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Application of nonequilibrium ecology to management of Mediterranean grasslands

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Abstract

The state and transition model and the ball and cup analogy are used to organize the vegetation dynamics knowledge base for California's annual-dominated Mediterranean grasslands. These models help identify irreversible transitions and alternate stable states. Mechanisms that facilitate movement between successional stable states are categorized as demographic inertia, seedbank and germination, grazing impacts, establishment and competition, fire feedback, and irreversible changes in soil conditions. While theoretical work needs to continue to further describe states and transitions, managers can begin to use existing knowledge to develop management plans with realistic species composition objectives and to select the appropriate tools for reaching objectives.

Key Words: stable states, transitions, vegetation dynamics, annual rangeland, native grassland

Vegetation dynamics observed in Mediterranean grasslands cannot be predicted by the traditional range succession model (Bartolome 1989). Climax-based models predict succession toward a plant community dominated by taller, perennial species as grazing intensity is reduced. However, in the absence of grazing, these grassland communities do not succeed toward a single steady-state dominated by "climax" species. Substantial empirical evidence in Mediterranean grasslands has accumulated that renders traditional assumptions invalid and of little predictive value (Biswell 1956, Heady 1958, Naveh 1967, White 1967, LeHouerou 1972, Bartolome and Gemmill 1981, Foin and Hektner 1986).

Contemporary ecological models provide for complex ecosystem dynamics including alternative stable states, discontinuous and irreversible transitions, nonequilibrium communities, and stochastic events (Drury and Nisbet 1973, Connell and Slatyer 1977, May 1977, Wiens 1977, Nobel and Slatyer 1980) The state and transition (Westoby et al. 1989) approach helps bring order to the complex body of knowledge and concepts describing vegetation dynamics in rangeland ecosystems. These models should be incorporated into land management schemes so that more information can be available for decisions.

Objectives of this analysis were to describe examples of mechanisms found on annual grasslands that can produce complex ecosystem dynamics, and to demonstrate the state and transition approach by describing vegetation dynamics in an annual grassland triggered by natural events and managerial actions.

Annual Grassland Vegetation Dynamics

While annual-dominated grasslands possess a certain amount of inertia that resists change to a perennial-dominated grassland, they also readily shift between dominant annual species. Mechanisms of vegetation change which produce complex ecosystem dynamics (Noy-Meir 1975, Westoby 1980, Walker 1988, Walker 1989) may be summarized into the following categories: seedbank and germination, grazing impacts, establishment and competition, fire feedback, and irreversible changes in soil conditions. Several of these examples can be found in California's annual dominated grasslands.

Overcoming Inertia

Established plant populations change slowly unless disturbed by managerial action or natural phenomena. Some plant populations require a rare event for establishment but the resulting cohort can persist for relatively long time periods (Westoby et al. 1989). Reestablishment of native perennial grasses has been a recurring objective of range managers on California's annual grasslands (Kay et al. 1981) and much has been learned from these efforts. The constraints imposed on perennial bunchgrass establishment, survival, and reproduction by alien annual grasses have limited their success. Heavy grazing; long, dry summers; and intense competition for limited soil resources favor the annual strategy.

Several events would have to occur to provide a window for natural reestablishment of native perennial grasses on California's annual grasslands. A seed source from remnant plants or a viable seed bank must be present. More frequent fire would reduce competition from annual plants (Hervey 1949, Zavon 1982, Ahmed 1983, Fossom 1990). A shorter dry season, which may result from late spring rains, would lengthen the growing season beyond the optimum for most annual competitors and provide conditions adequate for perennial seedling survival and development (Jackson and Roy 1986). Additionally, suspension of grazing during critical periods of carbohydrate storage and shoot development is critical for both sexual and asexual reproduction.

Simultaneous occurrence of these events would be rare, indicating that reproductive strategies may act to inhibit linear reversal of Mediterranean grassland retrogression. These events are more likely to occur on coastal sites with deep soils, longer rainy seasons, and lower summer temperatures. In fact, coastal prairies do possess the most prevalent native perennial grass populations in California's Mediterranean climate zone (Heady 1977, Bartolome and Gemmill 1981, Foin and Hektner 1986).

In California's annual grasslands blue oak (*Quercus douglasii* H. & A.) establishment was strongly associated with the occurrence of past fires (McClaren 1986). Fire suppression policies implemented in the 1940s may have contributed greatly to reduced blue oak seedling establishment. Gordon et al. (1989) suggest that oak seedlings grow poorly amidst dense annual grasses but may have grown more vigorously in interstitial spaces more common in a bunchgrass type.

Seedbank and Germination

Species phenology and short-term weather patterns, in addition to varying types and levels of disturbance, dictate that each patch in an annual grassland site is in almost constant change (Bartolome 1989). Annual grasslands are a mosaic of patches, often dominated

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by 1 or 2 species. Conditions during germination and establishment determine species composition. These dominants may change annually in response to weather, litter levels, soil fertility, and seedbank dynamics.

The seedbank changes in composition annually. Estimates of germinable seed could easily exceed 20,000 m^{-2} (Young and Evans 1989). A high proportion of the seeds are at or above the soil surface in litter. This placement exposes a large proportion of the seedbank to predation and wide variability in moisture and temperature on a diurnal as well as seasonal basis.

The intensity of herbivory influences aboveground and belowground (seed bank) species composition. Intensity of herbivory influences litter levels which in turn influence the seed bank's microclimate. Seedbank microclimate influences seed survival, germination cueing, seedling survival, and resulting aboveground species composition (Rice 1989). The progeny of the current year's species composition will influence species composition of the seed bank.

Within 3 weeks of a germinating precipitation event, 20 to 30% of the pregermination seed reserve is established as plants and only a small remnant of the seed reserve remains (Young and Evans 1989). Seedbanks of species that produce hard seed, such as rose clover (*Trifolium hirtum* All.), or have self-burial mechanisms, such as filaree (*Erodium cicutarium* (L.) L'Her), subterranean clover (*T. subterraneum* L.), and wild oats (*Avena fatua* L.) are less likely to be depleted during germination. Young et al. (1981) estimated that seed carryover from one year to the next was greatest for annual legumes, followed by annual forbs, and least for annual grasses.

Grazing Impacts

Plant abundance may vary discontinuously and irreversibly in response to changes in stocking rate (Noy-Meir 1975, 1978, 1982; Walker et al. 1981; Walker and Noy-Meir 1982; Crawley 1983). Thus, alternative persisting species mixes are possible. In California grasslands, annuals continue to dominate after grazing pressure is removed (Biswell 1956, White 1967, Bartolome and Gemmill 1981). Native perennials, once reduced below critical population densities by grazing and other disturbances, are unable to persist or reestablish even under lower stocking rates or protection from grazing. Continuous grazing during the growing season contributes to the failure of perennial species to increase in vigor and basal area, and remnant perennial grasses that persist in a matrix of annuals become the focus of heavy fall and spring grazing pressure, limiting reproduction.

Establishment and Competition

The initial abundance of species may influence the outcome of competition and eventually population mixes (Harper 1977). Established annual plants may have priority in competition over developing perennial grass seedlings. In California Mediterranean grasslands, annual plants dominate the seed bank (Major and Pyott 1966) and seeds of annuals germinate faster and roots grow faster than perennial grasses' (Harris 1977). Foliage of annuals may overtop and shade perennial competitors in more mesic systems (Borman et al. 1990).

Differences in germination date and early seedling vigor and development largely determine competitive ability (Salisbury 1942, Harper 1977, Fenner 1978). Therefore, changes in botanical composition of annual dominated vegetation are influenced strongly by short-term weather patterns (Heady and Pitt 1979). Species composition is determined before December and is largely a function of dates of autumn rains and autumn temperatures (Heady 1958). In drier years or in years of adequate but poorly distributed rainfall, filaree usually dominates. Filaree germination is improved by wide diurnal variation in summer temperatures (Rice 1985). High rainfall years and years with late spring rains may result in grass dominance. Early rains coupled with evenly spaced and adequate rainfall usually result in clover domination (Bentley and Talbot 1951).

Fire Feedback

Grass-dominated plant communities promote fire and in many cases are also promoted by fire (Mutch 1970). At the Jepson Prairie Preserve in southern Solano County, Calif., late summer burning increased fall regrowth and seed weight of purple needlegrass (*Stipa pulchra* Hitch.), a native perennial (Fossum 1990). Burning also increased the frequency of purple needlegrass seedling emergence and survival, which may be associated with larger seed size. Much of California grassland has been protected from burning by fire suppression policies and heavy grazing. Hence, where remnant perennial bunchgrasses remain, properly timed fire and grazing may improve seedling establishment and survival and increase basal area of established plants. Application of prescribed fire and grazing management in the absence of established perennial bunchgrass seeds will not result in bunchgrass establishment.

Irreversible Changes in Soil Conditions

Alteration of some soil properties may have a long lasting or permanent effect, especially on a time scale relevant to management. Grazing during the rainy season compacts some soils, which reduces infiltration, percolation, and water holding capacity, and concentrates roots near the surface (Menke 1989). Soil compaction also impedes root elongation, placing deep rooted species such as perennial grasses, shrubs, and trees at a disadvantage during seedling establishment. Oak seedling establishment success could be improved by planting acorns on top of a 60 to 90-cm hole refilled with soil (McCreary 1991).

Annual rangeland sites present a special erosion hazard because soils are often thin, topography steep, and they receive much of their precipitation as rain rather than snow. Consequently, there is the potential on some sites to lose a substantial proportion of the soil, resulting in permanent loss of production potential.

Application of a State and Transition Model

These mechanisms, alone or in concert, may produce alternative persisting vegetation states. Single, catastrophic events of weather, fire, grazing, or management action may change range ecosystems in ways not easily reversible and not consistent with the linear monoclimax succession model. Rangeland vegetation dynamics on a site may be described by discrete states and definable transitions between states (Westoby et al. 1989). In some cases it is convenient to recognize transient states in which vegetation does not persist indefinitely but changes to another persistent state, depending upon events during the transient state. Transitions between states may be triggered by natural events (weather, fire, etc.) or management (brush control, seeding, change in stocking rate, etc.), or combinations of the 2. Transitions may occur very quickly (fire) or over an extended period (biological invasions, climate change) (Svejcar and Brown 1991).

Figure 1 describes a state and transition example for a shallow gravelly loam site in the Sierra foothills of Yuba County, Calif. This approach provides a map for ecosystem management for use by land managers and a means for more quantifiably testing hypotheses about ecosystem response to disturbance and management.

The state and transition model can be applied in the field and used for planning managerial inputs. The transitions describe managerial actions (inputs) required to progress from one state to another. Resource value ratings can be assigned to stable states and potential products (outputs) can be projected. Probabilities of natural phenomena (disturbances) and managerial success can be assigned to transitions.

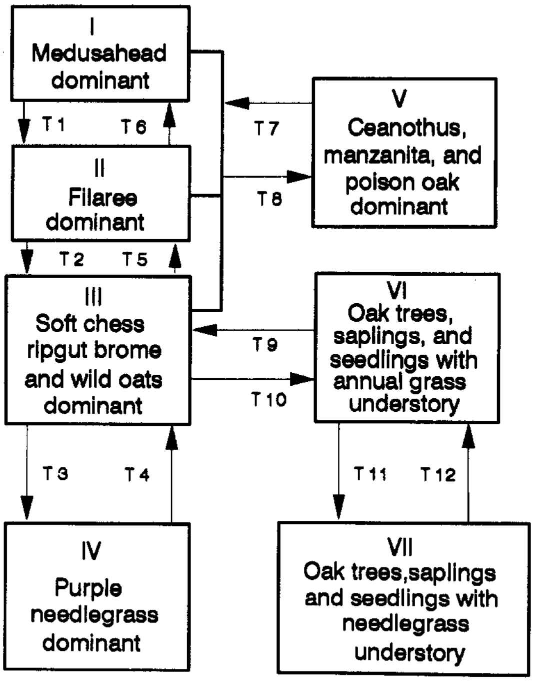

Fig. 1. State-and-transition description for a shallow gravelly loam foothill range site in Yuba County, California with 675–875 mm of annual precipitation.

Catalog of States

State I. Medusahead (*Taeniatherum asperum* Nevskii) forms nearly pure stands with heavy litter that effectively excludes most other annual grasses and forbs. High silica content is believed to slow decomposition, resulting in litter accumulation that effectively suppresses establishment of associated species. Late maturity allows medusahead to most effectively exploit soils containing clay (Young and Evans 1970).

State II. Filaree (*Erodium cicutarium* (L.) L'Her) dominates seedbank and the aboveground standing crop. Medusahead density is substantially reduced. Soft chess brome (*Bromus mollis* L.) is present in the seedbank and standing crop but in small amounts.

State III. Wild oats (*Avena fatua* L.), ripgut brome (*Bromus diandrus* Roth), and soft chess dominate patches. Filaree and other species are present in small amounts. Medusahead is infrequent or not present. Perennial grasses such as purple needlegrass (*Stipa pulchra* Hitchc.) may be present in small amounts.

State IV. Purple needlegrass dominates the grassland. While it is the most common native grass present in today's California annual grassland, it may not have been the dominant perennial grass in the original California grassland (Bartolome and Gemmill 1981). Nodding needlegrass (*S. cernua* Stebb. & Love) and blue wildrye (*Elymus glaucus* Buckley) may have been present in the original grassland.

State V. Wedgeleaf ceanothus (*Ceanothus cuneatus* (Hook.) Nutt.), whiteleaf manzanita (*Arctostaphylus viscida* Parry), and poison oak (*Rhus diversiloba* T. & G.) dominate the community.

State VI. Blue oak (*Quercus douglasii* H. & A.) and interior live oak (*Q. wislizeni* A. DC.) savanna with an annual grass understory dominated by wild oats, soft chess brome, and ripgut brome.

State VII. Blue oak and interior live oak savanna with a perennial grass (purple needlegrass) understory.

Catalog of Transitions

Transition 1. Medusahead seedbank reduced by 50 to 90%. This can be effected by several forms of disturbance (Major et al. 1960, Hilken and Miller 1980): including herbicide applications, cultivation, late May fire, or short duration high intensity grazing throughout the growing season for 2 consecutive years. These disturbances reduce litter and open the site for establishment of other species. Filaree will invade from surrounding patches or become established from residual hardseed. Subterranean (*Trifolium subterraneum* L.) and rose clover (*T. hirtum* All.) may partially replace filaree if medusahead control is followed by seeding these legumes. Low levels of litter in summer and fall lead to filaree dominance within patches. Litter abundance is primarily a function of the intensity of herbivory during spring and early summer. Low litter cover increases soil temperature and seed germination with the first fall rains (Rice 1989). Timing of fall precipitation can also influence filaree composition. Early germinating rains followed by several weeks of drought favor filaree. Filaree is more tolerant of drought than annual grass and forb competitors because of the ability to rapidly elongate a tap root.

Transition 2. Filaree dominance is reduced as other species, especially annual grasses, successfully invade and colonize the patch from adjacent patches. Increased aboveground production and light to moderate herbivory increase litter during summer and fall resulting in decreased summer soil temperatures and reduced fall filaree germination. Increased litter also improves grass seedlings' survival by reducing dessication. Regular or above-average rainfall through the fall and winter increases seedling survival. Application of nitrogen fertilizer may accelerate herbage production and litter accumulation.

Transition 3. Annual plant dominance is seemingly irreversible. Purple needlegrass recruitment and survival is suppressed by intense competition with annual species and season-long herbivory. Germination of purple needlegrass is suppressed by moisture stress and high levels of litter (Bartolome and Gemmill 1981). Reversal may be possible with a high level of managerial control of season and intensity of grazing and periodic prescribed burning. Fire reduces litter and annual plant density (Zavon 1982). Heavy early spring grazing followed by late summer burning increases the frequency of needlegrass seedling emergence and survival (Fossom 1990). Adequate rest between grazing periods improves needlegrass vigor.

Transition 4. Year-long continuous grazing, drought, and competition from annual species reduce needlegrass vigor and survival.

Transition 5. Filaree increases in response to low litter levels or early fall rains followed by several weeks without precipitation. Poor growing season production or heavy herbivory reduces litter levels. Long periods of inadequate rainfall within the normal growing season reduce grass as a component of the herbaceous composition.

Transition 6. Medusahead gradually increases in the patch. Plants produced from the post-fire seedbank produce seed, increasing medusahead in the seedbank. Medusahead increases and dominates the patch and gradually invades adjacent patches if clay content of the soil is adequate.

Transition 7. Summer wildfire or controlled burning removes shrubs. Grazing and recurring fire maintain grassland.

Transition 8. Protection from grazing and fire facilitates shrub invasion. Shrubs become dominant in 10 to 20 years. Herbaceous understory declines as shrub canopy increases (Johnson and Fitzhugh 1990).

Transition 9. Drought, wildfire, controlled burning, or herbicides remove blue and interior live oaks leaving an open grassland dominated by annual species.

Transition 10. High density of annual plants suppress oak seedling emergence and root growth. Competition for soil water with annual species contributes to the increased rate of blue oak seedling mortality (Gordon et al. 1989). Blue oak savannas are believed to be more xeric today than during pre-settlement conditions due to high annual plant densities and reduced litter associated with domestic livestock grazing (Welker and Menke 1990).

Transition 11. Same as Transition 3. Like purple needlegrass, oak recruitment and seedling survival is suppressed by competition with annual species.

Transition 12. Yearlong continuous grazing and drought reduce needlegrass vigor and survival.

For example, if a grassland is in State I (Fig. 1) and the objective was to convert to the grassland in State III, managerial inputs described in Transitions 1 and 2 would be prescribed. Early rains and favorable growing seasons would accelerate progress toward State III while drought and fire would tend to delay progress for 1 to 3 years. Removal of livestock earlier to leave more residual dry matter would facilitate progress from State II to State III. Application of nitrogen fertilizer may accelerate progress from State II to State III. At State III management inputs can be designed to maintain State III or to set course for a new objective.

The resource value for cattle grazing would increase with progress from State I to State III while State II would be of greater value for sheep grazing than cattle. Maintaining adequate cover while increasing forb populations (State II) would enhance upland bird habitat. Increasing cover (State III) would reduce habitat value for ground squirrels *(Spermophilus beecheyi)*. As the grassland progresses from State I to State III, increasing cover and residual dry matter may improve the grassland's value as watershed. The landowner's goals, enterprises, and markets would determine the most advantageous mix of patch states on the landscape.

Ball and Cup Analogy

The "ball and cup or trough" analogy (Hurd and Wolf 1974, Gordon and Forman 1983, Forman and Godron 1986, Laycock 1991) can be applied to this annual grassland state-and-transition model (Fig. 2). The ball represents a plant community. Highly

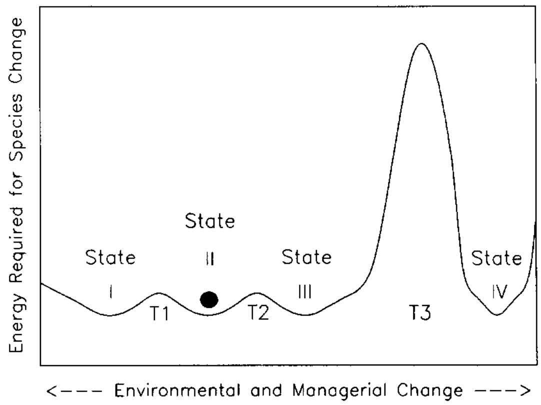

Fig. 2. Graphic representation of ball and cup or trough analogy.

stable communities take a great deal of disturbance to move from one stable condition (cup or trough) to another. California's remnant perennial bunchgrass community as represented by State IV may be a relatively stable community. Transition to an annual grass community as described in Transition 4 requires substantial environmental change (disturbance) and for this site probably is an irreversible transition. However, recent research by Fossum (1990) suggests that reversal (Transition 3) may be possible with application of prescribed grazing and fire where remnant perennial bunchgrasses are present. Inadequate perennial bunchgrass seed sources, infrequent fire, long dry seasons, and annual plant competition individually and collectively are tremendous barriers to reversal.

While the annual grasslands are generally considered to be stable (Heady 1977), communities are made up of several transient states (States I–III) within a trough that are the product of weather variation, amounts of litter, soil fertility, and grazing. Short generation times, species diversity in the seedbank, and differing requirements for germination and seedling establishment as influenced by variations in weather result in annual changes in species composition and dominance.

Conclusions

While there is insufficient information to describe all possible transitions, it is important to arrange what is known in a usable format. Some states may be quite stable while other states, especially annual-dominated states, will change frequently in response to prevailing natural and managerial actions. We may know the states but not factors that control the transitions. This model would help focus research on the transitions where the lack of information exists.

It is important for managers to recognize that irreversible conditions exist and that annual grasslands are capable of frequent change. Management plans on annual grasslands continue to emphasize the return to perennial-dominated grasslands as an objective and protection from grazing as the main tool for reaching that objective. No known management prescription will achieve that.

Range condition assessments continue to rate communities dominated by annual plants in low condition. Ecological site descriptions continue to be based upon species composition without acknowledging that composition may change annually. States and transition descriptions provide a new format to describe vegetation dynamics and acknowledge the transient nature of some vegetation states.

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