SYNECOLOGY AND DISTURBANCE REGIMES OF SAGEBRUSH STEPPE ECOSYSTEMS

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Abstract

The pre-Columbian mixed-growth form, composition, and structure of sagebrush steppes was mostly due to the highly variable semiarid climate and long fire-free intervals. The weak stability of this relatively complex vegetation was easily upset by excessive livestock grazing, especially in drought periods. After a few decades of uncontrolled livestock grazing, it was easy for introduced winter annuals, especially cheatgrass, to dominate the understory and alter the fire regime to larger, more frequent fires that occur earlier in the year. Accelerated soil erosion has caused many sites to lose the potential for management back toward native perennial dominance by controlling only livestock and fire. Major investments will probably be necessary to lengthen the current fire-free interval, as well as reduce the size of fires and their occurrence during late spring and early summer on large areas of cheatgrass dominance. Livestock could be used in some circumstances to help reverse the damage they did before grazing became regulated. Opportunities to apply genetic engineering to native plants and new herbicides to cheatgrass should also be explored before even more noxious biennials gain a major foothold.

Introduction

Durant McArthur (this volume) appropriately began by giving us background in sagebrush taxonomy, species distributions, and autecology. I now perceive my role as one of reviewing the synecology of an ecosystem type called "sagebrush steppe." This includes the disturbance regimes intrinsic to this ecosystem.

Definitions

I have restricted my coverage to the 45 million ha of sagebrush steppe (West 1983*a*) and alert you to the fact that not all areas currently or recently having vegetation with a woody *Artemisia* dominant are sagebrush steppe, particularly in the drier, less diverse, less productive, less resistant, less resilient sagebrush semi-desert to the south (West 1983*b*). I am purposely avoiding drawing on information from sagebrush semi-deserts in this paper.

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Ecosystem Structure

Climate - Sagebrush steppe occurs where there has been until recently, or still is, a sharing of dominance between shrub and herbaceous growth forms. The fundamental reason for this is that, on average, continental semiarid climates occur here. More important than the climatic means is the understanding that these climates have high coefficients of variation (~30%) in total annual precipitation, with rapid fluctuation between some more favorable years that promote the shallow, fibrous-rooted, herbaceous plants and droughty years that favor the more deeply rooted shrubs (Fig. 1). Herbaceous plants develop earlier in the growing season and thrive on spring rains, whereas shrubs lag in their phenological development because they can draw from deeply infiltrating moisture from snowmelt the previous fall and winter. While this leads to some compensation between species to produce a dampened yet higher level of production in shrub steppes than in semi-deserts, it also makes these systems much more difficult to understand and sustainably manage than either grassland or desert.

The fire-return interval in the Pre-Columbian condition probably varied between 25 years in wetter areas (Houston 1973) and 110 years on the central Snake River Plains (Whisenant 1990) (Fig. 2). Otherwise, the earliest observers would have called this the rabbitbrush steppe because the shorter-lived and root-sprouting *Chrysothamnus* spp. would have prevailed (Young 1983).

Soils - Soils give us some reflection of long-term climatic and vegetational influences. Most sagebrush steppe soils are Xerolls – that is, the most drought-affected Mollisols – if the surface layers haven't been eroded. Most soils of sagebrush semi-desert are Aridisols (West and Young 2000). Thus, where flora and fauna are highly altered, one can use soil profile characteristics to gauge the potential of sites for recovery through management or restoration.

Vegetation - The floristic diversity of the sagebrush steppe is moderate by regional standards. Daubenmire (1970) found an average of 20 vascular plant species in 1,000-m^2 plots on relict sites in central Washington. Tisdale et al. (1965) found from 13 to 24 vascular plant species in examples of three community types on an ungrazed site in southern Idaho. Mueggler (1982) found 24 to 41 vascular plant species in a set of 68 lightly grazed macroplots in the sagebrush steppe of western Montana.

The vertical and horizontal structure of the sagebrush steppe consists of shrub-dominated and herb-dominated phases (West 1983*a*). The shrubs usually vary in height from about 0.5 m for either young plants of the tall sagebrushes or mature low-statured species to more than 2 m for the tallest sagebrushes on the best sites. The fraction of ground surface covered by the various growth forms varies greatly depending on site and successional status.

Herbs on relict sagebrush steppe sites are usually perennial hemicryptophytes (Daubenmire 1975). The proportion of geophytes approaches 20%. Bork et al. (1998) claim that grasses are more often situated closer to the shrubs than the forbs. Annuals and microphytes are usually more abundant in the middle of the interspaces between shrubs.

The total phytomass standing crop of relictual stands varies between 2 and 12 t/ha, with about half of that occurring below ground. Only about 15% of the above-ground phytomass may be attributable to the current year's growth of shrubs. Above-ground net primary production varies from about 100 to 1,500 kg/ha/yr for relict areas (Passey et al. 1982).

Animals - Native vertebrate animals of the sagebrush steppe are a mixture of grassland and desert species. About 100 bird and 70 mammal species can be found in sagebrush habitats (Braun et al. 1976). Although the vertebrate community is most diverse when the pattern of plant communities is most structurally diverse (Parmenter and MacMahon 1983, Maser et al. 1984), the only tightly co-evolved and thus sagebrush obligate vertebrate species are the sage grouse, sage sparrow, Brewer's sparrow, sage thrasher, pygmy rabbit, sagebrush vole, sagebrush lizard, and pronghorn (Paige and Ritter 1999). While none of these is known to cause major negative feedbacks on the vegetation, jackrabbits can (Young 1994).

Over 1,000 species of insects have been found on example sites (West 1999), more than 76 species on sagebrush alone (Wiens et al. 1991). While some are known to alter the vegetation during occasional population explosions, e g., *Aroga* moth and cicadas (West 1999), grasshoppers and crickets (Yensen 1980) can do so more regularly. The functional importance of most invertebrates is yet to be discovered.

Microbes - We know very little about what microbes are present and how they influence ecosystem processes within the sagebrush steppe. Hopefully, these organisms and the work they do, mainly decomposition and nutrient cycling, will receive more attention in the future. Global environmental changes are likely to produce some unexpected interactions among plants, microorganisms, and soil degradation (West et al. 1994).

Ecosystem Dynamics

We now need to turn to consideration of how the above components interact and how the ecosystem has changed. In order to interweave the historical with the ecological, I will follow the recent example of Rapport and Whitford (1999) in organizing this overview of how sagebrush steppes have responded to stress. I will also tie the changes to a recent model of retrogression in the sagebrush steppe (West 1999). Only the major states and pathways are considered here.

Pristine Conditions (State I)

Pristine ecosystems (State I in Fig. 3) no longer exist, nor are they likely to be recoverable. The reasons for this view are:

1. Humans (indigenous peoples) are no longer hunting, gathering, and burning the areas. The previous fire regimes are no longer in place; and, as the vegetation has changed in response to fires, the hydrologic and nutrient cycles have been altered, as has the habitat for numerous animals and microbes.
2. The present climate is warmer and drier than the cooler, wetter Little Ice Age climate which prevailed from about 1500 to 1890. Thus, only heat- and drought-tolerant species may now thrive under global warming.
3. Atmospheric CO_2 has increased about 20% during the past century, altering the competitive balances in this vegetation as well as changing the nutritional qualities of the phytomass and litter (Polley 1997).
4. About 15% of the flora is new to the region. Since the close of the Pleistocene, extinctions have been minor.

Since we can reverse none of these influences, at least in the short term, we should learn to live with what remains and manage it toward the mix of desired plant communities we choose for each landscape (Paige and Ritter 1999).

Relictual Conditions (State II)

There are some remnants of the present landscapes that have escaped direct human influences. These relicts exist because they have no surface water, are surrounded by difficult topography, or are protected in special-use areas, e.g., Research Natural Areas. I place these in State II (Fig. 3). Passey et al. (1982) describe many examples. These relicts are not completely reliable as reference conditions because they are incomplete ecosystems. They lack indigenous humans as well as normal kinds and numbers of native animals and have usually experienced lengthened fire frequencies because of their isolation. Relicts are further influenced by air pollutants, climatic change, and invasion by exotics (Passey et al. 1982).

Most of the existing late seral sagebrush steppe with good perennial understory (State II in Fig. 3) has had light livestock use, especially earlier in the century when sheep were very abundant. Even light livestock use (T_1) puts inordinate pressure on a few highly palatable species ("ice cream plants"), partially explaining the lack of a return arrow from State II to State I. I estimate that less than 1% of the region remains in State II (Fig. 4). These shrub steppes with smaller, more scattered shrubs and almost complete perennial herbaceous understories are less susceptible to large-scale fires and subsequent invasion by cheatgrass (Peters and Bunting 1984).

Stagnant Sagebrush (State III)

Because livestock that graze native sagebrush steppe tend to avoid the unpalatable species (usually woody species), shrubs are freed from competition and achieve dominance quickly (10-15 years). With the removal of fine connecting fuels, the chance of fire is also reduced in State III (Fig. 3). About 25% of this ecosystem type is estimated to exist in this state (Fig. 4). In some places, feral horses, protected by law on most public lands, have created and maintain sagebrush stands with little remaining herbaceous perennial understory. Most of these stands can remain stagnant for decades (Rice and Westoby 1978, Sneva et al. 1984, Winward 1991). The dense, competitive stands of excess sagebrush prevent perennial herbaceous species from recovering when grazing is either reduced (T_3) or excluded over very long intervals (Bork et al. 1998).

Herb-dominated Stands (State IV)

Brush-choked or stagnant stands of sagebrush (State III) were usually chosen by both livestock and wildlife managers in the past for manipulation to diversify vegetation structure. Such treatments locally enhance a stand by concentrating livestock use and reducing pressure elsewhere, while simultaneously creating an advantage for some wildlife species through vegetation modifications via grazing systems, prescribed burning, brush-beating, or chaining (T_3). For example, grazing sheep only in the fall – because they consume more sagebrush then but cannot heavily impact the herbs – can help achieve a conversion from State III to State IV and even increase floristic diversity compared to adjacent exclosures ungrazed for decades (Bork et al. 1998). Prescribed burning (Harniss and Murray 1973) can also be applied to stands with sufficient remnant populations of perennial native herbs to quickly recover following brush kill. A rest-rotation grazing system or winter-only use (Mosley 1996) will often allow a slow return (T_6) to State II from State IV.

Reduction of brush also enhances water yields (Sturges 1977), and some seeps, springs, and streams reappear. When phenoxy herbicides are used alone (Evans et al. 1979) (T_4) or in conjunction with fire, the community becomes dominated by native grasses (State IV, Fig. 3) because phenoxy herbicides negatively impact all broad-leafed species. This conversion slowly returns (T_6) to State II only with conservative grazing. About 5% of the remaining sagebrush steppe is now estimated to be in State IV. This is a short-lived state, especially under heavy grazing (T_5). Mueggler (1982) found enhanced alpha diversity in moderately grazed sagebrush steppe communities in western Montana following prescribed fire, 2,4-D, and brush-beating treatments. Summer fires can damage some grass species (Young 1983) but encourage the resprouting rabbitbrushes (*Chrysothamnus* spp.) and horsebrushes (*Tetradymia* spp.) (Anderson et al. 1996).

The perceived will of a majority of Americans now is to identify remaining areas occupied by States II and III, especially those on public lands, and protect them from development. In other words, I agree with Paige and Ritter (1999) that no net loss of sagebrush should be a regional objective to prevent further declines in biodiversity (West 1999). Some advocate all such areas have livestock removed (Kerr 1994), whereas others (Bock et al. 1993) propose that 25% have livestock excluded. Rose et al. (personal communication) have, however, recently demonstrated that lightly grazed sagebrush steppe has higher species richness than adjacent exclosures dating to 1937. Others propose restoration efforts to bring further-degraded systems back to States I or II. Whether that is possible and economical is discussed in the remainder of this volume.

Regardless of one's view of the matter, State II and III areas will serve as a major "parts catalog" for restoration efforts. The Gap Analysis Program (GAP) of the U.S. Fish and Wildlife Service (Scott et al. 1993) and the various natural heritage programs initiated by the Nature Conservancy are well under way to identify such areas.

I expect to see physical modifications for enhancing production of food and fiber (formerly called range "improvements") to be more spatially limited than in the past. Such actions on public lands or with public monies on private land require environmental assessments or impact statements and, thus, public scrutiny and debate. The remaining sagebrush-dominated public lands will probably be consciously protected to provide the later seral condition patches necessary to hold a broader spectrum of all species and meet the special requirements for some featured and obligate species (Paige and Ritter 1999).

Rangeland managers in the past strove to reduce the land's limitations for producing livestock. These limitations were mainly topography, forage availability, and water. For example, trails were constructed into areas where topographic breaks limited previous livestock access. Natural water was supplemented by developing springs, building stock tanks and small dams, drilling wells, and piping and hauling water. Fences were constructed and salt distributed to control livestock movement and institute grazing management systems (e.g., rest-rotation grazing). All these "improvements" were designed to distribute livestock utilization more uniformly across the land, gain greater efficiency of food and fiber production, and divert livestock from the especially sensitive riparian areas (Elmore and Kauffman 1994, Laycock 1995). The net result has been progressively more widespread yet intensive use of a landscape that has become at least partially tamed from the wild. These assumptions need to be reexamined in the light of biodiversity concerns. Let us continue our consideration of these relationships in the mostly highly altered sagebrush steppe areas.

If accelerated soil erosion does not ensue and the fundamental potential of the site does not change, then State III can be maintained or managed toward States II or IV. However, as herbaceous plants, litter, and microphytes in the interspaces between perennials are reduced, soil aggregate stability declines, infiltration of precipitation diminishes, overland flow increases, and soil erosion frequently increases (Blackburn et al. 1992). When a probable threshold is exceeded, the site can irreversibly change to one of lesser potential. This explains the dashed line and downward arrows below States III and IV as permanent transitions, where the syndrome of desertification is most evident.

All the previously discussed states shown above the dashed line of Fig. 3 can be dealt with via management approaches using "soft" energy. Once this threshold is exceeded, however, subsequent management requires expensive, risky, "hard" energy solutions. Unfortunately, it is often easier to get political attention after major damage has been done rather than getting budgets and personnel to plan, monitor, and tweak the healthier, more natural systems at opportune times.

Desertified Sagebrush Steppe (State V)

The desertified sites are usually initially dominated by taller, thickened brush and have largely introduced annuals in their understory. The major adventive from 1870 onward has been cheatgrass (*Bromus tectorum*) (Billings 1990, Knapp 1996). I estimate that State V comprises about 25% of the current sagebrush steppe region (Fig. 4). Removal of livestock usually only hastens further degradation from State V because livestock remove part of the herbaceous fuel load and thus reduce the chance of fire destroying the sagebrush and the spots of enriched soil it protects (Charley and West 1975). Cheatgrass fundamentally changes the fire regime (Fig. 2), and most sagebrushes, not being root sprouters, only return slowly, if ever. Livestock can be used in the spring to reduce cheatgrass (Mosley 1996); however, grazing at that time also impacts any remaining native herbs. Where there are warm season (C_4) grasses and forbs, heavy livestock grazing in the spring with deferment in summer can be used to favor the recovery of those components (R. Budd, personal communication, 1999).

Introduced Bunch Grasslands (State VI)

If insufficient amounts of native grass remain in the sagebrush steppe to allow a reasonably short return to other desired plant communities, the usual response by land management agencies has been to destroy the sagebrush and replace it mechanically (T_7) with introduced wheatgrass and ryegrass, especially crested wheatgrass (Asay 1987). This has been done because the seed of introduced perennial grasses is more readily available and less expensive and their seedlings are much more easily established than the native grasses. They also grow quickly to provide more forage with a higher nutritional plane. The introduced perennial grass stands are also much more tolerant of subsequent heavy livestock use and last for many decades (Johnson 1986). There are some long-range concerns, however (Lesica and DeLuca 1996), because the introduced perennial grasses suppress the return of natives and, thus, richer plant species assemblages. Some large treatment areas are essentially monocultures of Eurasian perennial grasses (State VI, Fig. 3). I estimate about 5% of the original sagebrush steppe has already been transformed to State VI (Fig. 4).

Wildlife biologists have noted declines in the numbers of birds (Olson 1974; Reynolds and Trost 1979, 1981), small mammals (Reynolds and Trost 1979), and large reptiles (Reynolds 1979) on such seedings of introduced grasses in the sagebrush steppe area. It should be noted, however, that such studies present a worst-case scenario because samples came from the center of large treatments. Provision for increased diversity near edges (Thomas et al. 1979) is not usually mentioned in such studies. Present-day, more sensitized planners would provide for optimum edge effect and patchiness (McEwen and DeWeese 1987, Paige and Ritter 1999).

When society made the investment in repairing severely damaged sagebrush steppe, e.g., creating perennial grass-dominated pastures of species palatable to livestock (T_7) with much greater productivity, this compensated for livestock reductions and other management restrictions on lands where States II, III, and IV (Fig. 3) predominated. Because introduced grass pastures can take much heavier utilization in the spring than the native shrub steppe, livestock can be grazed on native sagebrush steppe in fall or winter with less impact, especially on the native herbaceous perennials.

Shrub-Reinvaded Introduced Grasslands (State VII)

Introduced perennial grass plantings in the sagebrush steppe region, especially if grazed by livestock, will eventually experience shrub reinvasion (T_8 to State VII, Fig. 3), largely in response to intensity and timing of livestock grazing. I estimate (Fig. 4) that about 5% of the sagebrush steppe region is currently represented by shrub-reinvaded introduced wheatgrass/ryegrass pastures (State VII).

Shrubs reinvading State VII are not being eliminated by herbicides, as was once attempted. All herbicide use in such circumstances on public lands has been suspended by judicial decree in the Pacific Northwest. Prescribed burning of the coarser, introduced grasses is difficult and leaves patches where the shrubs prevail. Therefore, there are opportunities to enhance edge effects in large areas that were formerly homogenized. As in the untilled native areas, patchy burning could enhance wildlife habitat across landscapes by providing a mix of successional stages over a landscape, providing both cover and forage for either featured species or total species richness (Maser et al. 1984). For example, some success has been attained in creating alternate leks for sage grouse following disturbance (Eng et al. 1979). Some crested wheatgrass pastures on U.S. Forest Service lands in northeastern California have recently been plowed and planted with native herbs in an attempt to enhance biodiversity. Aggressive annuals such as yellow starthistle were the dominant result (J. Young, USDA ARS, personal communication).

Annual Grasslands (State VIII)

Despite greatly increased attention to fire prevention and control, much of the depauperate sagebrush steppe (State V) has been burned (T_{10}) at least once during the past three decades and is now almost completely replaced by introduced annuals, mainly grasses such as cheatgrass and medusahead (State VIII, Fig. 3). The Bureau of Land Management (M. Pellant, Bureau of Land Management, personal communication) estimates that about 3 million acres of public lands in Idaho, Utah, Oregon, and Nevada are now dominated by cheatgrass and medusahead. I estimate that about 25% of the total sagebrush steppe has made these transitions (T_{10}, T_{11}).

Because of their short stature, restricted nutritional characteristics (short period of above-ground greenness), and greater susceptibility to recurring fires and drought than sagebrush steppe, such areas are undesirable from all viewpoints (Knick and Rotenberry 1997). Without nutritional supplementation, livestock can graze State VIII only during the short, early-spring growing season. Winter use is possible only in the lower-elevation areas near the Columbia River (Mosley 1996). Only the most generalist animals, such as the introduced chukars, horned larks, grasshoppers, and deer mice, seem to thrive on the annual grasslands (Maser et al. 1984). When such areas burn in early summer, soils are bared to wind and water erosion during the convectional storms of summer. The consequent needs for revegetation after fire are increasing while the budgets of federal land management agencies decline and pressure increases from environmentalists who are against proactive management.

Land dominated by annuals may provide fair watershed protection during years without fire and actually appear to be more productive of total plant biomass than the original sagebrush-native perennial grass and forb combination (Rickard and Vaughn 1988). This is likely, however, to be only a temporary situation based on the priming effect of decomposing litter (Lesica and DeLuca 1996) and the mineralization of nutrients from the enormous below-ground necromass of the original system. The formerly strong link of net primary production with precipitation becomes decoupled (Whitford 1995). The shrub-centered islands of fertility (Charley and West 1975) are now diluted in a horizontal direction by the interactions of fire, soil erosion, and tillage. When these reserves of nutrients and soil organic matter are finally respired away, the annual grasslands are likely to become much less productive. Similar transitions happened in the Middle East several millennia ago (Zohary 1973). Many other more noxious weeds from that region could find their way here, and we could witness a downward spiral of further degradation (T_{12}).

Repairing the Damage

Rather than allowing the annual grasslands derived from former sagebrush steppe (State VIII, Fig. 3) to remain and the land to degrade further, some land managers are attempting to intervene. A joint program among the USDA Forest Service, Bureau of Land Management, Agricultural Research Service, and University of Idaho has been under way this past decade to reduce these threats (Pellant 1990). The most notable component of this effort is the greenstripping program, which is particularly evident in southern Idaho. The basic approach is to begin breaking up the now vast stretches of cheatgrass and other annual dominance that have developed as fires have become earlier, larger, and more frequent (Fig. 2). Land managers are attempting to break the cheatgrass-dominated areas into smaller, burnable units, especially in proximity to cities and towns. The approaches used thus far include planting strips of vegetation that stay green (and thus wetter and less burnable) longer than cheatgrass.

Although the introduced wheatgrasses, ryegrasses, and forage kochia (*Kochia prostrata*) do stay green longer and burn less readily because of coarser aboveground structure, they are not native and thus are rejected as replacements by some interest groups. Because the genetic biodiversity of the native plants is so primitively understood, the best that can be done is to gather such seed locally and plant it on comparable sites. Such seed sources are undependable, however. Thus, a root-sprouting big sagebrush is seen as a potentially better keystone species to put back in this area. A few sagebrushes may actually help sustain perennial grasses by harboring the predators on black grass bugs (*Labops* spp.) (Haws 1987). Furthermore, total plant community production can be enhanced (Harniss and Murray 1973) because sagebrushes help trap blowing snow (Sturges 1977) and scattered sagebrushes moderate temperatures (Pierson and Wight 1991), benefit the reestablishment of native herbs, and protect them from excessive utilization (Winward 1991). Sagebrushes also harbor mycorrhizal fungi (Wicklow-Howard 1989), which helps them extract nutrients from deep in the soil and recycle them to the surface through litter production (Mack 1977, West 1991).

Whether or not we can accomplish restoration of sagebrush steppe (T_{13}, between States V and III in Fig. 3) is highly questionable. Even where funding is less limiting and topsoil is replaced on coal strip mines, early results are only partially encouraging (Hatton and West 1987). We must learn much more about how sagebrush steppe ecosystems are structured and how they function, and we must have access to vast budgets and more trained personnel before such efforts are routinely successful. It is cheaper and more feasible to foster good stewardship of land having late seral vegetation (manage while in States I, II, III, or IV of Fig. 3) rather than rely on restoration efforts after degradation has taken place (States V, VI, VII, and VIII of Fig. 3).

The future of the sagebrush steppe region is the concern of this volume. Can the damage of the past be reversed or mitigated? Is restoration or rehabilitation possible and affordable? Remember that we have lost some pieces, gained new ones, and have a new and further changing environment. New invaders, increased temperatures, atmospheric CO_2, and UV_B pose additional problems.

While we must acknowledge that unrestricted livestock grazing, especially during droughts, was the fundamental cause of degradation of most sagebrush steppe, it doesn't automatically follow that reduction or even entire removal of livestock will reverse the changes for highly altered sagebrush steppe (below the dashed line in Fig. 3). Most of this land area has had threshold-exceeding changes. Soils, their nutrient pools and water handling capabilities, seed reserves, and thus their vegetation-producing potential have been fundamentally lowered. Even removing livestock during droughts will not suffice in attaining recovery. In fact, removal of livestock during wet years may increase the risk of wildfires, further damaging on-site features, as well as those at some distance, through wind erosion (dust storms). If livestock are totally removed, I predict we will have to eventually pay for them to return. The point is to constructively use them as tools within a holistically conceived recovery plan.

We must break the positive feedbacks, which allow further damage to the sagebrush steppe. The major linkage is between cheatgrass and larger, earlier, and more frequent fires (Fig. 2). I suggest further expansion of greenstripping with further use of the herbicide OUST® to reduce cheatgrass competition and allow better shrub establishment. A resprouting sagebrush would be desirable. If not that, rabbitbrushes are better than cheatgrass. Unpalatable strains of bluebunch wheatgrass (e.g., Whitmar) could be replanted to prevent overuse by livestock in the future. Let's enlist the genetic engineers to build us some perennial plants that better capture and conserve the resources that are truly irreplaceable – the soils. With the soils in place, future generations will have more options as new science and technology become available.

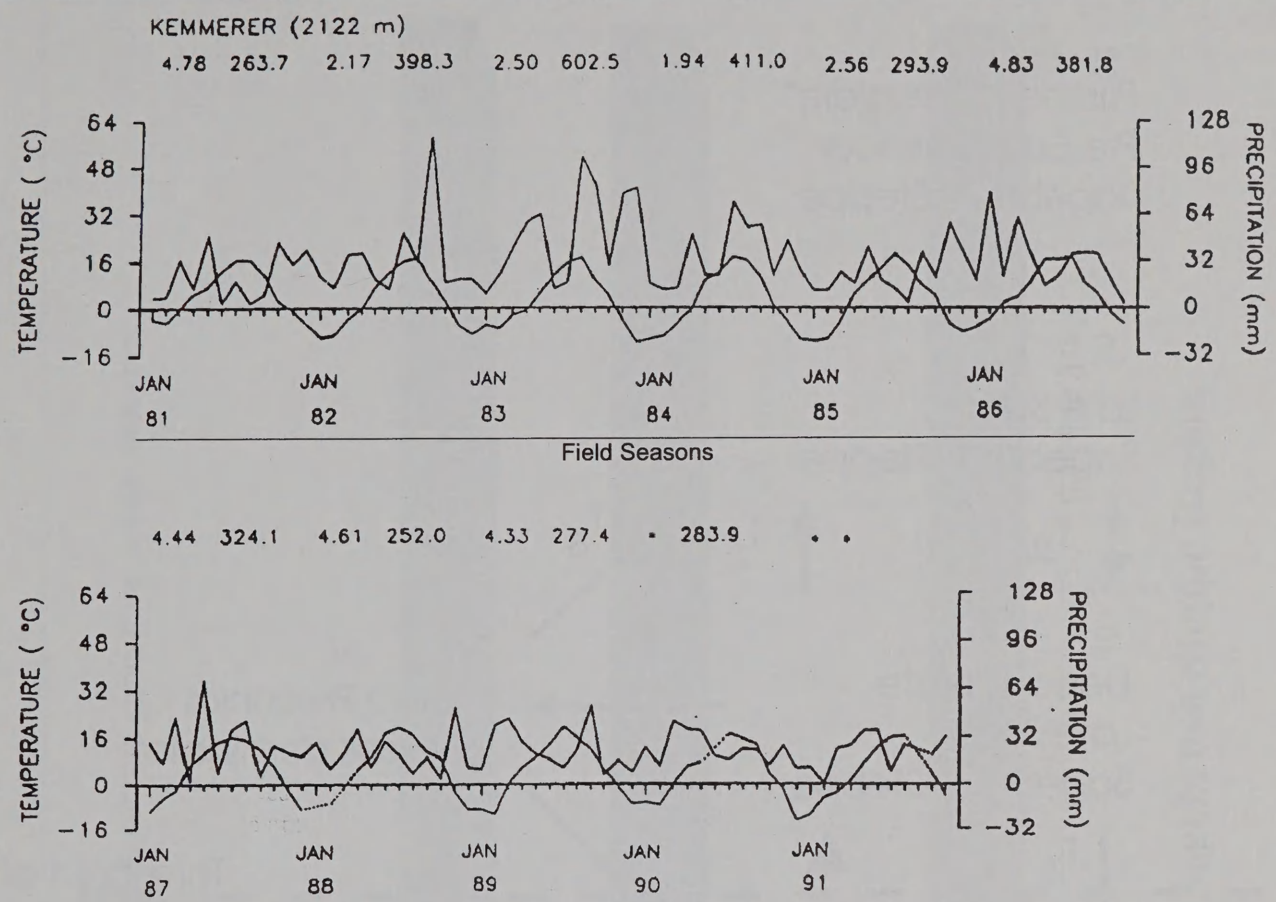

Figure 1. Patterns of mean monthly precipitation and temperature at Kemmerer, Wyoming, 1981 to 1991. Mean annual temperature (°C) and total annual precipitation (mm) are the numbers entered above the trend lines for each year.

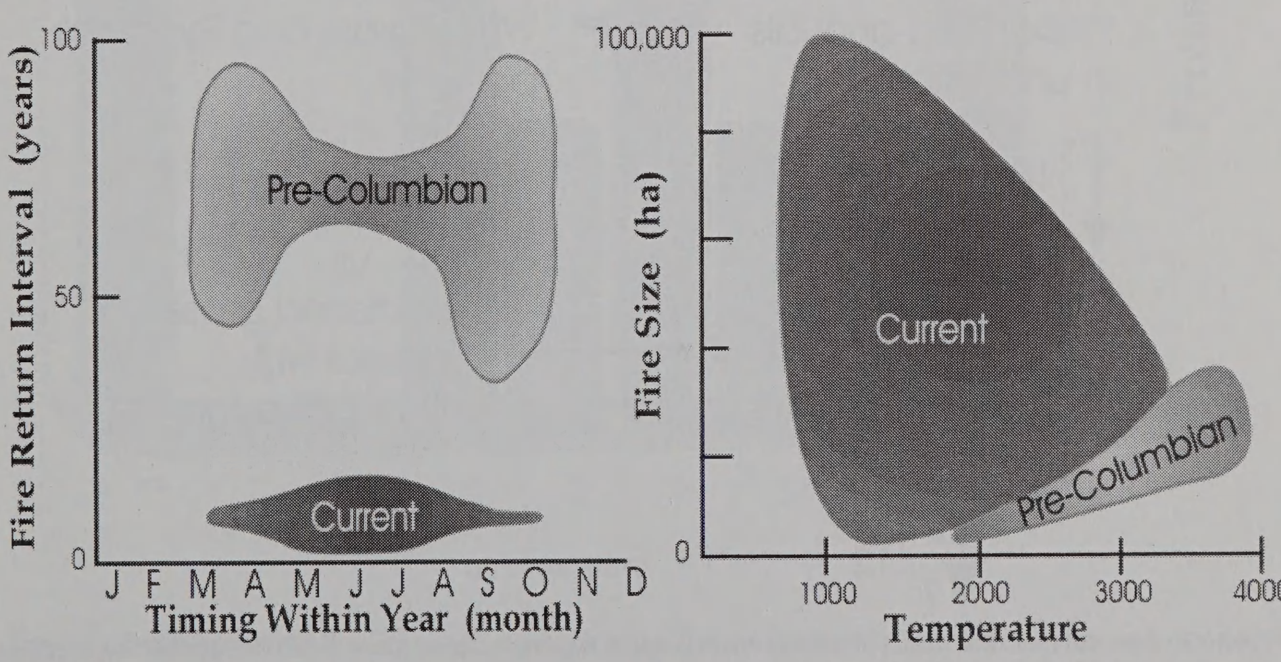

Figure 2. Estimated differences in the fire regime of sagebrush steppe in Pre-Columbian and current times.

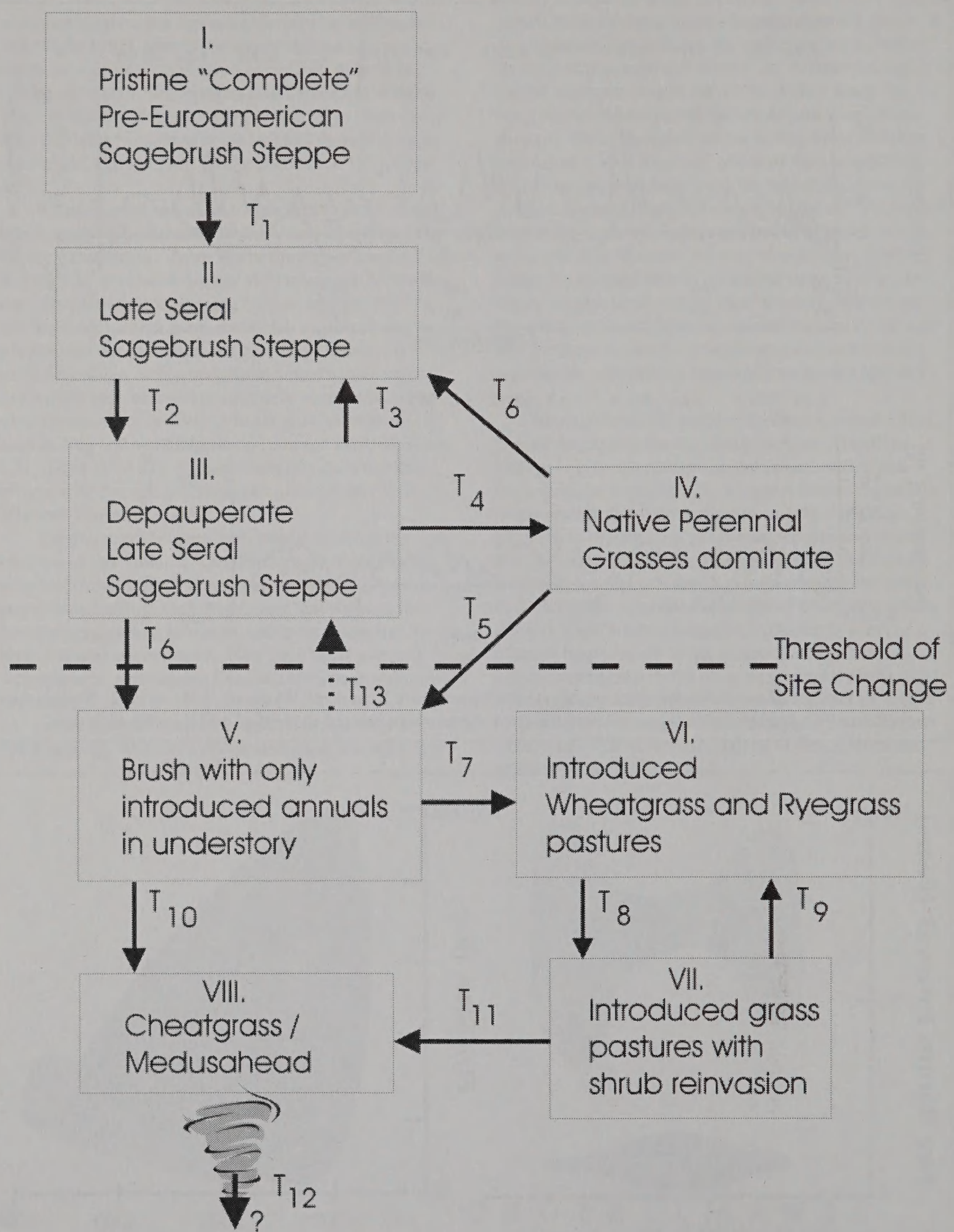

Figure 3. State and transition model of successional change in sagebrush steppe (from West 1999, permission to reprint from CRC Press).

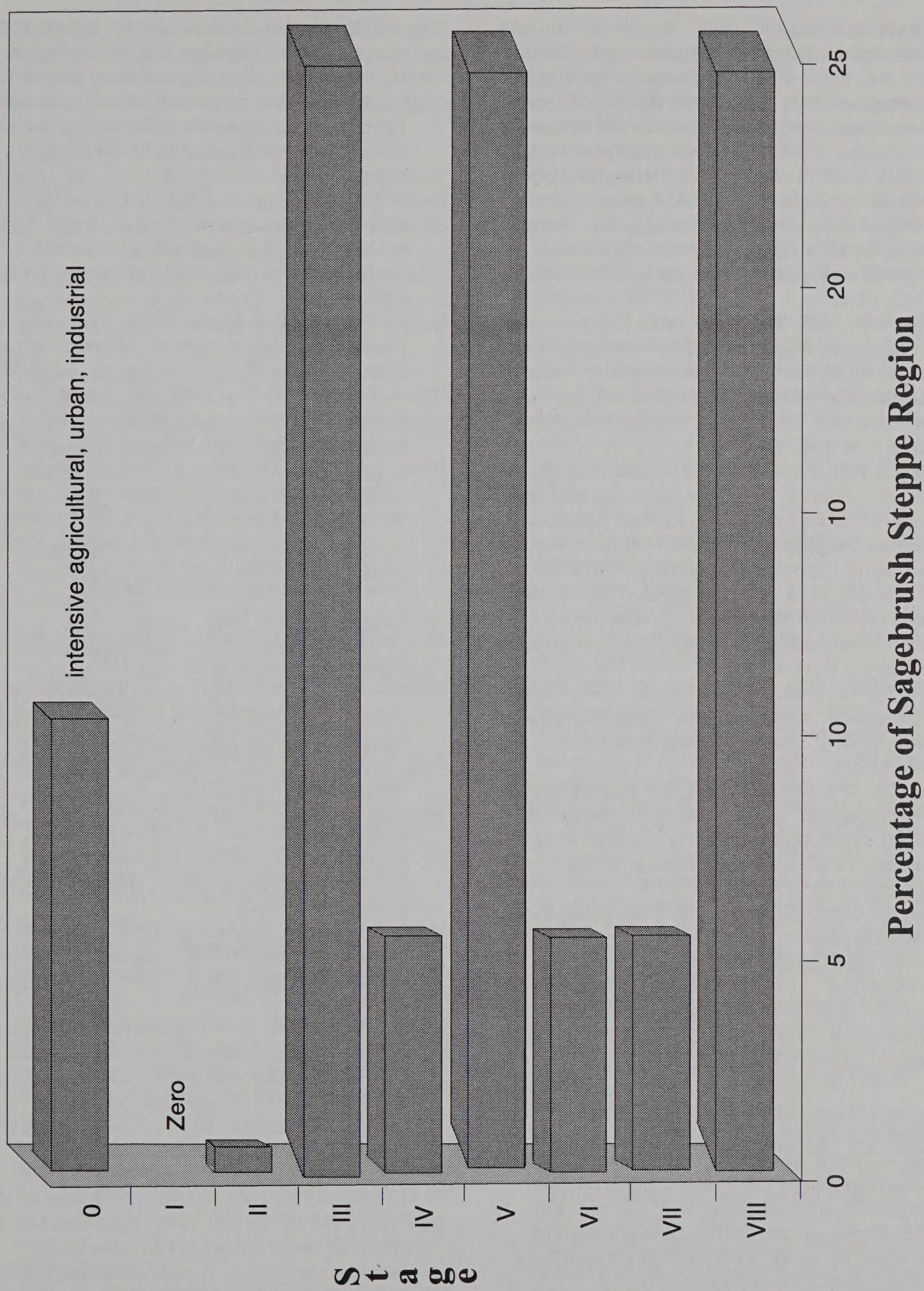

Figure 4. Percentages of the Pre-Columbian sagebrush steppe that are estimated to be occupied by the various states of Figure 3.

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