	0	1	3	1	0	5
<i>Pseudoroegneria spicata</i> – <i>Artemisia tridentata</i>	4	19	2	0	0	25
<i>Pseudoroegneria spicata</i> – <i>Bromus tectorum</i>	6	8	0	0	0	14
	14	56	21	1	1	
State-transition states	Range condition classes				<i>n</i>	
	E	G	F	P		
<i>Bromus tectorum</i>	2	2	25	20	49	
<i>Artemisia tridentata</i> – <i>Chrysothamnus</i>	0	0	1	4	5	
<i>Pseudoroegneria spicata</i> – <i>Artemisia tridentata</i>	2	1	19	3	25	
<i>Pseudoroegneria spicata</i> – <i>Bromus tectorum</i>	2	5	7	0	14	
	6	8	52	27		

Note: States (*Bromus tectorum*, *Artemisia tridentata*–*Chrysothamnus*, *Pseudoroegneria spicata*–*Artemisia tridentata*, and *Pseudoroegneria spicata*–*Bromus tectorum*) are defined in the ST model (Fig. 2); seral stages I through V are defined in the Classical model (Fig. 1); *excellent* (E), *good* (G), *fair* (F), and *poor* (P) are defined in the Range Condition model (Fig. 1). Values are the number of plots in each class as determined by the models. Seedlings are excluded.

effectively describe the most common nonlinear changes.

Our data suggest a new approach or line of inquiry concerning ST models. First is a time dependency and thus the apparent inadequacy of most data sets. For example, if we had a data set with two repeated measures in time, after 10 yr, we would find that no treatment resulted in nine sites changing from state *Bromus tectorum* to *Pseudoroegneria spicata*–*Artemisia tridentata* (T1), five sites staying in state *Bromus tectorum*, three sites staying in state *Pseudoroegneria spicata*–*Artemisia tridentata*, but two sites moving from *Pseudoroegneria spicata*–*Artemisia tridentata* to *Bromus tectorum* (T2). But as our results illustrate, another 10 yr with no change in management may very well result in the return of an area to its former state. Had we sampled 20 yr apart, we would have detected no change at all. Given that the life-spans of most dominant perennial species are on the order of a few decades (West et al. 1979), inventory on a 5–10 yr cycle appears appropriate to detect transitions.

The pattern of time dependency in the ST model is no longer linear, which has important implications for successional study. In the linear models the patterns of change in one direction can be used to infer changes in the opposite direction. This linear approach forms most of the information base for describing vegetation change in the sagebrush–grass type. Unfortunately, once multiple pathways are likely, as identified in the ST model, each pathway needs to be confirmed and understood separately.

CONCLUSIONS

The Classical model, by using very broad definitions of stages, accommodates most of the observed changes in vegetation. However, the required generality of the

model and the emphasis on linearly related seral stages severely limits its predictive value. It was not useful for classifying areas to be selected for treatment, determination of appropriate treatments, or predicting response to grazing because the categories were too broad.

The Classical and RC models are derived from a similar set of assumptions and, as expected, they exhibited closely related types of stages and changes between stages. The ST models previously developed, because they started with the same assumptions about community structure and development as the Classical and RC models, end up with the same basic set of limitations and resulting poor prediction of system behavior. Our data-driven ST model describes a quite different set of vegetation dynamics, and our observed states and transitions are generally not recognized as important in existing models for the sagebrush–grass type.

ST models offer the advantages of general applicability but require detailed, time- and site-specific data to fully exploit their capabilities for description and prediction. A difficult, but real, problem to overcome with realistic ST models is the lack of symmetry. The Classical and RC models, because they assume symmetrical changes over time, require only observations or data documenting change in a single direction. Because most of our information about rangelands system behavior is based on comparisons of deteriorated and protected areas, we really only have good information about the process of rangeland deterioration, not recovery. More and longer term studies of community behavior in response to changes in grazing, following fire, and following vegetation treatment, are sorely needed for rangeland ecosystems.

LITERATURE CITED

- Bartolome, J. W. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecological Applications* 1:27–29, Volume 3.
- Bartolome, J. W., B. H. Allen, and H. F. Heady. 1988. Changes in vegetation. Pages 36–53 in *The Vale Rangeland rehabilitation program: an evaluation*. PNW-RB-157. U.S. Forest Service, Pacific Northwest Station and U.S. Department of the Interior, Bureau of Land Management, USA.
- Bartolome, J. W., and H. F. Heady. 1988. Grazing management 1962–1986. Pages 54–64 in *The Vale Rangeland rehabilitation program: an evaluation*. PNW-RB-157. U.S. Forest Service, Pacific Northwest Station and U.S. Department of the Interior, Bureau of Land Management, USA.
- Blaisdell, J. P., R. B. Murray, and E. D. McArthur. 1982. Managing intermountain rangelands—sagebrush—grass ranges. U.S. Forest Service, General Technical Report INT-134.
- Branson, F. A. 1985. Vegetation changes on western rangelands. Society for Range Management, Denver, Colorado, USA.
- Brown, D. 1954. Methods of surveying and measuring vegetation. Bulletin 42. Commonwealth Bureau of Pastures and Field Crops, Hurler, Berkshire, UK.
- Brown, J. R. 1994. State and transition models for rangelands. 2. Ecology as a basis for rangeland management: performance criteria for testing models. *Tropical Grasslands* 28:206–213.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Publication 242, Washington, D.C., USA.
- Committee on Rangeland Classification. 1994. Rangeland health. National Research Council, Washington, D.C., USA.
- Daubenmire, R. F. 1970. The steppe vegetation of Washington. Bulletin 62. Washington Agricultural Experiment Station, Pullman, Washington, USA.
- Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2:104–115.
- Filet, P. G. 1994. State and transition models for rangelands. 3. The impact of the state and transition model on grazing lands research, management and extension: a review. *Tropical Grasslands* 28:214–222.
- Foran, B. D., G. Bastin, and K. A. Shaw. 1986. Range assessment and monitoring in arid lands: the use of classification and ordination in range survey. *Journal of Environmental Management* 22:67–84.
- Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management* 44:422–426.
- Friedel, M. H., G. N. Bastin, and G. F. Griffin. 1988. Range assessment and monitoring in arid lands: the derivation of functional groups to simplify vegetation data. *Journal of Environmental Management* 27:85–97.
- Frischknecht, N. C., and L. E. Harris. 1968. Grazing intensities and systems on crested wheatgrass in central Utah: response of vegetation and cattle. U.S. Department of Agriculture, Technical Bulletin 1388.
- Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, New York, USA.
- George, M. R., J. R. Brown, and W. J. Clawson. 1992. Application of nonequilibrium ecology to management of mediterranean grasslands. *Journal of Range Management* 45:436–440.
- Grime, J. P., J. G. Hodgson, and R. Hunt. 1988. Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London, UK.
- Heady, H. F., editor. 1988. *The Vale Rangeland rehabilitation program: an evaluation*. PNW-RB-157. U.S. Forest Service, Pacific Northwest Station and U.S. Department of the Interior, Bureau of Land Management, USA.
- Hill, M. O. 1979. TWINSPLAN-A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University Press, Ithaca, New York, USA.
- Hironaka, M., M. A. Fosberg, and A. H. Winward. 1983. Sagebrush-grass habitat types of southern Idaho. Forest, Wildlife, and Range Experiment Station Bulletin 35. University of Idaho Press, Moscow, Idaho, USA.
- Huntsinger, L., and J. W. Bartolome. 1992. Ecological dynamics of *Quercus* dominated woodlands in California and southern Spain: a state-transition model. *Vegetation* 99–100:299–305.
- Jenny, H. 1961. Derivation of state factor equations of soils and ecosystems. *Proceedings of the Soil Science Society of America* 25:385–388.
- Jones, R. M. 1992. Resting from grazing to reverse changes in sown pasture composition: application of the state and transition model. *Tropical Grasslands* 26:97–99.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- Lovell, B. B. 1980. Soil survey of Malheur County, Oregon, northeastern part. U.S. Department of Agriculture. USDA Soil Conservation Service, in cooperation with Oregon Agricultural Experiment Station. National Cooperative Soil Survey, Washington, D.C., USA.
- Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetation* 43:5–21.
- Norusis, M. J. 1993. SPSS for Windows. Version 6.0. Chicago, Illinois, USA.
- Pienseisel, R. L. 1938. Changes in weedy plant cover on cleared sagebrush land and their probable causes. U.S. Department of Agriculture, Technical Bulletin 654, Washington, D.C., USA.
- . 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. *Ecology* 32:53–72.
- Schacht, W. H. 1993. A new approach for range condition assessment is needed. *Rangelands* 15:245–247.
- Taylor, J., N. MacLeod, and A. Ash. 1994. State and transition models: bringing research, extension and management together. *Tropical Grasslands* 28:193–194.
- West, N., K. H. Rea, and R. O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. *Ecology* 60:376–388.
- Westoby, M., B. H. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- Whalley, R. D. B. 1994. State and transition models for rangelands. 1. Successional theory and vegetation change. *Tropical Grasslands* 28:195–205.
- Young, J. A., R. A. Evans, and P. T. Tueller. 1976. Great Basin plant communities—pristine and grazed. Pages 186–216 in *Holocene environmental change in the Great Basin*. R. Elston, editor. Nevada Archeological Survey Research Paper Number 5.