Cheatgrass (*Bromus tectorum L*) dominance in the Great Basin Desert: History, persistence, and influences to human activities

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Knapp, P.A. (1996) Cheatgrass (*Bromus tectorum L.*) dominance in the Great Basin Desert: History, persistence, and influences to human activities. Global Environmental Change 6:37-52.

Abstract:

Cheatgrass (Bromus tectorum L), an exotic annual, is a common, and often dominant, species in both the shadscale and sagebrush-steppe communities of the Great Basin Desert. Approximately 20% of the sagebrush-steppe vegetation zone is dominated by cheatgrass to the point where the establishment of native perennial species is nearly impossible. This paper discusses the historical factors that led to the establishment and dissemination of cheatgrass in the Great Basin, examines the processes that further cheatgrass dominance, provides examples of subsequent Influences of the grass to human activities, and links the ecological history with range condition models.

Evidence suggests that cheatgrass was introduced accidentally to the Great Basin as a grain contaminant at the end of the 19th century at the same time that large-scale domestic grazing was occurring. Imported from Mediterranean Europe and central and south-western Asia, seeds of cheatgrass exploited an ecological niche, as no native annual was dominant In the Great Basin. Cattle, sheep, and feral horses facilitated establishment, for they spread the seeds in the same areas that they disturbed. Once established, cheat-grass promoted the likelihood of fire to the detriment of the native species. In addition, other factors, such as the effects of the lack of vesicular arbuscular mycorrhizae and selective lagomorph grazing have worked in concert to further establish cheatgrass dominance.

The ecological consequences of cheat-grass establishment have been an increase in fire frequency and Intensity, a decrease in species diversity, and a landscape susceptible to severe erosion. Bunchgrasses interspersed with long-lived perennial shrubs now are replaced with either nearly pure patches of cheat-grass or swaths of cheatgrass and short-lived perennial shrubs. Some consequences to human activities involve the numerous ramifications of rangeland fires with costs of approximately US$20 million annually, the undependability of cheat-grass as a source of forage for cattle and sheep, and the value of biotic diversity as numerous plant and animals species undergo high amplitude population fluctuations. Management of these Great Basin vegetation communities should be approached using the state and threshold range condition model.

Article:

Nearly forty years have passed since the publication of W L Thomas' book *Man's Role in Changing the Face of the Earth*.[1] Although scholars had focused on human-biota interactions previously, this publication provided both empirical examples and a conceptual synthesis of ideas on the background, processes, and prospects of human alterations to the environment. The evolving dominance of the exotic annual grass, cheatgrass (*Bromus tectorum L*), in the Great Basin Desert provides yet another example of how humans constantly alter the environment and underscores a theme common in Thomas' book: that the unforeseen consequences of past human activities continue to make environmental impacts to the land, and that these impacts in turn, affect human activities in numerous, unanticipated ways. The purpose of this paper is fourfold: first, to survey the literature of the ecological history of cheat-grass in the Great Basin; second, to show how additional processes further cheatgrass dominance in the absence of continued grazing of domestic animals; third, to give examples of how these changes to the flora consequently have affected human activities in the region; and fourth, to place cheatgrass invasion in a theoretical context by examining range condition stable states and thresholds.

The capacity of humans to either accidentally or intentionally alter biota has occurred for several millennia and is well documented. Sauer[2] described early human influences on plants, where he showed how the introduction of exotic species, setting of fires, and clearing of brush and trees, all affected the landscape by allowing certain species new ecological advantages. Clearing of brush and trees favoured heliophytes (species requiring higher light levels), while aggressive exotic species exploited resource niches. Additional studies have shown the modifying ecological influence of domesticated animals.[3] Complimenting the studies on ecological impacts has been the growth in the field of environmental history, which has explored the relationship of human cultural influences in shaping the natural environment.[4]

Numerous examples exist chronicling anthropogenic alterations in the western United States during the last 150 years. Young and Budyt discussed the historical use of pinyon-juniper woodlands to support mining needs in Nevada. Rogers[6] studied vegetation changes caused by domestic livestock grazing and altered fire regimes during the last century in the eastern Great Basin. In south-eastern Arizona Bahre[7] studied the modifying effects of historic land use during the last 100 years to plant communities. All of these studies have shown the ability of humans to alter greatly the ecological balance of desert regions. What is equally interesting is that ecological modifications, in turn, can affect human activities.

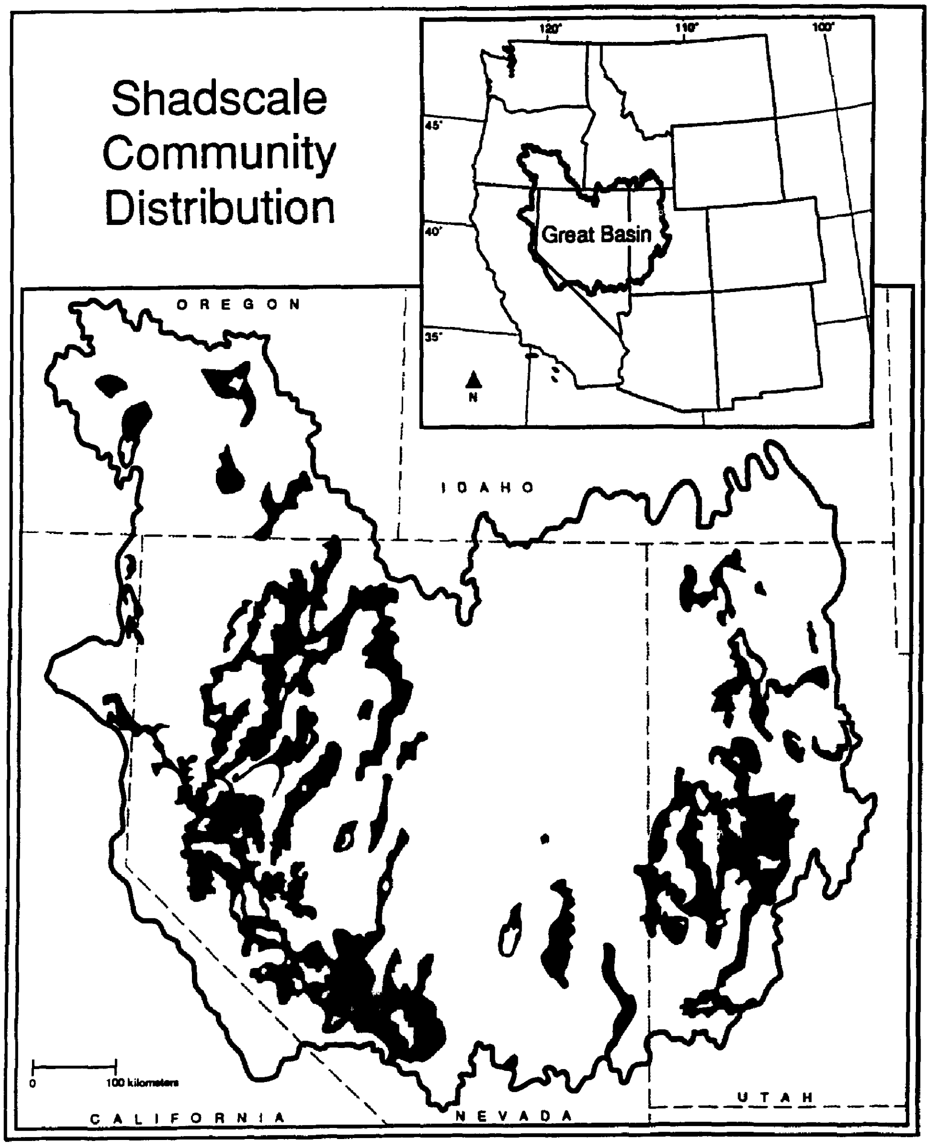

Figure 1. Shaded areas represent the distribution of *Atriplex confertifolia* (shadscale) in the Great Basin (bold black line). Adapted with permission from S Trimble, 1989. *Sagebrush Ocean*, University of Nevada Press, Reno.

The Great Basin is large, comprising parts of five states and an area greater than 390 000 km^2 (nearly two-thirds of it lies in Nevada); it is principally arid, averaging approximately 20 cm of precipitation annually; it is high, with average elevations greater than 1500 m; and it is mountainous, with over 300 distinct ranges. While human populations remain sparse (<2 million)[8] and concentrated within two urban areas (Reno, Nevada and greater Salt Lake City, Utah), numerous human activities have occurred that have altered severely the flora of the region. In particular, are the consequences of the introduction of cheatgrass for it represents an example of how easily humans can unintentionally alter the ecology of large areas.

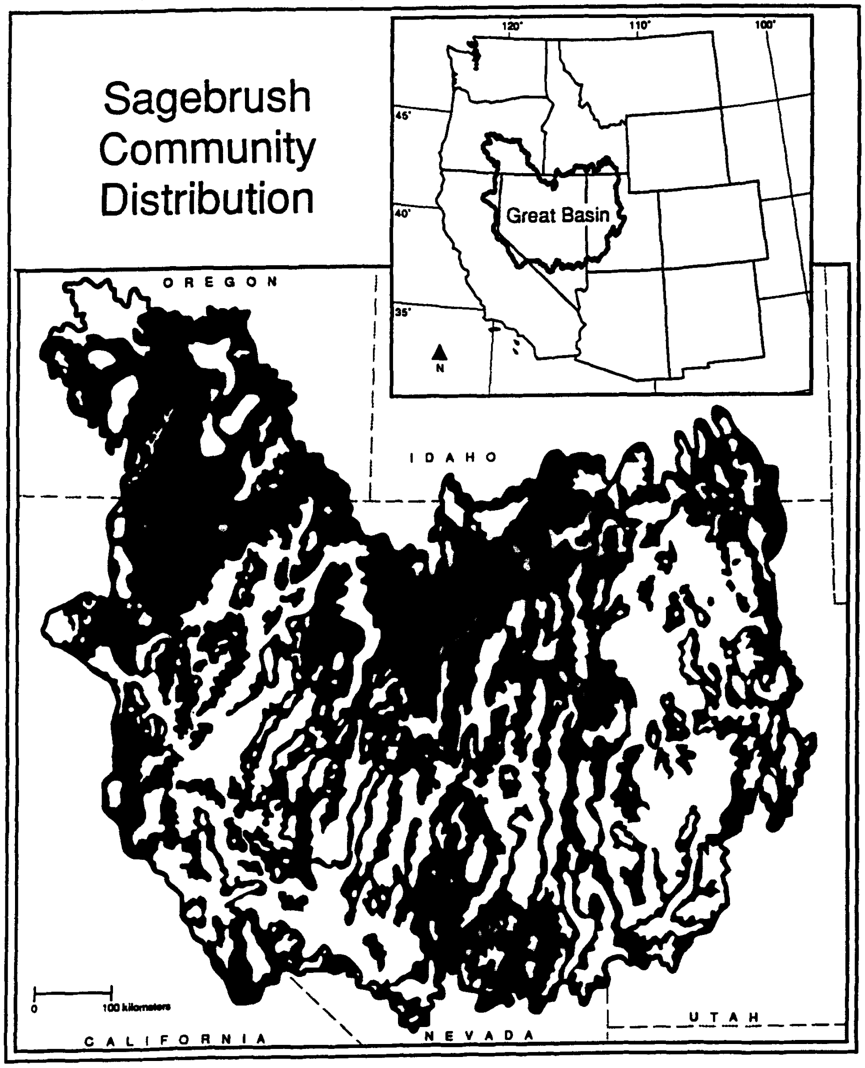

Figure 2. Shaded areas represent the distribution of *Artemisia tridentata* (sagebrush) in the Great Basin (bold black ine). Adapted with permission from S Trimble, 1989. *Sagebrush Ocean*. University of Nevada Press, Reno.

Domestic grazing is a common activity that has affected the biota in the broad expanse of the Great Basin Desert, and occurs primarily within two vegetation zones. The lowest, most arid zone is dominated by shadscale (*Atrixplex confertjfolia*), with subdominants such as winterfat (*Ceratoides lanata*), big greasewood (*Sarcobatus vermiculatus*), Indian ricegrass (*Oryzopsis hymenoides*), and the exotic annual cheatgrass (Bromus tectorum), called such because the presence of this grass in wheat fields 'cheated' farmers out of a full harvest.[9] This zone comprises approximately 30% of the Great Basin.[10] Grazing within the shadscale zone is more common in the upper (wetter) regions of this zone (Figure 1).[11] A slightly less arid region is the sagebrush- bunchgrass zone, which is dominated by big sagebrush (*Artemisia tridentata*). Other common species within the sagebrush zone are primarily bunchgrasses such as bluebunch wheatgrass (*Agropyron spicatum*), bottle-brush squirreltail (*Sitanion hystrix*), bluegrass (*Poa spp*), needlegrass (*Stipa spp*), Idaho fescue (*Festuca idahoensis*), and cheatgrass.[12] Approximately 45% of the Great Basin is in the sagebrush zone (Figure 2).[13]

Cheatgrass is ubiquitous throughout the Great Basin where it either has displaced competitively or replaced many of the annual and perennial grasses, and has decreased the dominance of ‘climax’ species.[14] Billings views the introduction of cheatgrass into the Great Basin as a ‘biotic cause of ecosystem impoverishment’ and decreased genetic diversity.[15] Others have questioned what type of impact the grass will have on livestock management.[16]

One result of cheatgrass dominance is a change in species richness and evenness of the Great Basin flora. For any given area there are likely to be fewer native bunchgrasses and annual forbs; and in areas where fires burn, cheatgrass is an early successional species preventing the re-establishment of native perennial shrubs. Areas (several km^2) of nearly 100% coverage by cheatgrass often lie in stark contrast to surrounding areas of shrubs and grass mix (Figures 3 and 4).

The introduction of cheatgrass has changed the floristic composition of thousands of km^2 in the Great Basin. In Nevada cheatgrass now is present on virtually all sagebrush-bunchgrass communities, and it is estimated that 20% of these communities are cheatgrass dominated to the point where root crown sprouting shrubs (eg, rubber rabbitbrush [*Chrysothamnus nauseosus*] and broom snakeweed [*Gutierrezia sarothrae*]) are unable to coexist.[17] In Nevada's shadscale zone, cheatgrass is rapidly becoming common, but less than 1% is cheatgrass dominated.[18]

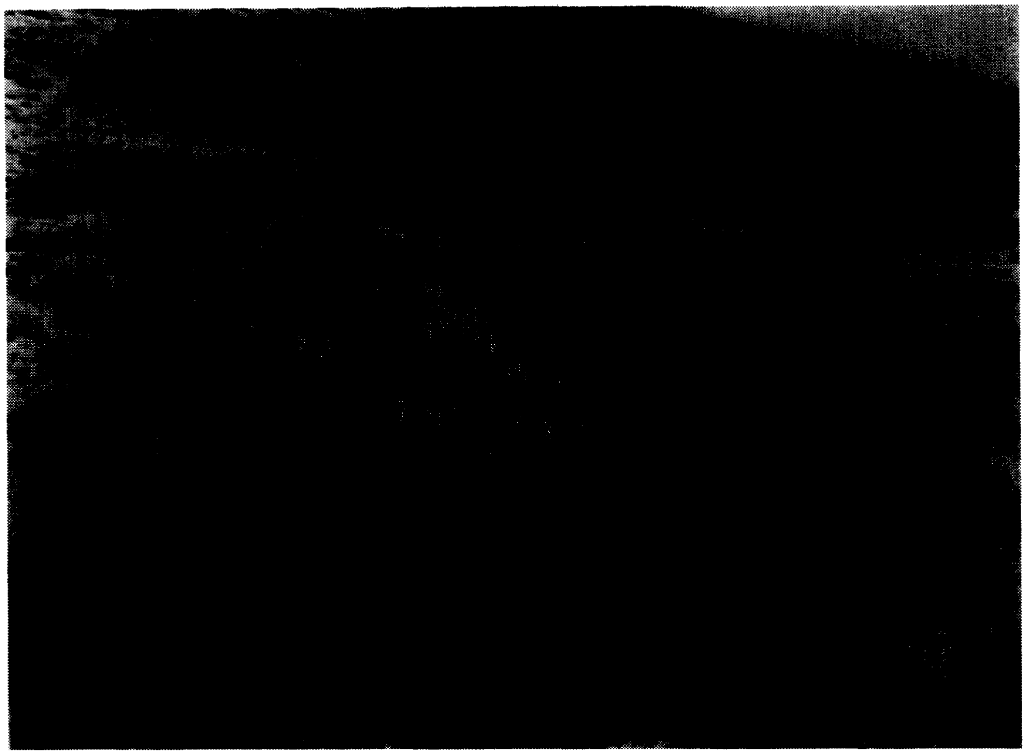

Figure 3. Foothills of Virginia Mountains near Reno, Nevada, elevation 1525 m. A potential sagebrush-bunchgrass community with a continuous coverage of *Bromus tectorum* interspersed with *Artemisia tridentata* and *Chrysothamnus nauseosus*. Extensive coverage of cheatgrass is common after wet years such as the winter of 1992–1993. Native bunchgrasses are absent.

Source: Photograph by author, 10 June 1993.

Ecological history of cheatgrass in the Great Basin

Presettlement vegetation and native grazers

Vegetation in the Great Basin prior to domestic grazing can be broadly discerned from the journals and diaries of early European-descent travellers through the Great Basin.[19] While John C Fremont collected plants and made casual observations during his trip into northern Nevada in the winter 1843-44, it was not until 1854 that a true scientific plant collection was made.[20] Lt Beckwith, 3rd Artillery, was in northwestern and north-central Nevada looking for a railroad route along the 41st parallel. Beckwith's report stated the abundance of bunchgrasses in the ranges and the dominance of sagebrush in the valleys. Reports by Schiel in 1859, Humphreys in 1871, and Simpson in 1876,[21] also state findings similar to Beckwith's.

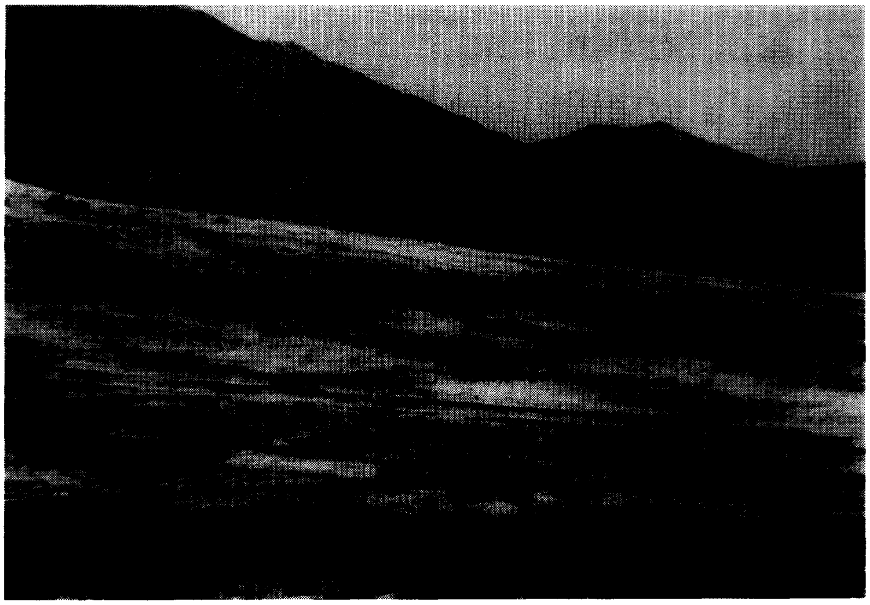

Figure 4. Looking north to north-west elevation 1250 m. Dominance of *Bromus tectorum* is shown in background (lighter areas are patches of dry cheatgrass) following a fire in 1989 in the Virginia Mountain foothills 25 km north of Reno, Nevada. Dark shrubs in foreground are *Gutierrezia sarothrae* (snakeweed) a common dominant following intense *Artemisia tridentata* fires.

Source: Photograph by author, 2 May 1992.

The Great Basin plant communities did not evolve with much grazing pressure. Bison seldom occupied the area, and herbivory had come from pronghorn antelope, bighorn sheep, mule deer, jackrabbits, rodents, and insects.[22] Collectively, the impact of native Great Basin animals was light and rarely damaging. This was essential, since C_4 sodgrasses, such as grama and buffalograss, which can support heavy grazing and protect the soil, were uncommon in the Great Basin. Instead, C_3 bunchgrasses (that evolved without heavy grazing) separated by fragile cryptogamic crusts were the norm.[23] Consequently, unlike the Great Plains where cattle replaced bison with little ecological impact, uncontrolled livestock grazing in the Great Basin was devastating to the native grasses.

A few examples exist in the Great Basin to show how vegetation appears without domestic grazing impacts. Vegetation composition surveys completed on kipukas (pristine areas of older landscape surrounded by lava flows that make access for ungulates impossible) in sagebrush-bunchgrass associations in southern Idaho and south-eastern Oregon have shown that cheatgrass is present in minor amounts in the plant communities.[24] Similarly, Passey et al[25] examined the composition of sagebrush-bunchgrass communities in thirty-two relict areas of the Intermountain West, and found that, based on a prevalence index (PI), cheatgrass ranked ninth. Five native bunchgrasses had a higher PI in the same study.

The value of studies completed in pristine areas of the Intermountain West cannot be underestimated, for additional evidence suggests that only minor disturbances can hasten major changes to vegetation composition. Driscoll,[26] for example, studied the vegetation composition on a semi-isolated plateau in central Oregon that had been grazed by sheep for only two summers in the 1920s. Driscoll found that cheatgrass dominated areas occurring immediately north and east of western juniper (*Juniperus occidentalis*) areas where sheep concentrations were high because of the afternoon shade protection provided by the trees.

Grazing

The introduction of thousands of domestic cattle into the western Great Basin began in 1864 to support the Comstock Lode mining operations around Virginia City, Nevada. Discovery of precious ores in Austin, Pahrangat, White Pine, and Eureka, Nevada during the 1860s additionally increased the demand for beef and subsequently led to domestic grazing activities into central and eastern Nevada.[27] Further, Nevada had no fence laws that made livestock owners liable for damage caused by their animals, which attracted many (California) ranchers in the early 1870s. Nevada became the new frontier for livestock operations, for pristine range was still abundant.[28] By 1874 there were at least 180 000 cattle grazing in Nevada.[29]

Sheep also were causing range damage in the Great Basin beginning in the 1850s. Sheep were valued for both their mutton and wool, and the expansion of the sheep industry into the Great Basin was heightened by development of mining camps during the 1860s and 1870s. The sheep industry grew rapidly with the number of head in Nevada rising from a few thousand in the late 1850s to nearly 400 000 by 1890 and approximately 1200 000 head from 1908 to 1928.[30] In the early 1990s, approximately 100 000 sheep were grazing in Nevada.[31]

While sheep and cattle competed for many of the same resources, the impact of the sheep on the landscape was probably even greater than that of the cattle. Cattle were primarily confined to the relatively gentle terrain of the shadscale and sagebrush-bunchgrass vegetation zones in the Basin where they could manoeuvre sufficiently to graze on bunch-grasses and palatable shrubs such as winterfat. Conversely, sheep were not solely confined to the lower vegetation zones. The mountain grasslands, which because of the steep terrain were not favourable cattle grazing areas, were heavily foraged by sheep during the summer. In the spring and fall, sheep competed with cattle on the sagebrush-bunchgrass, and in the winter similar competition existed in the shadscale zone. While grasses are major constituents of sheep diets, sheep are also efficient consumers of many of the browse species (shrubs) in the shadscale zone[32] and often eat plants to the rootstock.

Horses also caused range deterioration in the Great Basin from the 1870s through the 1930s.[33] Horse populations have varied considerably in the last century, with population fluctuations being as much a function of climatic events (ie, drought) as governmental policy. An estimated 100 000 horses were reported ranging in Nevada in 1910; 12 000 in 1950; 28 000 in 1982; and nearly 31 000 in 1989.[34]

The observation that many of the Great Basin ranges were overgrazed became common in the 1880s.[35] This was not surprising, however, given the circumstances. Ranching techniques used in the arid and semi-arid Great Basin evolved from Spanish herdsmen who came from a Mediterranean climate that supported different vegetation than that in the Great Basin. These ranching techniques were then applied by Anglo-Texas ranchers who had their animals graze on either the woodlands of southern and eastern Texas, or the sodgrass plains of west Texas. In either case, the environment was sufficiently resilient to resist major ecological damage, especially considering these areas evolved with grazing pressures from bison; however, when similar numbers of livestock were placed on the Great Basin ranges, severe overgrazing occurred.[36]

Overgrazing of rangelands continued to cause range deterioration in the Great Basin through the early 1930s.[37] Congress responded in 1934 with the Taylor Grazing Act (TGA), which was designed to 'stop injury to the public grazing lands by preventing overgrazing and soil deterioration'.[38] The TGA came under the jurisdiction of the Bureau of Land Management (BLM) in 1946. Since TGA jurisdiction was enforced by the same livestock ranchers who necessitated its creation, few were surprised that the implementation of TGA policies did little to ameliorate range conditions in Nevada.[39] More recently, a Government Accounting Office report[40] on range management of BLM and Forest Service lands in the western USA concluded that 50% of western rangelands remain in either poor or fair condition (the lower two of four categories).

Introduction, disturbance, and dissemination

The introduction of cheatgrass into western North America can be traced back to 1889 in the interior Pacific North-west[41] and, given it was found in agricultural fields, it likely came as a grain contaminant. Cheatgrass may have also been introduced to the West embedded in the wool/hide of Old World sheep or cattle. The latter means of introduction is speculation based on the fact that cheatgrass evolved in Mediterranean Europe and in the regions where cattle, sheep, and goats were first domesticated: central and south-western Asia.[42]

The first records of cheatgrass in the Great Basin came from Provo, Utah in 1894, Elko, Nevada in 1905, and Reno, Nevada in 1906. Once introduced, cheatgrass spread rapidly throughout the Intermountain West, and by the late 1920s the grass was common throughout the sagebrush-bunchgrass biome of the Great Basin.[43]

The original means of cheatgrass dispersion in the Great Basin were linked to direct human activity along the railroad lines. Cheatgrass was spread when discarded in the bedding straw and dung of cattle and when refuse straw was used for dry goods packing. Cheatgrass was additionally dispersed away from the railroad lines when mixed in cereal grains[44] although this impact may have been minor in the Great Basin because of the lack of water for extensive cropping. The original dispersion of cheatgrass probably was localized to small areas, since seeds of cheat-grass are most commonly dispersed only short distances (<1 m) from the parent plant by wind.[45] It was the influence of subsequent grazing by domestic livestock and feral horses that facilitated further dissemination of the grass.

Although cheatgrass is ubiquitous in the West, it has established its greatest dominance in the Great Basin for primarily two reasons.[46] First, there is a lack of a dominant native annual grass in the Great Basin, so an unoccupied resource niche was available for the annual cheatgrass to exploit following disturbances to the native vegetation. Cheatgrass exhibits a high degree of phenotypic plasticity in life history characteristics allowing the grass to overwhelm native species in the highly variable environments found in the Great Basin.[47] For example, the high germination rate (up to 99.5% success) of cheatgrass seedlings provides an advantage over native perennials.[48] Further, cheatgrass root growth is much greater in winter than bluebunch wheatgrass, which confers an advantage for cheatgrass in the spring because it can utilize soil moisture earlier and faster than the native grasses.[49]

A second reason for cheatgrass dominance is that precipitation patterns in the western Great Basin are similar to those in the areas where cheat-grass evolved. In all areas there is a wintertime precipitation maximum followed by dry summers. The timing of the western Great Basin precipitation pattern is particularly similar to that of central and south-western Asia, since summer thunderstorms are infrequent and bring little rainfall. Similar precipitation patterns allow cheatgrass to germinate in autumn with the first significant rain. Fall germinated plants can then grow into densely packed stands (up to 15 000 seedlings/m^2) with root systems elongating during the winter.[50] During the following spring when temperatures are sufficiently warm for shoot growth, the more developed cheatgrass root system effectively removes soil moisture to the competitive disadvantage of the native perennial grasses.[51]

The invasion of cheatgrass in western North America was thought to have reached its maximum range expansion (the sagebrush/bunchgrass zone) by 1930.[52] Hunter,[53] however, has shown that cheatgrass increased in frequency and dominance on the Nevada Test Site (NTS) in the last thirty years and that cheatgrass is now found at elevations below the sagebrush-bunchgrass zone. This latter result is supported by Knapp,[54] who reported cheatgrass in disturbed shadscale zones in western Nevada.

It is likely that the domination of cheatgrass would not be as great today without the introduction of livestock. Livestock facilitate the spread of cheatgrass by two means. First, excessive grazing reduces the native herbaceous vegetation by cropping the plant so closely that it is unable to capture enough sunlight for sufficient photosynthesis and/or to reach maturity, when it produces seeds for future germination.[55] Secondly, cheatgrass is easily dispersed by animals because the spikelet contains seeds that either easily adhere to animal hides, or may become embedded in animal hooves.[56] With hundreds of thousands of livestock grazing the open range every year, cheatgrass was exposed to virtually every available grazing site in the Great Basin.

Cheatgrass persistence following disturbance and dissemination

Disturbance and dissemination facilitated the establishment of cheatgrass, but the persistence of the grass once established is responsible for the cultural-ecological landscape of the Great Basin. Three factors work in concert to ensure the continued dominance of cheatgrass: the occurrence of fire; the temporary elimination of vesicular-arbuscular mycorrhizae; and lagomorph activity.

Fire

Fire is the most important factor in assuring and aiding the survival of cheatgrass. Fire within the xeric sagebrush-bunchgrass communities of the Great Basin occurs at intervals between approximately 60-110 years.[57] Fires within the shadscale zone are infrequent and may be nonexistent because of insufficient biomass to carry the fires from shrub to shrub.[58] Changes in the density of cheatgrass have led to commensurate changes in fire frequency. Hull[59] has estimated that cheatgrass rangeland is 10-500 times more likely to burn than native bunchgrasses, and that the fire season is extended by one to three months. Further, fires have shown a tendency to occur repeatedly within cheatgrass dominated areas. On a south-western Idaho rangeland over 50% of the fires that occurred between 1981 and 1987 were in previously burned, cheatgrass dominated areas.[60] Cheatgrass fires burning at recurrence intervals of less than five years are common on the Snake River Plain of southern Idaho.[61]

Cheatgrass fires are common because the amount of fine fuel that accumulates in cheatgrass dominated areas is far greater than occurs in either the pristine sagebrush-bunchgrass or shadscale zones. Cheatgrass can occur in such densities as to cover the ground completely.[62] Additionally, cheatgrass biomass may accumulate over several years because the arid conditions of the Great Basin inhibit rapid decomposition. The result of continuous fuel accumulations is a proliferation of wildfires during the summer in the Great Basin. In 1985 for example, over a million acres of rangeland burned in Nevada.[63]

Numerous studies[64] have shown that cheatgrass dominates plant communities after fire to the point where many native perennial plants are unable to re-establish. The success of cheatgrass following fire has been linked to the ability of the grass to fill an unoccupied resource niche following the fire. Many of the native perennial shrubs such as big sagebrush and shadscale are non-sprouting following fire and revegetate only through seeds.[65] If fires are less than a few years apart, cheatgrass quickly establishes dominance within a couple of years and excludes many of the common shrubs of the Great Basin such as antelope bitter-brush (*Purshia tridentata*), cliffrose (*Cowania mexicana*) and big sagebrush.[66] If fires are slightly less frequent, resprouting perennials such as rabbitbrush (*Chrysothamnus spp*) may share the disturbed site with cheatgrass.[67] Additional research done in northern Nevada, however, also suggests that productivity and water status of rabbitbrush and needle and thread (*Stipa comata*) may be affected adversely by cheatgrass because the root system of cheatgrass used soil resources that would have been used by the native species.[68]

Fires within the shadscale zone of the Great Basin may lead to even greater changes in vegetation composition. Until the early 1980s, cheat-grass was not considered an important species within the shadscale zone. It is now known, however, that cheatgrass is becoming an increasingly important element within this arid zone because the accumulation of cheatgrass phytomass has allowed fires to burn in areas where they had never burned before. The result of the fires has been an increase in cheatgrass, the native perennial Indian ricegrass, and other exotic annuals such as Russian thistle (*Salsola australis*) and halogeton (*Halogeton glomeratus*) at the expense of the native shrubs.[69] Young and Tipton[70] have speculated on the causes of the invasion of cheatgrass into the shadscale zone, including precipitation change, genetic changes, and grazing management change. The most credence was placed on the latter cause, where, since the 1960s, there has been a deferral of grazing for either an entire season or until after seedripe has occurred. This grazing strategy has allowed cheatgrass phytomass to accumulate because less cheatgrass is consumed and the seedbed is replenished annually with cheatgrass seeds. The cheatgrass increase comes at the expense of native perennial grasses because prior heavy grazing caused a greater depletion of the seed bank for perennial grasses as opposed to cheatgrass.

Role of vesicular-arbuscular mycorrhizae

Within the Great Basin, three non-native annual species have an interesting relationship with vesicular-arbuscular mycorrhizae (VAM). VAM are symbiotic fungi that, upon infection on plant roots, extract carbon from the plant, but in return facilitate nutrient and water absorption via the hyphal network.[71] Plants vary in their dependence on the fungi, with species such as Russian thistle and halogeton being non-mycotrophic, while most grasses such a cheatgrass are facultatively mycotrophic, and most shrubs such as big sagebrush are obligately mycotrophic.[72]

Disturbance of land that facilitates topsoil erosion, such as excessive grazing, can either reduce or eliminate propagules of mycorrhizal fungi, and the establishment of secondary successional species may be related to propagule density.[73] Work done on Wyoming sagebrush-bunchgrass[74] indicated that following disturbance there was a severe depletion of mycorrhizal infection in the soils, and species from different seral stages had different physiological responses to the subsequent re-infection of mycorrhizae. Study results showed that Russian thistle and halogeton were pioneer seral stage species that exhibited reduced growth and water vapour conductance following the addition of mycorrhizal fungi (within one to two years after disturbance) on their rhizospheres. Mycorrhizal re-infection then favoured cheatgrass in the second sere of succession because the grass was not physiologically affected by the presence of mycorrhizal inoculum.[75] Mycotrophic species, such as Indian ricegrass and bluebunch wheatgrass, were expected to dominate the secondary sere because of the addition of VAM inoculum, but the competitive superiority of cheatgrass did not allow these species to establish successfully. Although the duration of the study was not sufficient to examine the successional stages leading to a sagebrush-bunchgrass community, seral development to climax shrubs was viewed as unlikely because succession was halted by cheatgrass dominance.

Lagomorph grazing pressure

Cheatgrass may continue dominance in sagebrush-bunchgrass communities because grazing pressures applied by jackrabbits and rodents alter the population dynamics of the grass.[76] On a study of plant successional dynamics on two exclosures within the sagebrush-bunchgrass zone of southern Idaho, Hironaka and Tisdale[77] found that the return of perennial grasses to a formerly disturbed site only occurred after blacktail jackrabbits (*Lepus californicus*) were excluded. Furthermore, at the same site Hironaka[78] found that even though livestock grazing could be removed, the presence of small mammals either could delay or prevent secondary succession (beyond the cheatgrass sere) from occurring.

Prevention of secondary succession is caused by the severe damage and destruction from lagomorph and rodent grazing. In a study of the influence of mountain meadow mouse (*Microtus montanus*) on the population dynamics of cheatgrass and bluebunch wheatgrass in eastern Washington, Pyke[79] found that bluebunch wheatgrass was more sensitive than cheatgrass to the intensity and time of grazing and the growth response following grazing. The result of the differential response of these grasses led to cheatgrass dominance.

Influences to human activities

Costs of fire

While humans have altered the flora of the Great Basin, the invasion of cheatgrass has also influenced human activities. Perhaps the greatest attention has been placed on fire control and the costs of fire fighting, since the importance of cheatgrass in causing fires cannot be underestimated. In an examination of a 31-year fire record (ending in 1988) for the BLM Shoshone District in southern Idaho, Whisenant[80] found that 90% of burned acreage had occurred in areas dominated by cheatgrass. Because of the numerous ramifications of increased fire intensity and frequency caused by cheatgrass, considerable effort is placed on prescribed burning, and presuppression activities such as construction of fire fuel breaks, increased awareness of fire safety measures, and the allocation of aerial and foot patrols in areas likely to burn.[81] In addition, in years of extreme fire danger, many areas are closed to public access (eg, no off-road vehicles), and activities are limited (eg, no campfires) in other areas. All of this occurs in an environment where, prior to cheatgrass invasion, fire was an infrequent event.

The annual costs of fires are prohibitive and can be broken into five categories: resource losses, suppression costs, presuppression costs, rehabilitation and fire management (Table 1). Based on 1991 Vale (OR) BLM District values, resource losses — which include forage loss, wildlife impacts, visitor impacts, fish habitat impacts and post-fire soil erosion — average US$35.88/acre burned.[82] Suppression costs, which include construction of active fuel breaks, payroll for crews, and all equipment are US$12.75/acre burned.[83] Resource loss and suppression costs vary only slightly throughout the BLM districts in the Great Basin. Presuppression activities (eg, hiring fire fighters, stocking water tanks, buying fire trucks) vary more by district, ranging from zero to US$1.5 million annually, but average US$500 000 per district in the Great Basin.[84]

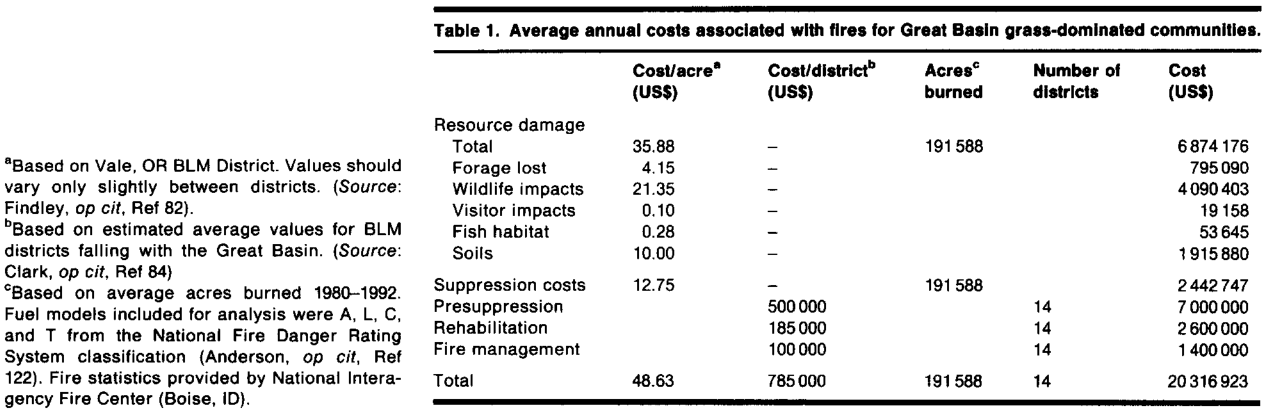

Table 1. Average annual costs associated with fires for Great Basin grass-dominated communities.

	Cost/acre[a] (US$)	Cost/district[b] (US$)	Acres[c] burned	Number of districts	Cost (US$)
Resource damage					
Total	35.88	–	191 588		6 874 176
Forage lost	4.15	–			795 090
Wildlife impacts	21.35	–			4 090 403
Visitor impacts	0.10	–			19 158
Fish habitat	0.28	–			53 645
Soils	10.00	–			1 915 880
Suppression costs	12.75	–	191 588		2 442 747
Presuppression		500 000		14	7 000 000
Rehabilitation		185 000		14	2 600 000
Fire management		100 000		14	1 400 000
Total	48.63	785 000	191 588	14	20 316 923

[a] Based on Vale, OR BLM District. Values should vary only slightly between districts. (*Source*: Findley, *op cit*, Ref 82).

[b] Based on estimated average values for BLM districts falling with the Great Basin. (*Source*: Clark, *op cit*, Ref 84)

[c] Based on average acres burned 1980–1992. Fuel models included for analysis were A, L, C, and T from the National Fire Danger Rating System classification (Anderson, *op cit*, Ref 122). Fire statistics provided by National Interagency Fire Center (Boise, ID).

Significant effort is placed on rehabilitation of burned rangeland because of the severe erosion problems that work in concert with fire cycles. While cheatgrass is an effective stabilizer of topsoil, the grass does little to curb erosion after burning and loss of vegetation cover following fire creates numerous watershed problems such as increased susceptibility to flooding, siltation of rivers and streams, and loss of soil nutrient status.[85] For the Great Basin, fire rehabilitation of burned areas, including reseeding, construction of fences to exclude livestock, and labour, average approximately US$2.6 million annually.[86]

Fire management involving prescribed fire, smoke management and fuels management (green stripping) is an additional cost associated with fires. This cost is also site specific like rehabilitation, but averages approximately US$100 000 annually per BLM district.[87]

To give a rough estimate of the annual cost of fires in the Great Basin, I used fire statistics from 1980-1992 of the total acres burned in grass-dominated communities of all the 14 BLM districts that lie (at least partially) in the Great Basin boundary. Based on an average of 191 588 acres burning annually (values ranged from 31 983 acres in 1991 to 687 175 acres in 1985) the annual cost of fire was US$20 million of which approximately 'one-half can be attributed to cheatgrass'.[88]

Effects to ranching

The ranching industry has also been affected by the invasion of cheat-grass. Considerable debate exists as to the value of cheatgrass as a source of forage, especially in comparison to the native bunchgrasses.[89] Cheatgrass is a nutritious and palatable forage crop,[90] particularly in the winter. Since cheatgrass germinates in the autumn and continues growth throughout winter, it provides green grass during a period that few other grasses do.[91] In addition, it is one of the few grasses that grows on the alkaline soils associated with the drier (lower elevation) areas of the Great Basin.[92]

A major shortcoming of cheatgrass is that it is an undependable source of forage.[93] Ranchers who do rely on cheatgrass as a major source of feed are vulnerable to the extreme flammability of the grass, since either a lightning strike or spark from a catalytic converter could easily start a fire that would destroy a source of forage for a year.[94] In addition, cheatgrass productivity is affected more by annual precipitation than are perennial grasses.[95] In an examination to determine grazing capacity on cheatgrass, Stewart and Young[96] found that herbage production was double for perennial grasses in comparison to cheatgrass during wet years and twelve times greater than cheatgrass during droughts. A further problem with cheatgrass is that when dry, its stiff awns or sharp seeds can puncture either the eyes, causing blindness, or the mouth and throat of livestock, causing lumpy jaw.[97]

An ironic twist to cheatgrass dominance is that to reduce fire probability, grazing is necessary to remove the cheatgrass that allows fire to carry. In the Lahontan Basin of Nevada, Young and Tipton[98] found that the reduction of grazing because of shifts in management policy had led to a condition where sufficient (cheatgrass) fuel was present to carry fire in the shadscale communities. Since fire was rare in these communities prior to cheatgrass establishment, the communities are particularly susceptible to changes in vegetation composition after a burn.

Influences to biological diversity

A substantial number of plant and animal populations have been altered in the Great Basin by the presence of cheatgrass. In studies on the Snake River Birds of Prey area in south-western Idaho, Groves and Steenhof[99] and Yensen et al[100] found that in areas where cheatgrass had increased fire intensity and frequency, that the number of active burrows of the Townsend's ground squirrel (*Spermophilus townsendii idahoensis*) had significantly decreased. These squirrels are an important prey base for a number of animals including nesting prairie falcons (*Falco mexicanus*), red-tailed hawks (*Buteo jamaicensis*) ferruginous hawks (*B regalis*), badgers (*Taxidea taxus*) and rattlesnakes (*Crotalus viridis*). Results suggest that the loss of the squirrels has led to an environment with high amplitude population fluctuations: the type of fluctuations that make the affected animal populations extinction-prone.[101] Additional impacts have occurred with the fire-induced loss of forage for pronghorn and rabbits and subsequent influence on the birds (eg, bald and golden eagles) that utilized the rabbits as prey base.[102]

There is numerous evidence that when certain populations are led to near extinction, even on a local scale, that there are many unanticipated consequences. Ehrlich[103] has suggested that removal of just one plant species probably eliminates approximately ten animal species, and Myers[104] has illustrated that species not kept in check by competition flourish by adapting to human culture and technology (eg, the Norway rat [*Rattus rattus*] and the German cockroach [*Blatella germanic*]). In the Great Basin, Billings[105] has addressed the problems of biotic impoverishment as a result of cheatgrass.

Conclusions

The invasion of cheatgrass in the Great Basin Desert presents one example of a major ecological alteration to large areas. The grass now dominates approximately one-fifth of the potential sagebrush-bunchgrass habitat and is rapidly increasing within the shadscale zone. Fires, once either infrequent or virtually non-existent within the vegetation zones are common. The fire-scarred land often revegetates with exotic annuals, particularly *B tectorum*. Great Basin Desert flora is now typically characterized by fewer species per area, single species dominance, a paucity of bunchgrasses, and a patchwork mosaic of areas where perennial shrubs have burned and have been replaced with annuals. Young et al[106] have described the processes that have led to increased *B tectorum* dominance as a 'downward spiral of concentric cycles of degradation'. The cause of this was the accidental introduction of *B tectorum*, the ability of cattle, sheep and feral horses to facilitate the dissemination and establishment of the grass, and the subsequent ability of the grass to exploit niches in disturbed areas. Other factors, such as changed fire regimes, the lack of VAM, and the role of small mammals provide *B tectorum* with a competitive advantage over many native annual and perennial species and have further established the dominance of this species within the Great Basin.

Many lessons are learned regarding the management of human induced landscapes such as are found in the Great Basin. Foremost, is relating these events to other disturbed arid environments in an effort to apply appropriate range condition models necessary for wise management decisions. Several have noted the inadequacies of the traditional Clementsian range succession mode1,[107] which views alterations of plant communities as temporary, and assumes the return of rangelands to a predisturbed climax condition following the cessation of disturbance (eg, drought, overgrazing). The range succession model has severe limitations because plant communities may be changed irreversibly; recovery is neither consistent nor continuous; multiple stable states may exist; non-equilibrium communities are possible; and, stochastic elements (eg, introduction of exotics, fire) can alter or truncate succession.[108] Several alternative range condition models have emerged in the last decade that incorporate multiple stable states and non-equilibrial conditions.[109] Among these models are the 'state and transition',[110] 'thresholds and state',[111] and the 'non-equilibrial persistene.[112]

While it may be difficult to pinpoint with certainty which model is most appropriate for the Great Basin, the thresholds and state model appears to represent best the current understanding of Great Basin ecology. This model assumes either multiple states or conditions can be found on a rangeland where distinct communities exist. The transition from one plant community to another typically involves crossing a threshold (eg, initiated by fire, grazing, introduction of exotic species) where the changes are irreversible in the absence of intervention.[113] Pellant and Hall[114] examined the distribution of cheat-grass and another exotic annual (medusahead wildrye) on BLMmanaged rangeland in the Intermountain West (primarily within the Great Basin) and found that over 80% of the public lands were infested with annual grasses. More revealing, however, were the categories in which they delineated three levels of infestation based on the weight of the species composition: (1) 'monoculture', with greater than 60% annual grasses; (2) `understory', with 10-59% annual grasses; and (3) 'potential', with less than 10% annual grasses. They found that more than 60% of the Intermountain BLM rangelands were classified as 'potential' and were 'at risk of invasion' by the annual grasses if disturbed.

History suggests that the transition to greater cheatgrass dominance is incomplete and likely to continue. In particular, is the cheatgrass/fire cycle that acts as the catalyst to cross the threshold into a different stable state, such as from 'potential' to `understory' classes. Knapp[115] examined climatic predictors of fire in the grass-dominated communities of the Intermountain West between 1980 and 1992, and found weather conditions that either increased the amount of fine fuels, or suppressed favourable fire season conditions (thereby allowing greater fuel accumulations), and were conducive to promoting fire. These results suggest that given a fire-favourable series of weather conditions, even areas that are less prone to fires such as those classified as 'potential', are susceptible to change towards a new stable state.

The impacts on human activities in the Great Basin and the difficulty of rangeland stewards to mitigate the expansion of exotic grasses are not unique, and ecological parallels are found in other North American rangelands. In the Central Valley of California, the historical advance of annuals into the native grasslands has followed a similar path to cheat-grass in the Great Basin.[116] The transformation of the native grassland was caused by two factors. First, overgrazing of domestic livestock in the mid-1800s coupled with a decade-long drought altered the vegetation dynamics of the region. Second, the degraded grasslands became susceptible to the establishment of exotic annuals from Eurasia, which commonly outcompete natives.[117] Recovery of native perennials appears unlikely even in the absence of domestic grazing,[118] and natural resource managers are being encouraged to apply state and transition models to understand better rangeland dynamics.[119] Similarly, in south-eastern Arizona, an exotic perennial from South Africa, Lehmann lovegrass (*Eragrostis lehmanniana*), has substantially reduced native grass cover, and reduced biodiversity in areas where the exotic dominates.[120] Although Lehmann lovegrass has been used by several governmental agencies for reseeding damaged rangelands and transportation rights-of-ways, the expansion of Lehmann lovegrass has been hastened by the selective grazing pressures of cattle whose preferential foraging on native grasses provides the exotic with a competitive advantage.[121]

There is little doubt that human activities in the Great Basin will continue to be influenced by the ecological ramifications of cheatgrass invasion. The establishment of exotic species, whether accidentally or intentionally, has occurred globally for several millennia and has invariably altered human activities — often with undesirable consequences. The dominance of cheatgrass in the Great Basin serves as another example that not only do humans alter the flora of large areas, but that these modifications in turn affect human activities.

Notes:

1 W L Thomas (ed) Man's Role in Changing the Face of the Earth, University of Chicago Press, Chicago, 1956
2 C O Sauer, 'Early relation of man to plants', The Geographical Review, Vol 37, 1947, pp 1-25
3 J D Brotherson and W T Brotherson, 'Grazing impacts on the sagebrush communities of southern Utah', Great Basin Naturalist, Vol 41, No 3, 1981, pp335-340; W P Cottam, 'Is Utah Sahara Bound?' Bulletin of the University of Utah, Vol 37, 1947, pp 1-40; F F Darling, 'Man's ecological dominance through domesticated animals on wild lands', in W L Thomas, op cit, Ref 1, pp778-787
4 R White, 'American environmental history: The development of a new historical field', Pacific Historical Review, Vol 54, 1985, pp297-335; D Worster, Dust Bowl: The Southern Plains in the 1930s, Oxford University Press, New York, 1979
5 J A Young and J D Budy, 'Historical use of Nevada's pinyon-juniper woodlands', Journal of Forest History,

Vol 23, 1979, Pp 113-121

6 G F Rogers, Then and Now, University of Utah, Salt Lake, 1982

7 C J Bahre, A Legacy of Change, University of Arizona Press, Tucson, 1991

8 US Bureau of the Census, Census of Population and Housing, Bureau of the Census/Economics and Statistics Administration, Washington, 1992

9 P T Tueller, 'Vegetation and land use in Nevada', Rangelands, Vol 11, 1989, pp 204-210

10 S Trimble, The Sagebrush Ocean, University of Nevada Press, Reno, 1989; Tueller, op cit, Ref 9

11 R J Tausch, Adjunct Professor, Range, Wildlife and Forestry, University of Nevada, Reno, 89557, personal communication August and September, 1992

12 Tueller, op cit, Ref 9

13 Trimble, op cit, Ref 10

14 R N Mack, 'Invasion of Bromus tectorum L into western North America: An ecological chronicle', Agro-Ecosystems, Vol 7, 1981, pp 145-165

15 W D Billings, 'Bromus tectorum, a biotic cause of ecosystem impoverishment in the Great Basin', in G M Woodwell (ed) The Earth in Transition: Patterns and Processes of Biotic Impoverishment, Cambridge University Press, New York, 1990, pp 301-322

16 J D DeFlon, 'The case for cheatgrass', Rangelands, Vol 8, 1986, pp 14-17; R Devine, 'The cheatgrass problem', Atlantic Monthly, Vol 271, 1993 pp 40-48; J A Young, R A Evans, R E Eckert Jr and B L Kay, `Cheatgrass', Rangelands, Vol 9, 1987, pp 266-270

17 K P Price and J D Brotherson, 'Habitat and community relationships of cliff rose (Cowania mexicana var stansburiana) in central Utah', Great Basin Naturalist, Vol 47, 1987, pp 132-151; J A Young, Adjunct Professor, Range, Wildlife and Forestry, University of Nevada, Reno, personal communication, August and September, 1992

18 Young et al, op cit, Ref 16; J A Young and F Tipton, 'Invasion of cheatgrass into arid environments of the Lahontan Basin', in E D McArthur, E M Romney, S D Smith and P T Tueller (compilers) (eds) Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, US Department of Agriculture, General Technical Report INT 256, Intermountain Research Station, USFS, Ogden, Utah 1990, pp. 37-40; Young, op cit, Ref 17

19 T R Vale, 'Presettlement vegetation in the sagebrush-grass area of the Intermountain West', Journal of Range Management, Vol 28,1975, pp 32-36

20 Billings, op cit, Ref 15

21 Vale, op cit, Ref 19

22 R N Mack and J N Thompson, 'Evolution in steppe with few large, hooved animals', The American Naturalist, Vol 199, No 6, 1982, pp 757-773; Billings, op cit, Ref 15; B A Haws, G E Bohart, C G Riley, and D L Nelson, 'Insects and shrub die-off in western states: 1986-89 survey results', in E D McArthur et al, op cit, Ref 18, pp 127-151

23 Mack, op cit, Ref 14; Billings, op cit, Ref 15; Haws et al, op cit, Ref 22

24 E E Tisdale, M Hironaka, and M A Fosberg, 'An area of pristine vegetation in Craters of the Moon National Monument, Idaho', Ecology, Vol 46, 1965, pp49-352; R R Kindschy, 'Pristine vegetation of the Jordan Crater kipukas: 1978-1991', in S B Monsen (ed) Proceedings—Symposium: Ecology, Management and Restoration of Intermountain Annual Rangelands, US Department of Agriculture, Intermountain Research Station, USFS, Ogden, 1994, pp 85— 88

25 H B Passey, V K Hugie, E W Williams, and D E Ball, Relationships Between Soil, Plant Community, and Climate on Rangelands of the Intermountain West, Technical Bulletin No 1669. USDA-Soil Conservation Service, Washington, DC, 1982

26 R S Driscoll, 'A relict area in the central Oregon juniper zone', Ecology, Vol 45, 1964, pp 345-353

27 J A Young and B A Sparks, Cattle in the Cold Desert, Utah State University Press, Logan, 1985

28 Ibid

29 B Hazeltine, C Saulisberry, and H Taylor, A Range History of Nevada, American Society of Range Management, Reno, 1965, Nevada Section

30 Young and Tipton, op cit, Ref 18; B W Sawyer, Nevada Nomads, Harlan-Young Press, San Jose, 1971

31 Young and Tipton, op cit, Ref 18

32 Young and Sparks, op cit, Ref 27
33 Hazeltine et al, op cit, Ref 29
34 Ibid; J Berger, Wild Horses of the Great Basin, University of Chicago Press, Chicago, 1986; Bureau of Land Management, Public Land Statistics, US Department of Interior, Washington, DC, 1990
35Young and Sparks, op cit, Ref 27
36 Ibid
37 T R Vale, 'Sagebrush conversion projects: an element of contemporary environmental change in the western United States', Biological Conservation, Vol 6, 1974, pp 274-284
38 T R Vale, Report by Bureau of Land Management on range conditions and grazing in Nevada, Biological Conservation, Vol 8,1975, pp 257-260
39 Ibid
40 General Accounting Office, Rangeland Management: More Emphasis Needed on Declining and Overstocked Grazing Allotments, US General Accounting Office, Washington, DC, 1988, RCED-88-80
41 Mack, op cit, Ref 14
42 L A Morrow and P W Stahlman, 'The history and distribution of downy brome Bromus tectorum in North America', Weed Science, Supplement 32, 1984, pp 2-6; Young et al, op cit, Ref 16; J A Young, R A Evans, and J Major, 'Alien plants in the Great Basin', Journal of Range Management, Vol 25,1972, pp 194-201
43 Billings, op cit, Ref 15
"Mack, op cit, Ref 14
45 D A Pyke and S J Novak, `Cheatgrass (Bromus tectorum L) demography: establishment attributes, recruitment, ecotypes, and genetic variability', in S B Monsen, op cit, Ref 24, pp 12-21
46 Young et al, op cit, Ref 42
47 R N Mack and D A Pyke, The demography of Bromus tectorum: variation in time and space', Journal of Ecology, Vol 71, 1983, pp 69-93; Pyke and Novak op cit, Ref 45
48 S A Warg, 'Life history and economic studies on Bromus tectorum'. Unpublished thesis, University of Montana, Missoula, 1938; L C Hulbert, 'Ecological studies of Bromus tectorum and other annual brome grasses', Ecological Monographs, Vol 25, 1955, pp 181-213
49 G A Harris, 'Some competitive relations between Agropyron spicatum and Bromus tectorum', Ecological Monographs, Vol 37, 1967, pp 89-111; N E West, 'Western intermountain sagebrush steppe', in N E West (ed) Temperate Deserts and Semideserts, Elsevier Scientific, Amsterdam, 1983, pp. 351-374
50 G Stewart and A C Hull, 'Cheatgrass (Bromus tectorum L) an ecologic intruder in southern Idaho', Ecology, Vol 30, 1949, pp 58-74; Young et al, op cit, Ref 16
51 Harris, op cit, Ref 49; G Melgoza, R S Nowak, and R J Tausch, 'Soil water exploitation after fire: competition between Bromus tectorum (cheatgrass) and two native species', Oecologia, Vol 83, 1990, pp 7-13
52 Mack, op cit, Ref 14
53 R Hunter, Bromus invasions on the Nevada Test Site: Present status of B rubens and B tectorum with notes on their relationship to disturbance and altitude', Great Basin Naturalist, Vol 51, 1991, pp 176-182
54 P A Knapp, 'Secondary plant succession and vegetation recovery in two western Great Basin Desert ghost towns', Biological Conservation, Vol 60, 1992, pp 81-89
55 Young et al, op cit, Ref 16; Young and Sparks, op cit, Ref 27
56 Young et al, op cit, Ref 16
57 S G Whisenant, 'Changing fire frequencies on Idaho's Snake River Plains: Ecological and management implications', in E D McArthur et al, op cit, Ref 18, pp 4-10
58 T R Vale, 'Plants and people: Vegetation change in North America', Resource publications in Geography, Association of American Geographers, Washington, DC, 1982; Young and Tipton, op cit, Ref 18; Young et al, op cit, Ref 16
59 A C Hull, Jr, 'Cheatgrass — a persistent homesteader', in Proceedings—Symposium on Management of Cheatgrass on Rangelands, US Department of the Interior, Bureau of Land Management, Portland, 1965, pp 20-26
60 M Pellant, 'The cheatgrass-wildfire cycle — Are there any solutions?', in E D McArthur et al, op cit, Ref 18, pp 11-18
61 Whisenant, op cit, Ref 57

62 Stewart and Hull, op cit, Ref 50
63 Young et al, op cit, Ref 16
64 J A Young, R A Evans, and R E Eckert, Jr, 'Population dynamics of downy brome', Weed Science, Vol 17, 1969, pp 20-26; Young et a/, op cit, Ref 16; Whisenant, op cit, Ref 57
65 West, op cit, Ref 49
66 R C Holmgren, 'Competition between annuals and young bitterbrush (Purshia tridentata) in Idaho', Ecology, Vol 37, 1956, pp 371-377; Price and Brotherson, op cit, Ref 17; D C Thill, K G Beck, and R H Callihan, 'The biology of downy brome (Bromus tectorum)', Weed Science, Vol 32, 1984 pp 7-12
67 West, op cit, Ref 49
68 G Melgoza and R S Nowak, 'Competition between cheatgrass and two native species after fire: Implications from observations and measurements of root distribution', Journal of Range Management, Vol 44, 1991, pp 27-33
69 Young and Tipton, op cit, Ref 18
70 Ibid
71 M J Crawley, 'Life history and environment', in M J Crawley (ed) Plant Ecology, Blackwell Scientific, Oxford, 1986, pp 253- 290; J Goodwin, 'The role of mycorrhizal fungi in competitive interactions among native bunchgrasses and alien weeds: A review and synthesis', Northwest Science, Vol 66, 1992, pp 251-260
72 E B Allen and M F Allen, 'The mediation of competition by mycorrhizae in successional and patchy environments', in J B Grace and D Tilman (eds) Perspectives on Plant Competition, Academic Press Inc., San Diego, 1990, pp 367-389
73 C L Powell, 'Mycorrhizal infectivity of eroded soils', Soil Biology and Biochemistry, Vol 12, 1980, pp 247-250; E B Allen and M F Allen, 'Competition between plants of different successional stages: mycorrhizae as regulators', Canadian Journal of Botany, Vol 62, 1984, pp 2625- 2629; E B Allen and M F Allen, 'Facilitation of succession by the nonmycotrophic colonizer Salsola kali (Chenopodiaceae) on a harsh site: Effects of mycorrhizal fungi', American Journal of Botany, Vol 75, 1988, pp 257-266
74 E B Allen, 'Some trajectories of succession in Wyoming sagebrush grassland: implications for restoration', in E B Allen (ed) The Reconstruction of Disturbed Arid Lands, Westview Press, Boulder, 1988, pp 89-112
75 Ibid
76 Stewart and Hull, op cit, Ref 50
77 M Hironaka and E W Tisdale, 'Secondary succession in annual vegetation in southern Idaho', Ecology, Vol 44, 1963, pp 810- 812
78 M Hironaka, 'Piemeisel exclosures', Rangelands, Vol 8, 1986, pp 221-223
79 D A Pyke, 'Demographic responses of Bromus tectorum and seedlings of Agropyron spicatum to grazing by small mammals: Occurrence and severity of grazing', Journal of Ecology, Vol 74, 1986, pp 739-754; D A Pyke, 'Demographic responses of Bromus tectorum and seedlings of Agropyron spicatum to grazing by small mammals: The influence of grazing frequency and plant age', Journal of Ecology, vol 75, 1987, pp 825-835
80 Whisenant, op cit, Ref 57
81 S C Bunting, B M Kilgore, and C L Bushey, 'Guidelines for prescribed burning sagebrush-grass rangelands in the northern Great Basin', USDA General Technical Report INT 231. Intermountain Research Station, Ogden, 1987; L D Mahaffey, National fuels and smoke management specialist, Bureau of Land Management, Boise Interagency Fire Center, Boise, ID 83705, Personal communication, December, 1993
82 L Findley, personal communication, January, 1994
83 Ibid
84 Robert Clark, State fire management officer, Idaho Bureau of Land Management, Boise, personal communication, January, 1994
85 Morrow and Stahlman, op cit, Ref 42; G D Pickford, 'The influence of continued heavy grazing and promiscuous burning on spring-fall ranges in Utah', Ecology, Vol 13, 1932, pp 159-171; Cottam, op cit, Ref 3
86 Clark, op cit, Ref 84
87 Ibid
88 Ibid
89 DeFlon, op cit, Ref 16; Young et al, op cit, Ref 16; Devine, op cit, Ref 16
90 R B Murray, H F Mayland, and P J Van Soest, Growth and Nutritional Value to Cattle of Grasses on

Cheatgrass Range in Southern Idaho. USDA Forest Service Research Paper INT-199. Intermountain Forest and Range Experiment Station, Ogden, 1978
91 DeFlon, op cit, Ref 16
92 Ibid
93 T C Roberts, 'Cheatgrass: Management implications for the 90's', Rangelands, Vol 13, 1991, pp 70-72
94 Young et al, op cit, Ref 16
95 Roberts, op cit, Ref 93
96 G Stewart and A E Young, 'The hazard of basing permanent grazing capacity on Bromus tectorum', Agronomy Journal, Vol 31, 1939, pp 1002-1015
97 Morrow and Stahlman, op cit, Ref 42; Devine, op cit, Ref 16; Young et al, op cit, Ref 16
98 Young and Tipton, op cit, Ref 18
99 C R Groves and K Steenhof, 'Responses of small mammals and vegetation to wildfire in shadscale communities of southwestern Idaho', Northwest Science, Vol 62, 1988, pp 205-210
100 E Yensen, D L Quinney, K Johnson, K Timmerman and K Steenhof, 'Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels', American Midland Naturalist, Vol 128, 1992, pp 299-312
101 S L Pimm, H L Jones, and J M Diamond, 'On the risk of extinction', American Naturalist, Vol 132, 1988, pp 757-785
102 Roberts, op cit, Ref 93
103 P R Ehrlich, 'Extinctions and ecosystem functions: Implications for humankind', in R J Hoage (ed) Animal Extinctions: What Everyone Should Know, Smithsonian Institution Press, Washington, DC, 1985, pp 159-173
104 N Myers, 'A look at the present extinction spasm and what it means for the future evolution of species', in R J Hoage, op cit, Ref 103, pp 47-57
105 Billings, op cit, Ref 15
106 Young et al, op cit, Ref 16
107 J E Ellis and D M Swift, 'Stability of African pastoral ecosystems: alternate paradigms and implications for development', Journal of Range Management, Vol 41, 1988, pp 450-459; M B Westoby, B Walker, and I Noy-Meir, 'Opportunistic management for rangelands not at an equilibrium', Journal of Range Management, Vol 42, 1989, pp 265-274; W A Laycock, 'Stable states and thresholds of range condition on North American rangelands: a viewpoint', Journal of Range Management, Vol 44, 1991, pp 427-433; J L Dodd, 'Desertification and degradation in sub-Saharan Africa. The Role of livestock', BioScience, Vol 44, 1994, pp 28-34
108 Westoby et at, op cit, Ref 107 139Laycock, op cit, Ref 107; Dodd, op cit, Ref 107
110 Westoby, op cit, Ref 107
111 M H Friedel, 'Range condition assessment and the concept of thresholds: A viewpoint', Journal of Range Management, Vol 44, 1991, pp 422-426; Laycock, op cit, Ref 107
112 Ellis and Swift, op cit, Ref 107
113 Dodd, op cit, Ref 107
114 M Pellant and C Hall, 'Distribution of two exotic grasses on intermountain rangelands: Status in 1992', in S B Monsen, op cit, Ref 24, pp 109-112
115 P A Knapp, 'Intermountain West lightning-caused fires: Climatic predictors of area burned', Journal of Range Management, Vol 48, 1995, pp 85-91
116 M Barbour, B Pavlik, F Drysdale and S Lindstrom California's Changing Landscapes, California Native Plant Society, Sacramento, California, 1993
117 Ibid
118 Ibid
119 M R George, 'Annual rangeland management principles and practices: The California experience', in S B Monsen, op cit, Ref 24, pp 392-395
120 Bahre, op cit, Ref 7
121 Ibid
122 H E Anderson, Aids to Determining Fuel Models for Estimating Fire Behavior, US Department of Agriculture, General Technical Report INT 122, Intermountain Research Station, USFF, Ogden, Utah, 1982