

A state-transition approach to understanding nonequilibrium plant community dynamics in Californian grasslands

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Abstract

Using a spatially and temporally replicated dataset, we built a state-transition model for Californian grasslands. We delineated vegetation states by allowing TWINSPAN to classify plot-level ($\approx 10 \text{ m}^2$) species cover data collected over 3 to 5 consecutive years on 9 sites in an experimental design that incorporated 5 residual dry matter (RDM) treatment levels representative of the range of grazing management prescriptions for this type (0, 280, 560, 841, 1121 kg RDM-ha⁻¹). We identified and described a new California annual grassland subtype—Coast Range Grassland—that is distinct from the previously described Coastal Prairie and Valley Grassland. Classification and regression tree (CART) analysis correctly classified 63% of TWINSPAN-created vegetation transitions among states with interactions among site and monthly climate averages as the main driving factors. The RDM variable (a surrogate for grazing intensity) was important in model refinement, but only at a few site \times year combinations and predictions were rarely attributable to the grazing intensity gradient. The equilibrium-based conclusion that grazing intensity manipulation creates distinctive community structure was restricted in application to a few sites. The results suggest that equilibrium models may be appropriate for predicting system productivity but not the community composition, details of which require a nonequilibrium approach. The non-equilibrium state-transition model offers considerable potential for improving the development and testing of hypotheses about vegetation change and the limitations of management controls, but will require relatively large spatially and temporally replicated datasets.

Introduction

In arid and semiarid ecosystems, vegetation tends to be highly responsive to short-term environmental fluctuations (Wiegand and Milton 1996) and relatively unresponsive to grazing (Ellis and Swift 1988; Behnke and Scoones 1993). Because stochastic fluctuations overwhelm grazing effects on community composition (Stafford Smith 1996; Perevolotsky and Seligman 1998), an equilibrium state rarely has time to become established; community structure and change are seldom attributable to biotic interactions. This is the primary cause for the failure of grazing management in nonequilibrium systems (Oba et al. 2000). Management practices can still work, but they

need to be developed and evaluated within the framework of nonequilibrium dynamics (for a review see Illius and O'Connor (1999)).

Wiens (1984) listed characteristics of ecosystems at either end of an equilibrium – nonequilibrium continuum indicating that nonequilibrium systems should display 1) biotic decoupling, 2) abiotic limitation, and 3) density independence while equilibrium systems should show 1) biotic interactions, 2) resource limitation, and 3) density dependence. In summary, equilibrium-type communities are predominantly shaped by plant-plant and plant-animal interactions while nonequilibrium systems are dominated by environmental factors like weather. Wiens stressed that ecosystems are typically distributed along this continuum

with arid and semiarid rangelands clustering towards nonequilibrium. However, any given system may exhibit nonequilibrium traits at some observational or organizational scales, but equilibrium characteristics at other scales. Fernandez-Gimenez and Allen-Diaz (1999) demonstrated that on Mongolian rangelands different vegetation parameters (e.g., cover, biomass, richness, etc.) fell out along Wiens' continuum at different places – some more closely resembled equilibrium dynamics, decreasing with increasing grazing intensity – while others apparently did not respond to the grazing gradient. Moreover, it is plausible that equilibrium dynamics are evident at a given spatial or temporal resolution, while nonequilibrium dynamics are manifested at alternative levels of organization. Thus, an evaluation of models describing vegetation dynamics must explicitly consider the spatial and temporal scales under examination (Bartolome 1989a).

State-transition models

The rejection of equilibrium models for arid and semiarid rangelands has left a void where the theoretical underpinnings of climax-succession-retrogression models previously provided the context for management models such as the range condition model (Dyksterhuis 1949). State-transition (S-T) models have been proposed to fill this void by providing an organizational framework for cataloging and quantifying hypotheses about temporal variations in community composition (Westoby et al. 1989). They are simple box-and-arrow diagrams that can be theoretical, empirical, or some mixture of both (Archer 1996). Their utility derives from their 1) generalizability to a range of community dynamics, e.g., the equilibrium – nonequilibrium continuum, 2) ability to incorporate ecosystem parameters other than plant species composition, e.g., soil characteristics, economic considerations, climate change scenarios, and 3) applicability to any desired level of detail or scale, i.e., the end-user defines which is useful for management or understanding.

The most important aspect of S-T models as applied to vegetation change is their ability to explicitly incorporate site × time interactions that may modify community responses to environmental or managerial inputs. This is the major shortcoming of equilibrium-type models; they tend to predict similar responses to proximate factors such as grazing or fire regardless of larger scale, distal controllers like weather.

When developed as a model of vegetation dynamics, we strongly believe that the S-T model should explicitly define spatial and temporal scale, should not assume symmetry and predictability of successional change, and should be driven by objective community description and classification. Attempts to apply the S-T model to rangeland community dynamics have met with limited success primarily because, with one exception (Allen-Diaz and Bartolome 1998), the model has still used equilibrium model assumptions (Laycock 1991), a priori notions of community types (George et al. 1992), or coarse-scale vegetation data that offered little utility to site managers (Hunt-singer and Bartolome 1992).

Californian grasslands

Temporal variability – Species composition in Californian grasslands fluctuates seasonally and annually at multiple scales (Heady 1956). These large inter- and intra-annual fluctuations obscure patterns of longer-term and directional changes in the community and constrain the precision of equilibrium-based predictions about succession (Bartolome 1989a). Variations of species composition and biomass in annual-dominated Californian grasslands have long been known to be associated with weather patterns (Talbot et al. 1939; Bentley and Talbot 1948; Pitt and Heady 1978). The intraannual pattern of biomass increase over the growing season has been well described in numerous publications because of the effects on livestock production (see Heady et al. (1992)). Intraannual changes in species composition are less well described (Heady 1958; Ratliff and Heady 1962; Bartolome 1979). Composition at peak standing crop is categorized as “grass”, “filaree”, or “clover” depending on dominant cover of either annual grasses or *Erodium* spp. and the relative contribution of annual legumes. Although it is widely accepted that weather patterns influence temporal variability in species composition, the association is poorly documented (Pitt and Heady 1978) and is properly linked neither to a predictive model nor to controlling factors (Bartolome 1989a).

Spatial variability – Spatial variability in Californian grasslands has been treated on a regional basis as being comprised of 2 main subtypes, Valley Grassland and Coastal Prairie (Heady 1977; Heady et al. 1992). McClaran and Bartolome (1989) further stratified the herbaceous understory component of Californian oak woodlands finding significant species differences between open grassland and oak canopy under-

story plots. Open grassland tended to support greater annual grass cover while oak canopies maintained more forb cover. Others have examined this dichotomy on a site basis (Saenz and Sawyer 1986; Jackson et al. 1990; Maranon and Bartolome 1993, 1994) always showing relatively large compositional differences.

Management – The absence of an effective model describing changes in community structure has hampered good predictions of the impact of grazing or other environmental factors on local species composition. Managers and researchers use residual dry matter (RDM) as a surrogate for grazing effects (George et al. 1985) and accept very broad generalizations about grazing impacts on composition. At a northern California site, Heady (1956) examined the effects of RDM manipulation on species composition at the spatial scale of the plot ($\approx 10 \text{ m}^2$), where livestock management is most likely to influence community structure (Bartolome 1984, 1989a). Heady (1956) found that the annual grass *Bromus hordeaceus* was dominant with greater RDM, while intermediate RDM levels resulted in a greater proportion of annual legumes (mostly *Medicago polymorpha*). Oddly, RDM treatment levels had no interpretable effect on *Erodium botrys* (filaree) cover. That study was later expanded to include 9 sites throughout the state from which Bartolome et al. (1980) reported the impacts of RDM on forage production, but not composition.

Menke (1989) reviewed the effects of management on annual grassland productivity and composition stating that many studies have shown that underutilized forage (i.e., light to no grazed range) tends to favor grasses over shorter stature legumes resulting in a depauperate or lost legume component. If annual grassland behaves as predicted under an equilibrium model, then livestock grazing management practices should be effective. Unfortunately, the examples of successful management controls are all from annual systems at the most productive and wettest end of the Mediterranean climatic regime's range, hence, they more closely resembled equilibrium type responses (Bartolome 1993).

Some believe that reducing or removing livestock use is necessary to check alien species invasions (Belsky and Gelbard 2000) in order to return California's grasslands to perennial grass dominance; a putative vegetation state that livestock overgrazing is thought to have demolished (Heady 1977; Bartolome et al. 1986; Heady et al. 1992) but see Hamilton (1998). These views all fall under the equilibrium rubric, that

the plant community can be re-structured via grazing intensity manipulation.

Californian grassland community structure changes rapidly and unpredictably over small spatial and short temporal scales (Bartolome 1989a) and is subject to frequent disturbance (Heady 1977; Hobbs and Mooney 1995), therefore S-T models that are able to incorporate nonequilibrium dynamics at the correct spatial and temporal scales should be more useful for understanding vegetation change or the lack thereof. Equilibrium-based models have proven adequate for managing forage quantities for livestock (Bartolome et al. 1980; Clawson et al. 1982; George et al. 1985), but have been ineffective for managing forage quality (i.e., species composition) or for predicting directional change in Californian grasslands (Bartolome 1993).

Objectives

We used an existing robust dataset to build a S-T model whose vegetation states objectively place interannual plant community variability at the proper scale to evaluate the importance of environmental and management controls. We hypothesized that plant community dynamics would respond more to environmental factors than simulated grazing intensity simulation manipulations of residual dry matter (RDM). Because transitions among vegetation states were numerous (we found 70 transition types), we show how the use of classification and regression trees (CART) can help uncover important site \times time interactions allowing for more robust assessment of the role grazing intensity plays in driving transitions among vegetation states.

Methods

Study sites

We used herbaceous cover data collected between 1968 and 1973 at 9 California sites located along a latitudinal gradient ranging from 35 to 40° N (Figure 1). Site names are given in all capital letters throughout this paper. Figure 1 also shows the timing of sampling at each site. UC Integrated Pest Management weather stations nearest to each of our sites were identified and daily precipitation and temperature data were downloaded from the world wide web (<http://axp.ipm.ucdavis.edu>). Monthly averages were

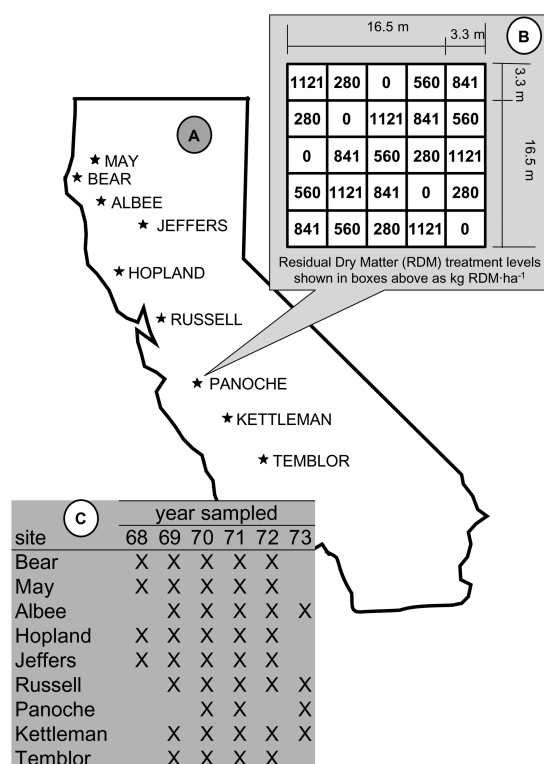


Figure 1. Study site locations (A), Latin square experimental design implemented at each site (B), and sampling date matrix showing sampled years for each site (C).

calculated for minimum and maximum temperature and precipitation for use as site-weather proxies (Table 1). Further transformations of weather variables for potential and actual evapotranspiration were calculated using the method of Thornthwaite et al. (1957).

California's climate is Mediterranean, characterized by hot dry summers and cool wet winters. The annual species that dominate Californian grasslands possess phenologies that are well adapted to this climatic regime. Annual species mainly follow the pattern of autumn germination, slow winter growth, and rapid spring growth, bolt, and seed set (George et al. 1985). These plants are mostly dead by June 1 each year, except for a few late-season annuals that exist into the dry summer months.

Soils of the Californian Coast Ranges are derived from sedimentary oceanic crust comprising the Franciscan Melange complex (Norris and Webb 1976). These soils are prone to erosion due to their unconsolidated nature and are often intruded by serpentinite (Bartolome 1989b).

Grazing simulation treatments and vegetation sampling

A 5 × 5 Latin square experimental design was established at each site. Treatments were applied by hand-clipping 3.3 × 3.3 m (10.89 m²) plots to 5 residual dry matter (RDM) treatment-levels (0, 280, 560, 841, and 1121 kg RDM·ha⁻¹; Figure 1). Each plot received the same treatment each September throughout the study period. After hand-clipping to approximately the desired level, two 30 × 30 cm samples were clipped to ground level and weighed. Addition of material saved from each clipping or subtraction of mulch (RDM) resulted in the desired residue. Care was taken to avoid disturbing the soil surface during clipping; thus, the treatment levels include a small but unquantified additional RDM amount. Once mulch manipulations were made, a 30 × 30-cm sample was returned to the laboratory to determine the oven-dry weight of RDM applied. This amount was usually ± 25 kg·ha⁻¹ of the prescribed treatment.

Clipping and grazing had similar effects on annual grassland biomass production and composition in previous studies (Bartolome et al. 1980; Bartolome and McClaran 1992) on California's north coast. For this study, clipping and mulch treatments were applied in late summer-early autumn because past research had shown that the quantity of mulch residue remaining at this period was of primary importance in determining ensuing year's productivity and in some cases composition (Heady 1956, 1965). However, herbivory is a more gradual process than our single clipping treatment with potentially significant effects on soil compaction and erosion at high grazing intensities. All sites were historically grazed by cattle or sheep at moderate intensities, but were excluded from livestock at the study's inception. More detailed descriptions of historical grazing regimes were not available.

Absolute percent cover was calculated as double the number of first-foliar-hits out of 50 sharpened points lowered through a 1-m long, 10-point frame that was randomly located 5 × on each 10.89-m² plot (Heady et al. 1959). Species cover data were recorded in plot centers where plant biomass samples were never clipped.

Data analyses

Species names were updated according to Hickman (1993). Plant species groupings were identified with

Table 1. Study site locations and UC Integrated Pest Management weather station proxies.

Site	Latitude (N)	Longitude (W)	Elevation (m)	IPM station code	Latitude (N)	Longitude (W)	Elevation (m)
BEAR	40° 30'	124° 06'	670	RICHGRV.C	40° 48'	124° 10'	500
MAY	40 25	123 48	640	RICHGRV.C	40 48	124 10	500
ALBEE	40 20	123 47	550	RICHGRV.C	40 02	124 10	500
HOPLAND	39 00	123 07	305	UKIAH.C	39 09	123 47	623
JEFFERS	39 55	122 33	365	ORLAND.C	39 45	123 12	254
RUSSELL	37 50	122 07	215	ANTIOCH.C	37 59	122 12	60
PANOCHÉ	36 40	120 51	455	FIVE_PTS.C	36 22	121 44	285
KETTLEMAN	36 05	120 08	215	COALINGA.C	36 09	120 09	670
TEMBLOR	35 00	119 41	760	MARICOPA.C	35 05	120 21	675

the classification program twinspan (Hill 1979). TWINSpan uses cover classes delimited according to *cut-levels* that specify class ranges. Default cut-levels were doubled to minimize leveraging by rare species resulting in absolute cover classes of 1 to 4%, 5 to 10%, 11 to 20%, 21 to 40%, and > 40%. TWINSpan uses each cover class \times species combination to create *pseudospecies*, e.g., *Bromus hordeaceus* 5-10% is considered a different taxon than *B. hordeaceus* 11–20%. Pseudospecies are then used to drive a divisive classification, each level of which is the result of bifurcating groups produced by previous divisions. The relative strength of a division, hence the resultant 2 groups, was denoted by an eigenvalue (λ) showing increasing strength from 0.00 to 1.00 (Gauch 1982). Eigenvalues approximate the percentage of pseudospecies not common to each group, i.e., $\lambda = 1$ denotes 2 groups with no pseudospecies overlap (Jongman et al. 1995). Eigenvalues provide an objective criterion for determining the merit of each division. Subjectivity is introduced into this analysis when the researcher decides upon some critical λ . Published λ 's vary widely and depend upon the research question. Ter Steege et al. (1993) developed a plant community classification for South American tropical rainforest with λ 's ranging from 0.53 to 0.24 while Bork et al. (1997) determined important plant groupings for Lower Boreal Mixedwood and Aspen Parkland regions with λ 's from 0.24 to 0.16. We initially set a critical λ value of 0.20 based on these and other published studies. However, interesting divisions usually involving annual legume pseudospecies were apparent below this level. Because of our interest in the “grass – clover – filaree” trichotomy and the role of annual legumes in this model, we deemed these divisions important enough to re-establish λ at

0.15 in order to include more subtle compositional variability.

Vegetation state nomenclature was based on compositional distinction; not necessarily species dominance. Vegetation state names are denoted in bold and were created using the 1st and 2nd letters from both species genus and specific epithet or the first 3 to 6 genus letters where species distinctions were not made, i.e., *Aira caryophyllea*=**Aica**, *Trifolium* spp.=**Trifol**, etc. Transitions are denoted by an arrow (\rightarrow) inserted between the vegetation state of the previous year and that of the year noted, e.g., “...the transition **Aica** \rightarrow **Trifol** dominated in 1969...” indicates the state **Aica** dominated a plot in 1968 while the state **Trifol** dominated the same plot in 1969. Table 2 lists codes and binomials for all species cited herein, i.e., this is not a complete species list for the study. Transitions among states were inferred from interannual species composition changes on a given plot.

Classification and regression tree (CART) analyses (Breiman 1984) were performed using transitions among vegetation states derived from TWINSpan output as the categorical response variable. Predictor variables included in the analysis were site, year, RDM, monthly mean daily minimum temperature, mean daily maximum temperature, mean daily average temperature, total precipitation, and potential and actual evapotranspiration. Response variable data from a given year were coupled with predictor variables from July of the previous year through June of that given year creating a July-June weather year.

CART models have been used extensively in the social sciences and have recently been applied in the medical sciences (Dobbertin and Biging 1998) as well as ecology (Andersen et al. 2000). S-plus (1993) is computer software that handles CART models. S-plus

Table 2. List of taxa and their codes found in text, tables, and figures

Code	Taxon	Authority
Aica	<i>Aira caryophylla</i>	L.
Amte	<i>Amsinckia tessellata</i>	A. Gray
Brca	<i>Bromus carinatus</i>	Hook. & Arn.
Brdi	<i>Bromus diandrus</i>	Roth
Brho	<i>Bromus hordeaceus</i>	L.
Brma	<i>Bromus madritensis</i>	L.
Ceso	<i>Centaurea solstitialis</i>	L.
Cyec	<i>Cynosurus echinatus</i>	L.
Daca	<i>Danthonia californica</i>	Bolander
Elgl	<i>Elymus glaucus</i>	Buckley
Erbo	<i>Erodium botrys</i>	(Cav.) Bertol.
Erci	<i>Erodium cicutarium</i>	(L.) L'Her.
Hype	<i>Hypericum perforatum</i>	L.
Hyra	<i>Hypochaeris radicata</i>	L.
Letr	<i>Leymus triticoides</i>	(Buckley) Pilger
Lomu	<i>Lolium multiflorum</i>	Lam.
Lowr	<i>Lotus wrangelianus</i>	Fischer & C. Meyer
Lubi	<i>Lupinus bicolor</i>	Lindley
Mepo	<i>Medicago polymorpha</i>	L.
Plno	<i>Plagiobothrys nothofulvus</i>	(A. Gray) A. Gray
Ruac	<i>Rumex acetosella</i>	L.
Taca	<i>Taeniatherum caput-medusae</i>	(L.) Nevski
Trifol	<i>Trifolium</i> spp.	–
Viam	<i>Vicia americana</i>	Willd.
Vulpia	<i>Vulpia</i> spp.	–

cites the following advantages of tree-based CART models over both linear and additive models:

They are,

- easy to interpret when the predictors are a mix of continuous and categorical variables.
- invariant to monotonic re-expressions of predictor variables (i.e., multicollinearity not a problem).
- adept at treating missing values.
- adept at capturing nonadditive behavior.

They also,

- allow more general interactions between predictor variables (i.e., they do not assume a particular multiplicative form such as linear combinations).
- model categorical response variables with more than 2 levels (cf. logistic regression).

The consequence of the 2nd item in the list above, absence of multicollinearity problems, made CART particularly attractive for our situation which included 63 potentially correlated predictor variables. Because

CART uses a recursive partitioning algorithm that essentially treats each predictor variable separately (i.e., not linear combinations), the total number of predictors entered into the analysis is inconsequential. The true value of CART analyses lies in its ability to combine both categorical and continuous predictors with a single categorical response variable. Overspecification of the model was avoided by pruning terminal nodes of the tree where a variable predicted identical vegetation states. Our final CART model was assessed by examining the misclassification rate associated with the number of tree nodes incorporated into the model.

Where RDM was deemed important by CART, we further explored functional group and species responses to the gradient with Latin square ANOVA. Significant differences were determined at a 95% confidence level for each model. Mean separation was performed with non-simultaneous, Fisher's LSD with a 5% comparison-wise error rate.

Results

Delimiting vegetation states

The finest TWINSpan classification level used (usually level 4 with λ 's ≥ 0.15) produced 23 vegetation states indicative of plot-level temporal variability, i.e., the same plot classified differently from 1 year to the next. At this classification level, we began to observe the waxing and waning of annual legume cover as important drivers of the classification, i.e., indicator pseudospecies. This was also the 1st level at which various plots within sites were regularly classified differently indicating plot-level spatial variability.

The initial TWINSpan division ($\lambda = 0.83$) separated the 3 southernmost sites (PANOCHE, KETTLEMAN, and TEMPLOR) from all northern sites based on *Erodium cicutarium* and *Bromus madritensis* endemism in the south. This southern group of sites comprised the Valley Grassland, which also contained a significant *Vulpia* spp. component. The remaining 6 northern sites were then split based on presence of the perennial grasses *Danthonia californica* and *Bromus carinatus* co-dominant with *Cynosurus echinatus* ($\lambda = 0.69$). This grouping comprised the Coastal Prairie consisting of most plots from the 3 northernmost sites (BEAR, MAY, and ALBEE).

Northern sites not classified as Coastal Prairie were distinguished by *Erodium botrys* presence. This

grouping encompassed such a large number of plots and sites, and was separated with such a high λ (0.69) that we determined it as representative of a 3rd Californian grassland subtype, Coast Range Grassland, that is usually grouped into the Coastal Prairie subtype (Heady et al. 1992). The dominant grasses, found at Coast Range Grassland sites (HOPLAND, JEFFERS, and RUSSELL) were *Vulpia* spp. (mostly *V. myuros* C. Gmelin) and *Bromus hordeaceus*. Coastal Prairie sites contained little or no *Erodium* while Coast Range Grassland sites maintained limited perennial grass cover. Annual clover species (*Trifolium* spp.) were interspersed among plots and years for Coast Range Grassland but were not found on Coastal Prairie. The ALBEE site was the only site with a subset of plots classified into Coast Range Grassland with the remainder grouped as Coastal Prairie.

It is important to note the limitations of TWINSPAN arising from its hierarchical symmetry. The northern sites split was a 2nd-level division whose resulting groups we have elevated to equal status with the initial N-S split. We based this decision on the exceptionally high λ of 0.69. The only other instances of λ 's > 0.30 were the splits setting apart RUSSELL for *Centaurea solstitialis* invasion ($\lambda = 0.56$) and the *Taeniatherum caput-medusae* – invaded ALBEE plots ($\lambda = 0.53$). Final vegetation state delimitations are described in Table 3.

Assessing transitions

The typical S-T model development protocol is to catalog transitions observed among states once they have been defined (Westoby et al. 1989). However, we observed 70 different transition types (Figure 2) making this scheme rather burdensome. Instead, we employed classification and regression tree (CART) analysis to uncover potentially important relationships among the plant community and a suite of environmental and management factors.

Our CART model (Figure 3) accurately discriminated among 63% of the plot-level vegetation transitions. Figure 4 shows the reduction in misclassification as the number of terminal nodes increased, e.g., our model included 34 terminal nodes corresponding to a 37% misclassification rate. It was clear from Figure 3 that *location* followed by *year* were the most important predictors of vegetation transition. The 1st predictor variable included in the CART model was site. Next, weather variables that essentially continued separating sites, and then years within sites, were

important discriminators. For example, 1969 HOPLAND plots were distinguished from 1970 through 1972 HOPLAND plots based on January maximum temperatures (JANMAT) < 12.8 °C where the transition **Brdi** → **Trifol** dominated 1969 and **Trifol** → **Aica** dominated 1970 through 1972. This indicated that not all 1970 or 1971 plots transitioned, but that in each year, the majority of those remaining *Trifolium*-dominant transitioned into the grass dominated **Aica** state.

In some cases, vegetation transitions within regions and/or sites were further predicted based on RDM treatment-levels (Figure 3). In only 2 instances did the RDM gradient appear meaningful, KETTLEMAN 1973 and BEAR 1970. KETTLEMAN 1972 transitions were all towards vegetation state **Erci** regardless of the 1971 vegetation state. Though these various transitions were all predicted by the RDM variate, no trend along the experimental RDM gradient was evident indicating that weather, specifically the combination of relatively poor growing conditions in both autumn and spring (OCTMIT < 8.95 °C, DECPET < 11.6 mm, and MARPPT < 2.5 mm), drove all of these transitions. At KETTLEMAN 1973, all plots except the 1121 kg-ha⁻¹ (highest RDM treatment level) plots transitioned from **Erci** vegetation state to **Lowr.Erci**. The 1121 kg-ha⁻¹ RDM treatment plots at KETTLEMAN 1973 underwent **Erci** → **Lowr.Vulpia** transition showing that the prevailing climate determined the legume component while the highest RDM treatment-level conferred a grass advantage over filaree.

At BEAR 1970, lower RDM levels (0 and 280) appeared to facilitate *Hypericum perforatum* invasion, as 100% of the plots under these conditions (i.e., site = BEAR, year = 1970, RDM = 0 & 280) underwent the transition **Daca.Hyra** → **Daca.Hype**. Curiously, 60% of the plots from the highest RDM level from the same site × year combination made the same transition. Only moderate RDM (560 & 841) plots were spared this invasion in 1970.

CART incorporated RDM into the classification tree in several other instances. However, in these situations transitions being predicted were either all towards the same state (as in the KETTLEMAN 1972 example cited above) or fell out along the RDM gradient in an uninterpretable way. For example, at RUSSELL 1969, 1970, and 1973; RDM levels 280 and 841 predicted a **Ceso.Mepo** → **Lomu.Lubi** transition while RDM levels 0, 560, and 1121 (the lowest, middle, and highest levels, respectively) predicted

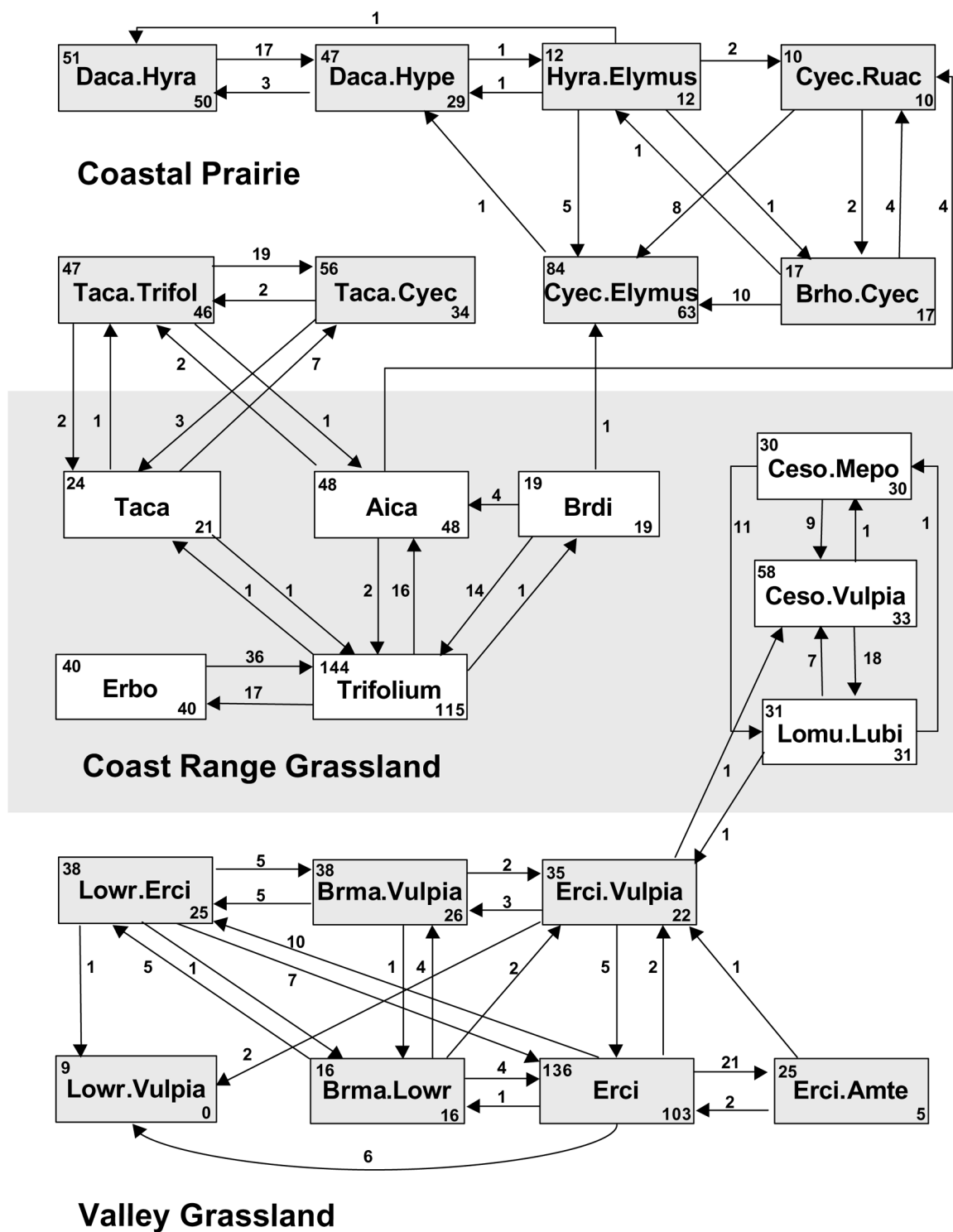


Figure 2. State-transition model for Californian grasslands. Number of plots with observed state shown inside boxes (upper left = all years, lower right = all but last year sampled since transitions from last year were unknown). Transition occurrences are given adjacent to arrows.

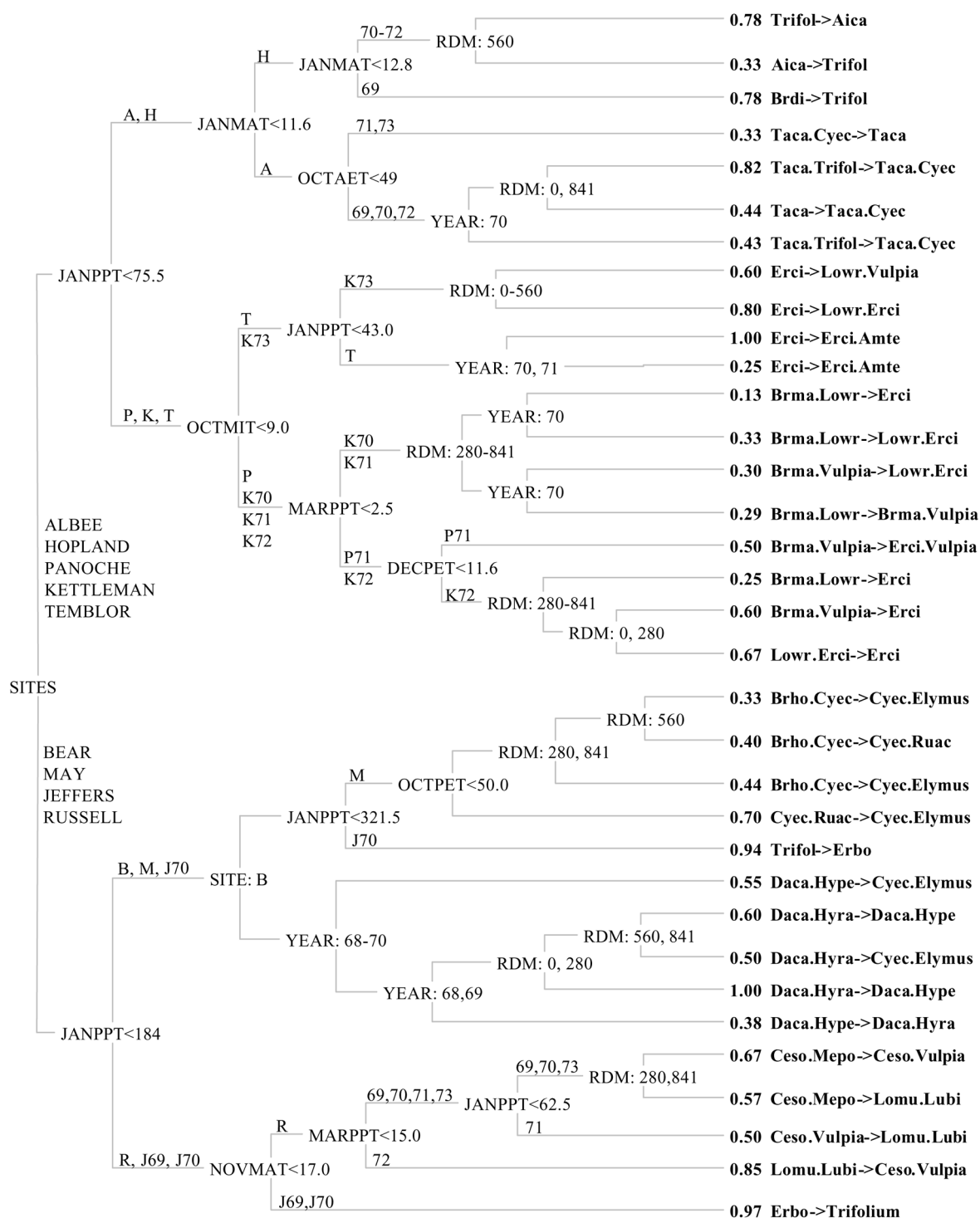


Figure 3. Classification and regression tree analysis (CART) results. If logical statement at node is true, follow lower path to daughter node for next logical statement until terminal nodes are reached. Sites and years found exclusively under given conditions are shown along pathways to nodes, e.g., K72 = KETTLEMAN 1972. Terminal nodes show probability that following transition was observed given preceding conditions. Predictor variables were: site, year, RDM, total monthly precipitation (mm; e.g., JANPPT), average monthly minimum and maximum temperature (°C; e.g., OCTMIT and NOVMAE), total monthly potential and actual evapotranspiration (mm; e.g., DECPET and OCTAET).

Table 3. Vegetation states, number of plots classified into each state, and species richness within each state. Shown below each state are the absolute-cover classes (%) used to distinguish and define states.

State:	Daca.Hyra	Daca.Hype	Hyra.Elymus	Cyec.Ruac	Brho.Cyec	Cyec.Elymus	Taca.Cyec	Taca.Trifol
Sites where state occurred:	BEAR	BEAR	MAY	MAY	MAY	MAY	ALBEE	ALBEE
n (# plots in this state):	51	47	12	10	17	84	56	47
spp richness:	29	28	23	21	27	33	26	30
Key species (% cover classes):	11-40 DACA	0-40 DACA	6-20 HYRA	11-40 CYEC	6-40 BRHO	>20 CYEC	20-40 TACA	11-40 TACA
	0-20 HYRA	6-40 HYPE	0-10 ELGL	6-10 RUAC	6-20 CYEC	0-10 ELGL	11-40 AICA	0-10 TRIFOLIUM
	1-10 BRCA	11-40 BRCA	0-10 LETR	0-10 AICA	0-10 LETR	0-10 LETR	0-40 CYEC	6-20 DACA
	1-10 CYEC	11-40 CYEC	6-20 CYEC		0-10 DACA	0-10 DACA	6-20 BRHO	0-10 ERBO
	0-10 VULP	0-10 AICA	0-20 BRHO		0-10 LOAM	0-10 LOAM	6-20 VULP	0-10 AICA
	0-5 AICA	0-10 VULPIA			0-10 VIAM	0-10 VIAM	0-20 DACA	0-10 BRHO
	0 HYPE	0 HYRA			0 BRHO	0 BRHO	0-10 ERBO	0-10 VULPIA
							0 TRIFOLIUM	0 TRIFOLIUM
State:	Brdi	Aica	Taca	Trifolium	Erbo	Ceso.Vulpia	Lomu.Lubi	Ceso.Mepo
Sites where state occurred:	HOPLAND	HOPLAND	HOPLAND	HOPLAND	HOPLAND	RUSSELL	RUSSELL	RUSSELL
n (# plots in this state):	16	47	25	144	40	61	31	30
spp richness:	20	27	27	34	16	18	14	17
Key species (% cover classes):	1-20 BRDI	0-10 AICA	6-40 TACA	0-20 TRIFOLIUM	6-40 ERBO	21-40 CESO	6-40 LOMU	11-40 CESO
	1-20 BRHO	11-20 ERBO	6-20 ERBO	10-40 VULPIA	6-10 VULPIA	21-40 VULPIA	6-20 LUBI	6-20 MEPO
	1-10 ERBO	0-10 TRIFOLIUM	0-20 BRHO	10-40 ERBO	1-20 PLNO	1-40 BRHO	11-40 VULPIA	6-20 LOMU
		0-10 BRHO	0-10 AICA	0-10 LUBI	0 TRIFOLIUM	0-10 LOMU	6-10 BRHO	1-20 VULPIA
		0-20 HYGL	0-10 VULP	0-10 BRHO		<10 LUBI	0-10 BRDI	1-20 BRHO
			0-10 TRIFOLIUM			<5 MEPO	0-10 VIAM	0-10 BRDI
							0-10 MEPO	0-5 LUBI
							>6 CESO	

Table 3. Vegetation states, number of plots classified into each state, and species richness within each state. Shown below each state are the absolute-cover classes (%) used to distinguish and define states.

State:	Erci.Vulpia	Brma.Vulpia	Brma.Lowr	Lowr.Vulpia	Lowr.Erci	Erci.Amte	Erci
Sites where state occurred:	PANOCHÉ KETTLEMAN TEMBLOR	PANOCHÉ KETTLEMAN TEMBLOR	PANOCHÉ KETTLEMAN TEMBLOR	PANOCHÉ KETTLEMAN TEMBLOR	PANOCHÉ KETTLEMAN TEMBLOR	PANOCHÉ KETTLEMAN TEMBLOR	PANOCHÉ KETTLEMAN TEMBLOR
n (# plots in this state):	35	38	16	9	38	25	140
spp richness:	5	11	13	9	14	5	15
Key species (% cover classes):	6–20 VULPIA 11–20 ERCI 1–10 BRMA 0 LOWR	11–20 BRMA 6–20 VULPIA 6–10 ERCI 0 LOWR	11–40 BRMA 1–10 LOWR 6–20 ERCI 0–5 VULPIA	21–40 LOWR 11–20 VULPIA 6–10 ERCI 0–10 BRMA	1–10 LOWR 6–20 ERCI 1–10 VULPIA	1–10 BRMA 1–10 AMTE 1–10 ERCI	11–40 ERCI 0–10 BRMA 0–5 VULPIA

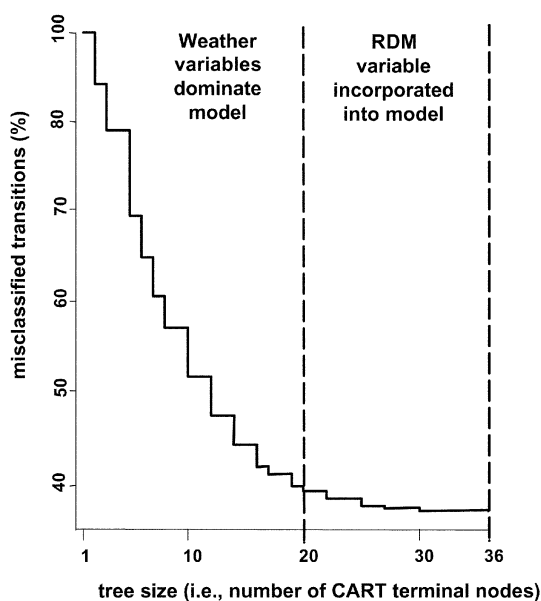


Figure 4. Misclassified plots as a function of CART model tree-size (number of terminal nodes). Weather variables were deemed most important factors in tree construction as their incorporation reduced the transition misclassification to 43%. Incorporation of the RDM variable resulted in a further reduction of 6%, i.e., overall model misclassification of 37%.

Ceso.Mepo → **Ceso.Vulpia**. Reasons why these transitions were distributed among RDM treatments in this manner were not evident.

Given the apparent importance of RDM at KETTLEMAN 1973 and BEAR 1970, we assessed its effects on several functional groups and species at these settings using Latin square ANOVA. Annual grasses and legumes followed similar trends at KETTLEMAN 1973, increasing with increased RDM (Table 4). At the species level, *Lotus wrangelianus* was the taxon accounting for this positive relationship while *Vulpia* spp. were the annual grasses responding to RDM. Although CART indicated BEAR 1970 as potentially responding to RDM treatments, ANOVA showed no significant differences in *H. perforatum* ($P = 0.43$) cover across these treatment levels.

Discussion

State-transition approach

Our S-T modeling approach provided more detailed descriptions of normal variability and its causes within the Californian grassland than have been pre-

viously reported. McClaran and Bartolome (1989) described regional differences in herbaceous understory of oaks at 5 sites but did not treat temporal variability. George et al. (1988) developed a model that predicted species composition from the variable *degree-days*, a combination of temperature and time during the autumn germination period, but this effort did not take a community perspective as we have done.

Our use of TWINSpan as the classification tool followed by CART analyses on the defined transitions is only one of many possible techniques that can be applied to uncover patterns and identify states and transitions in these types of data. However, we feel strongly that S-T approaches should use some quantitative, rule-based classification scheme to derive vegetation states. Reliance on preconceived notions of stable plant communities are likely to lead to oversimplified states and/or overlooked transitions (Allen-Diaz and Bartolome 1998).

CART explicitly incorporates interactions between mixtures of continuous and categorical variables. This ability allowed us to separate several site × time × treatment interactions that may have otherwise been masked by parametric techniques that build linear combinations of predictor variables. Distal controlling variables like climate and geography were accounted for before the effects of more proximal variables like RDM were addressed. Applying CART within sites or other strata would provide no extra power or benefit over applying it to the entire dataset because the algorithm finds the most important grouping variables first, then examines variation within these groupings, i.e., *post hoc* stratification.

Our dataset spanned 5 years per site (3 for Valley Grassland sites) and only contains species composition at peak standing crop, limiting temporal scale observations to interannual patterns over a 5-year maximum for each site. Intraannual or seasonal sampling of the plant community would result in even more transient vegetation states. If this level of detail is necessary to identify functionally significant states and transitions, the utility for management is questionable.

It was apparent that a longer-term dataset is necessary to fully describe invasion dynamics for this system. Two of the 3 invasion scenarios inferred, *Centaurea solstitialis* and *Taeniatherum caput-medusae* had either already occurred or not fully run their course over our 5-year sampling period so that the actual sequence of the invasion was not documented. Hence, we were not able to observe transitions into

Table 4. Fisher's LSD non-simultaneous mean separation (5% comparison-wise error rate) for significant response variables from KETTLEMAN 1973. Significant differences denoted by differing letters among treatment means within rows. Trend column indicates direction of increasing cover with increasing RDM treatment levels

Variable	RDM (kg·ha ⁻¹)					trend
	0	280	560	841	1121	
Annual legumes	0.4 (a)	4.8 (a)	10.4 (b)	15.6 (c)	15.6 (c)	->
<i>Lotus wrangelianus</i>	0.4 (a)	4.8 (a)	10.4 (b)	15.6 (c)	15.6 (c)	->
Annual grasses	1.6 (a)	8.0 (a)	8.0 (b)	14.0 (c)	16.8 (c)	->
<i>Vulpia</i> spp.	0.4 (a)	4.8 (b)	7.6 (b)	10.0 (b)	14.0 (b)	->

the vegetation states dominated by these species. However, we did observe the *Hypericum perforatum* invasion of 1970 at BEAR. A moderate level of RDM appeared to stave off invasion as the lowest and highest RDM plots were overtaken. Intermediate biomass levels may create a more species rich community thereby conferring greater resistance to invasion by reducing niche space available to invaders (Elton (1958); but see Levine (2000)). Past research has demonstrated greater species richness at intermediate biomass levels in Californian annual grassland/oak woodlands (Bartolome et al. 1980; Heady et al. 1992; Maranon and Bartolome 1993, 1994) following the model of Grime (1979) and discussed by Maranon and Garcia (1997) and Garcia et al. (1993). Because it maintains enough shade for favorable water conditions and ample mulch for nutrient cycling, while simultaneously reducing light competition from high litter levels, moderate biomass levels maintain the highest species richness levels. Maranon and Bartolome (1994) listed optimum biomass levels for maximum alpha or species diversity on Californian annual grassland/oak woodlands at 3500 to 5700 kg·ha⁻¹. In our study at BEAR 1970, species richness was uniformly distributed across the RDM gradient indicating that the above phenomenon was not at work.

Spatial scales for this study included only those ≥ 10.89 m², but we were able to reveal important features of regional community structure and the relationships between environmental and interannual variation that dominate intermediate spatial and temporal scales. The effects of grazing showed up only at the lower limits of resolution in this study suggesting that even smaller spatial and temporal scale are needed for a more complete understanding of this system.

Serendipitous vegetation subtypes

Employing a data-driven approach, S-T modeling resulted in several novel inferences about the spatial and temporal variability of Californian grasslands. This community is most commonly divided into 2 geographically separated subtypes – Valley Grassland and Coastal Prairie (Heady et al. 1992). In our dataset, an additional subtype – Coast Range Grassland – was useful for distinguishing between geographical and climatic areas containing significant amounts of perennial grass cover and annual grasslands that are without this component. As Heady et al. (1992) noted, the term *prairie* usually refers to graminoid communities dominated by perennial species while *grassland* is the more general term often reserved for annual herbaceous systems. The combination of annual grass dominance with a mesic, coastal influence is pervasive throughout the western slopes of both the northern coast range and the coast ranges S of the San Francisco Bay Area and N of the Los Angeles Basin (Sawyer and Keeler-Wolf 1995). Floristic comparison that encompasses the normal range of temporal variability of herbaceous subtypes of these 2 ranges is lacking, as are basic herbaceous subtype descriptions for Sierra Nevada foothill annual grasslands.

Our 9 plots included only parts of the Californian grassland and are representative of heavy to moderate grazing intensity. We found many more identifiable states and transitions than previously reported (George et al. 1992). Future data-driven, S-T approaches in these grasslands will undoubtedly reveal additional subtypes, either as subsets of previously described types or novel groupings. These site-specific descriptions of Californian grassland structure will be required for adequate management of composition at any level. Where no control of composition is possible, management should allow for stochastic

fluctuations with flexible, opportunistic planning (sensu Westoby et al. (1989)).

Grazing effects on community structure

Our results place the limited but significant effects of grazing (proxied by RDM manipulation) on plant community structure in a better context. On the same 9 sites we have described, Bartolome et al. (1980) demonstrated significant positive relationships between RDM and annual aboveground net primary production. That relationship was weakest at the drier Valley Grassland sites. Yet, RDM unambiguously influenced the annual community composition in our study only twice – on KETTLEMAN plots in 1973, the driest Valley Grassland site and BEAR 1970, the *H. perforatum* invasion site. Lower RDM (i.e., higher grazing intensity) translated to filaree dominated plant groupings while higher RDM resulted in grass dominance at KETTLEMAN 1973. The CART model included RDM in several other cases, but the differences in vegetation transition were never consistent along the grazing intensity gradient. We conclude that Californian grasslands exhibit nonequilibrium dynamics at the plant community organizational scale measured as species composition on a site. Grazing intensity consistently controls aboveground net productivity, which is more consistent with equilibrium dynamics.

These conclusions support the findings of Fernandez-Gimenez and Allen-Diaz (1999) who showed that a grazing gradient separated some but not all vegetation parameters on Mongolian steppe and mountain-steppe rangelands. Their cautionary note about overzealous acceptance of the nonequilibrium paradigm is important and consistent with our conclusions. Grazing intensity can be an important management tool for California's range managers because of the effect on ecosystem productivity. In addition, our species-level results from KETTLEMAN 1973 and BEAR 1970 show that grazing intensity does significantly influence the relative composition of some taxa under limited environmental conditions. However, we reject the notion that the overall composition of a given year's plant community can be manipulated via grazing intensity manipulation. It is clear that community-level response is primarily entrained by seasonal weather patterns.

The annual flush of vegetation in any given year is the product of germinating and growing conditions of autumn, winter, and early spring (Bartolome 1979).

While our study measured grazing effects on community types taken as a whole, a decidedly Clementsian approach, we appreciate the Gleasonian perspective that each year's community is simply the aggregation of individual species responses to growing conditions. Our results show that although grazing may alter the response of one to several taxa in some predictable way, the overall suite of species, ranging from an average of 5 in Valley Grassland to 36 in Coastal Prairie, cannot be controlled by grazing intensity modification. Livestock producers can rely on classical range management by manipulating grazing effects on RDM to achieve desired production levels. Vegetation managers may also manipulate grazing intensity to alter desirable or nondesirable populations but only if site-specific data show this to be achievable (sensu Meyer and Schiffman (1999)); under some specific conditions, a particular species may respond. However, the highly variable, idiosyncratic nature of plot-scale responses in Californian grasslands will require the tedious development of site-specific, time-dependent models for predicting most management effects on plant community structure. Even then, the species of most concern may not be responsive (Hatch et al. 1999).

The invasion of exotic species appears to be controlled at spatial and temporal scales larger than that which grazing effects may be observed (i.e., $< 10 \text{ m}^2$). We base this on the observation that invasions were independent of grazing intensity manipulations at the 10-m^2 scale, but that they occurred nevertheless. In the case of the BEAR site, the invasion appeared as a wave of transitions into and out of the *Hypericum perforatum* dominated state.

Efforts to convert Californian grassland areas from exotic annual to native perennial bunchgrass dominance have failed (Dyer et al. 1996; Dyer and Rice 1997). Removal of livestock grazing as a general method for restoration to putative pre-invasion composition fails as management not because of uncertainty about the supposed climax or equilibrium state (native perennial grass dominant), but because grazing intensity does not control composition (Stromberg and Griffin 1996). Indeed, long-term observations in annual grasslands on California's north coast (50 years exclusion) and Sierra Nevada foothills (40 years excluded) show no overall directional change in composition (Bartolome and Gemmill 1981); sites maintain exotic annual grass and forb dominance regardless of grazing reductions and favorable rainfall (White 1967). Likewise, any specialized grazing

management system that seeks to control overall composition will also likely fail because few species on only a few sites respond to grazing intensity modification (Bartolome 1984, 1993). They may achieve desirable results at some sites during selected periods, but their general utility is dubious. These are nonequilibrium predictions.

The level of detail necessary to link most management to community structure is impractical for general range management application because of the high degree of variability at very small spatial and temporal scales – although forage productivity can be maintained using the general RDM model. A further limitation of nonequilibrium S-T models is that they require more data with explicit definition of scale to provide effective management guidelines. We were fortunate to possess such a dataset and although these data were not originally collected with development of a S-T model in mind, these types of data will be required for a more detailed understanding of this system. Multivariate analysis tools such as CART and TWINSpan can help untangle the complexity of data-driven models.

State-transition modeling for Californian grasslands has great potential for success as a practical management guide because it can objectively identify what is feasible. It offers a means for organizing information and developing testable hypotheses about the processes of vegetation change. However, it was clear from the large number of states and transitions we observed on 9 sites along a latitudinal gradient over 5 years that any one general model for Californian grasslands, either equilibrium or nonequilibrium, will have limited utility.

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