

APPENDIX B1: ANNOTATED BIBLIOGRAPHIES OF LIVESTOCK GRAZING IMPACTS IN WESTERN NORTH AMERICA

General/Background (mainly for Chapters 1 and 5)

Agriculture, Food and Rural Revitalization. 1993 –
www.agr.gov.sk.ca/DOCS/livestock/beef/production_information/lvskgraze.asp

Location: Saskatchewan

Habitat types – grassland, range

Exp. Design – overview/fact sheet

Taxa/objects: none

Key findings: livestock are reluctant to use slopes >15% and in rolling terrain seldom graze at elevations >70 m above water. Grazing is also limited by horizontal distance from water – livestock rarely graze further than 2.5 km from water. They readily seek shade during hot summer periods resulting in high use of forested and riparian areas. Grazing systems: High-intensity low-frequency (high stocking densities, long grazing and long recovery periods); short-duration (high stocking densities with short grazing periods); and time-controlled (similar to short duration in terms of stocking and grazing times vary with growth rate of plants; grazing periods are brief (1-3 days) during rapid growth and longer (7-14 days) during slow growth.

BLM and USFS 2000. Interpreting indicators of rangeland health. Technical reference 1734-6 2000 Version 3. US Department of Interior Bureau of Land Management National Science and Technology Center, Denver, Colorado.

Location: N/A

Habitat types – rangelands

Exp. Design – methodological overview.

Taxa/objects: N/A

Key findings: qualitative assessments of rangeland health are important for communicating with the public. The technique, in association with quantitative monitoring, and inventory information, can be used to provide early warning of resource problems. The approach uses rangeland health surrogates related to soils, hydrology, bare ground, erosion, plant community composition, litter development, and invasive plants to compare grazed areas to ecological reference areas. It is used in conjunction with proper functioning condition monitoring, making use of a qualitative checklist to assess proper functioning condition of riparian areas. The approach is designed to provide a preliminary evaluation of soil/site stability, hydrologic function, and integrity of the biotic community (at the ecological site level); help managers identify areas that are potentially at risk of degradation; provide early warnings of potential problems and opportunities; and be used to communicate fundamental ecological concepts to a wide variety of audiences in the field. It is not meant to be used to: (1) identify the cause (s) of resource problems; (2) make grazing and other management decisions; (3) monitor land or determine trend; and (4) independently generate national or regional assessment of rangeland health (see p. 1). Ranking categories (extreme, moderate to extreme, moderate, slight to moderate, none to slight) are used to compare grazed sites with departure from ecological reference areas and proper functioning state (see p. 15).

Variance within categories is high in some indicators – e.g., dominant vegetation is defined by roughly 41-100% composition (p. 30). In general, changes in management are not appropriate based solely on the evaluation of range health per the procedures in this document (see p. 39).

Wuerthner, G. 2005. Birds and livestock grazing – a review (www.publiclandsranching.org/htmlres/plr_bird_impacts.htm).

Location: western US

Habitat types – NA

Exp. Design – literature overview.

Taxa/objects: birds

Key findings: ~578 million out of 1.9 billion acres in the West are grassland pasture or range; an additional 140 million acres of forests are grazed; nearly half of grazed landscapes are publicly owned; nearly 90% of federal lands administered by BLM and 69 % managed by the Forest Service are leased for livestock. In total, 700 million acres or slightly more than a third of the land area of the contiguous US may be grazed by domestic animals (Wuerthner, G., and M. Matteson eds. 2002 – Welfare ranching: the subsidized destruction of the American West. Island Press, Covelo, CA). In addition, 80% of croplands used for livestock – thus as much as 900 million acres or nearly ½ acreage of contiguous US are used for livestock production.

Ecosystem Dynamics

Madany, M.H., and N.E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah (Ecology 64(4):661-667)

Location: Zion National Park, UT

Habitat types – p. pine, juniper, grass/forb

Exp. Design – heavily grazed plateau vs. never grazed mesas (isolated)

Taxa/objects: vegetation structure and fire regimes

Key findings: heavy grazing by livestock and associated reduction of the herbaceous ground layer promoted establishment of less palatable tree and shrub seedlings. Pine oak and juniper sapling density and cover much higher on grazed than ungrazed; herb species dominated mesas savannas.

Other – pervasive increase of unpalatable shrubs and trees at expense of perennial grasses on western rangelands is attributed to heavy grazing, cessation of frequent fires, and climatic change. Grazing and fire cessation are inextricably intertwined. Major structural changes have taken place over the last century in conversion of Ponderosa pine savanna to forest – reason for changes cannot be attributed mainly to absence of fire. Mesa has experienced fire exclusion yet there were no sizeable thickets of forest. Dense sod of perennial grasses in ground layer of savannas is the primary controlling agent of tree regeneration. While fire important secondary factor in maintaining savanna, key factor in widespread conversion of savanna to forest seems to have been livestock grazing.

Fleischner, T. 1994. Ecological costs of livestock grazing in western North America (Conservation Biology 8(3):629-644)

Location: western US

Habitat types – broad diversity of ecosystem types

Exp. Design – overview/synthesis

Taxa/objects: provides taxa overviews by region with tables

Key findings: livestock grazing is most widespread influence on native ecosystems of western NA: 70% of western US (MT, WY, CO, NM, and westward) is grazed, including wilderness, wildlife refuges, national forests, and even some national parks. Ecological costs are dramatic: loss of biodiversity, lowering of population densities for a wide variety of taxa; disruption of ecosystem functions (nutrient cycling and succession); change in community organization; and change in physical characteristics of both terrestrial and aquatic habitats. Losses are highest in riparian ecosystems where livestock congregate, especially in arid areas. In 16 western states, ~165 million acres of BLM land and 103 million acres of Forest Service land are grazed by 7 million head of livestock, primarily cattle; 94% of BLM lands are grazed, 35% of wilderness is grazed (nationwide). Ungrazed land is extremely rare and very few studies of truly ungrazed lands exist (even exclosures were previously grazed). Autoecological, synecological, and geo-morphological studies confirm that native ecosystems pay a steep price for livestock. Ecological costs include: **(1) alteration of species composition (including decreases in density and biomass of species, reduction of species richness, and changing community organization); (2) disruption of ecosystem functioning (including interference in nutrient cycling and ecological succession); and (3) alteration of ecosystem structure (changing vegetation stratification, soil erosion, and decreasing availability of water to biotic communities).**

Other: by virtually any measure, livestock grazing has serious ecological costs in western NA – **reduced density and biomass of many plant and animal species, reduced biodiversity, aided spread of exotics, interrupted ecological succession, impeded cycling of most important limiting nutrient (nitrogen), changed habitat structure, disturbed community organization, and has been the most severe impact on one of the biologically richest habitats in the region – riparian areas. Livestock grazing has been described as “the single most important factor limiting wildlife production in the West (Smith 1977) and “one of the primary threats to biological diversity” (Cooperrider 1991).** Deleterious effects of grazing observed in all vertebrate classes, usually, indirectly through effects on habitat structure and prey availability (several additional references provided). Bock et al. (1993b) found increasingly negative effect on abundance of bird species in grassland, riparian woodland, and intermountain shrub-steppe (almost equal numbers of species with positive and negative responses in grassland, 6 times as many with negative responses in shrub-steppe). Birds may be better able to cope than mammals due to mobility and visual orientation. Complete type conversions reported in several areas due to history of grazing, especially in riparian zones. Spread of weeds – (1) dispersal of seeds in fur and dung; (2) opening habitat for weeds like cheatgrass; (3) reducing competition from native species by eating them. Invasions by many species in west associated with grazing. Disruption of microbiotic soils crusts, especially in desert areas. Disruption of succession – maintains early seral vegetation, prevent cottonwood and willow regeneration in riparian areas; riparian areas

highly affected, including width of riparian zone. Livestock are a major factor contributing to failure of riparian communities to propagate themselves. Also once successional thresholds are crossed (e.g., severe erosion), successional changes may become irreversible. Physical structure of ecosystems, including vegetation stratification, is often changed by grazing. In central WA, grazing was responsible for changing structure of Ponderosa pine from open park-like overstory with dense grass to dense pine and lack of grasses. Numerous authors noted extreme erosion and gullying when comparing heavily grazed to ungrazed sites – accelerated soil erosion, soil compaction, increased runoff, and changes in channel morphology. Livestock, like humans, are adapted to mesic habitats – riparian areas – shade, cool temperatures, water, and abundance of food. Cattle spend disproportionate time in riparian areas (many additional references provided); ecological stakes highest in riparian areas due to disproportionately higher wildlife use (western riparian areas most productive habitats for wildlife). Livestock affect 4 main components of riparian habitats: (1) streamside vegetation; (2) stream channel morphology; (3) shape and quality of water column; and (4) structure of stream bank (several additional references provided). No evidence in western systems that grazing is needed to stimulate plant productivity or that cows can be used beneficially as a management tool – results depend on species used as indicator. Riparian areas often demonstrate dramatic recovery from grazing but xeric lands less so (several additional references provided by region). **In numerous studies of riparian grazing, investigators concluded that total removal of livestock was necessary to restore ecosystem health** (several additional references provided by region). **Reductions in grazing have limited benefits (p. 638).**

Belsky, J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology 11(2):315-327.

Location: interior West, mainly upland forests

Habitat types – upland forests, grasslands, riparian

Exp. Design – literature overview, case studies.

Taxa/objects: ecosystem wide

Key findings: livestock grazing alters forest dynamics by: (1) reducing biomass and density of understory grasses and sedges, which otherwise out compete conifer seedlings and prevent dense tree recruitment; and (2) reducing the abundance of fine fuels, which formerly carried low-intensity fires through forests. Grazing has contributed to increasingly dense western forests and changes in tree species composition. Enclosure studies indicate livestock alter ecosystem processes by reducing cover of herbs and litter, disturbing and compacting soils, reducing water infiltration rates, and increasing soil erosion.

Other: extensive scientific literature beginning as early as the 1920s (Pearson 1923, Leopold 1924), suggests livestock played a major role in altering forests. Domestic grazing currently occurs on approximately 115 million ha (91%) of all federal lands in 11 contiguous western states. Impacts of grazing on western ecosystems in terms of species losses, soil erosion, and degradation of wildlife habitat have been widespread and severe (Flather et al. 1994, Fleischner 1994), primarily in western rangelands, arid woodlands, and riparian areas (several additional references provided). Livestock have had a profound influence on stand dynamics, species composition, soils, and stability of forests.

Prior to Euro-settlement, two natural phenomena maintained trees at low densities: (1) competitive exclusion of tree seedlings by dense understory grasses, and (2) frequent thinning of understory trees by low-intensity surface fires. The vigorous graminoid understory was important in maintaining low tree densities because established grasses with extensive root systems out competed tree seedlings for soil moisture and nutrients (several additional references provided). A large number of studies suggested that fire began to decline in frequency and forests began to increase in density soon after livestock were first introduced into the Interior West. By early 1800s in the southwest and late 1800s in the northwest, virtually all plant communities that supported grass and sedge production, including Ponderosa pine and mixed conifer, were heavily stocked with cattle and sheep (several additional references provided). Cows also reduce the frequency of surface fire by consuming the herb layer that otherwise would have dried into the fine fuels necessary to carry fire (several additional references provided).

Case Study 1 – Meeks Table, central WA (Rummell 1951) – isolated plateau never grazed compared with similar plateau with continuous grazing for 40 years. Ungrazed plateau had park-like Ponderosa pine conditions with dense grasses and low tree regeneration. The grazed area had large numbers of small trees maintained by heavy grazing and lack of fire because neither table had burned in 125 years. Many young trees became established following heavy grazing. Case Study 2 (Zinnerman and Neuenschwander 1984) – compared grazed and ungrazed Ponderosa pine and Douglas-fir in foothills of Bitterroot Mountains, ID. Found that grazed Ponderosa pine outside exclosures had twice as many trees in smaller size classes (< 5 cm dbh) as ungrazed and small trees came in following grazing. Cascade effect of grazing – as grazed stands grew denser, they became shadier, benefiting the more shade-tolerant Douglas-fir – species composition shifted from fire tolerant Ponderosa pine to more fire-sensitive and disease-prone Douglas-fir. Denser stands produced more litter from shaded branches and dying trees, accumulated more woody fuel, and became more vulnerable to intense fire. Stands with no livestock had much greater herb cover. Case Study 3 (Madany and West 1983) – compared Ponderosa pine on plateau in Utah grazed vs. ungrazed (isolated by steep cliffs). Found that during the 100 years prior to study, tree recruitment of grazed sites had increased by a factor of 10 or more while on ungrazed mesas it remained unchanged. Vigorous understory of ungrazed mesa inhibited tree recruitment whereas grazing and reduction in fire frequency favored dense small trees. Case Study 4 (Savage and Swetnam 1990) – reconstructed fire history of Ponderosa pine in Arizona-New Mexico – mean fire interval before sheep grazing (1700-1830) was 4.2 years; during grazing only 2 fires per year. Livestock instrumental in decline in fire frequency occurred 100 years before effective suppression. High Ponderosa pine densities during this time were the result of combination of livestock grazing, reduced fire frequency, abundant seed crops, and warm, wet conditions. Cattle preferences - in general, cattle show strong preferences for certain environments, avoiding steep slopes and increasingly dense forests while selecting riparian areas and meadows. Forage utilization by livestock was 7.5 times higher in riparian meadows than adjacent uplands (Gillen et al. 1984). Riparian areas in OR forested watershed comprised only 1.9% of allotment but produced 21% of available forage and 81% of forage consumed. Livestock also tend to concentrate in open forests, clearcuts, and open meadows (several additional references provided). Exclosure studies show cattle reduce vegetation cover, especially perennial bunchgrasses (several

additional references provided). In uplands, grazing has fewer effects on shrubs than grasses, but in riparian areas grazing dramatically reduces number and total biomass of shrubs and trees critical for shading. Livestock also select more palatable species, altering understory communities. Forest soil effects include lower litter cover and more bare ground, compaction and infiltration (increased runoff, increased sedimentation, and decreased water storage). In general, livestock grazing has had produced effects over a wide range of conditions – have actively participated in the destabilization of Ponderosa pine and mixed conifer forests throughout interior west.

Harrison, S., B.B., Inouye, and H.D. Safford. 2003. Conservation Biology 17(3):837-845.

Location: n. California

Habitat types – grasslands

Exp. Design – studied interaction of grazing and fire on productive and serpentine soils using 80-100 grazed vs. ungrazed sites before and after fire.

Taxa/objects: species composition of plants

Key findings: fire enhanced total and exotic species richness more on nonserpentine soils and enhanced native species richness more on serpentine soils. Grazing increased native species richness on **serpentine soils** but not on **non-serpentine soils**. Soil-disturbance interactions warrant careful consideration of fire and grazing to manage native species diversity in wildlands. Citations given for livestock grazing effects on fuel loads (two studies cited as reducing fuel loads). In general, grazing tended to have a homogenizing effect on non-serpentine soils. On non-serpentine soils, exotics generally out compete natives by preempting the pulse of available space and light created by disturbance and thus reduced the response in the richness of native species. On serpentine soils, where exotics are few and lack a general competitive advantage, natives may be better able to exploit the opportunities created by disturbance. **Disturbance may tend to increase invasion in precisely those habitats or communities that are already most invaded. Protecting grassland sites of outstanding native diversity may generally be more important than whether or not they are grazed or burned.**

Murray, M.P. 2003. Losing ground: wilderness meadows and tree invasion over a 55-year period in California's Klamath Range. Pp. 81-97, In: K.L Mergenthaler, J.E. Williams, and E.S. Jules (eds). Proceedings of the Second Conference on Klamath-Siskiyou Ecology. Siskiyou Field Institute, Cave Junction, OR.

Location: Marbled and Trinity Mountains, n. California

Habitat types – montane meadows

Exp. Design – aerial photo GIS analysis to confirm meadow loss.

Taxa/objects: NA

Key findings: 6 broadly defined meadow communities (sedge, sedge-bunchgrass, lush-herbaceous; corn-lily, bentgrass, and dry sparse types). Meadows historically supported “meager” tree cover either in patches or few individuals. Observations dating back to 1900s confirm tree encroachment into meadows. Meadow loss for 6 meadows (totaling 477.5 ha) during 55-year period varied from 2-13% among sites. Tree establishment was observed along meadow edges and interior. Shrub expansion also noted. **Combination of tree and shrub increases equate to 4-26% meadow loss (similar phenomenon**

observed in the Sierra and Rockies). Combination of factors involved trigger tree/shrub invasions – climatic fluctuations; livestock grazing (includes citations); and fire suppression. Grazing reduces meadow cover, thus reducing plant competition while enabling trees to flourish.

Freilich, J.E., J.M. Emlen, J.J. Duda, D.C. Freeman, and P.J. Cafaro. 2003. Ecological effects of ranching: a six-point critique. *Bioscience* 53(8):759-763.

Location: Great Plains and WY

Habitat types – western grasslands and shrublands (general)

Exp. Design – synthesis/overview

Taxa/objects: NA

Key findings: authors raise 6 points that summarize grazing impacts previously not addressed or downplayed by range managers: (1) control of “problem animals,” (2) truncation of food web; (3) fragmentation of rangelands from fencing and roads; (4) exotic weed and poisons to treat them; (5) alteration of fire regimes; and (6) impacts to water supplies and riparian areas. They question ecological sustainability of ranching and raise doubts about its potential as a conservation tool. **Problem animals** – predator control has had major ecological effects through persecution of a broad suite of predators – wolves, wolverine, grizzly, and other “problem” animals – ground squirrels, pocket gophers, snakes, raptors, and many other species “are destroyed at the whim of individuals.” Some areas have organized hunts that purposely kill coyotes or other target animals in the belief that they are performing a public service. Over the long run this cannot help but alter the entire rangeland. **Truncation of food web** – many predators and their carcasses are gone from the prairies. Diverse strands of food web formerly occupied by decomposers and scavengers dependent on large carrion – wolves, carrion beetles, wolverine, ants, vultures, and countless others are missing and often this is overlooked. Removal of biomass results in less material for nutrient cycling. **Fencing, roads, and fragmentation** – development by ranchers and others has fragmented rangelands – native ungulates especially vulnerable to fencing effects, weeds tend to follow roads. **Exotic weeds and poisons** – exotics flourish in disturbed areas, livestock producers and agencies have historically seeded large areas with nonnative species intended to improve the range. Western rangelands contain significant areas of disturbed, infested, or ruderal vegetation caused directly or indirectly by livestock production. Although there are time of the year and species specific strategies that can be used to put livestock to work eating weeds (Olsen 1999), victories are few, and each year the acreage of infested land expands. **Alteration of fire regimes** – mainly through fire suppression and introduction of non-native plants caused by ranching and other disturbances. **Impacts to water supplies and riparian areas** – two water-related factors are central to ranching in the arid West: provision of drinking water for livestock and irrigation of hay meadows for winter feed – well documented impacts to small streams from these activities – conversion of native marshes, willow thickets, and wet meadows into hay meadows has been extensive. Loss of riparian areas is extensive and may be persistent in some places. **Even if livestock are fenced to prevent riparian trampling, water must be diverted for animals.**

Other: a substantial literature exists on ecological effects of livestock grazing (Kauffman and Krueger 1984, Belsky 1986, Milchunas and Lauenroth 1993, Belsky et al. 1999,

Jones 2000). Many authors, however, rely on relatively small exclosures. No studies exist comparing biodiversity and ecosystem function in ranches and unranch lands. Bock et al. (1993) recommend large (100- 1000 ha) exclosures on fed lands to test effects. **Exactly how different is today's landscape – this is the central question rangeland scientists should be working on by comparing ranch lands to protected areas. Although many still view ranching as relatively innocuous, pastoral pursuit and historically valuable part of the Old West, these six points suggest that it is not ecologically benign.**

Neff, J.C., R.L. Reynolds, J. Belnap, and P. Lamothe. 2005. Multi-decadal impacts of grazing on soil physical and biogeochemical properties in southeastern Utah. Ecological Applications 15(1):87-96.

Location: southeastern Utah, Canyonlands NP

Habitat types – grasslands

Exp. Design – compared never grazed grassland in National Park with 2 historically grazed sites with similar ecologic, geomorphic, and geochemical characteristics that were grazed from the late 1800s until 1974.

Taxa/objects: biological soil crusts

Key findings: despite almost 30 years without livestock grazing, surface soils in the historically grazed site had 38-43% less silt and 14-51% less total elemental soil content relative to soils never exposed to livestock disturbances. Differences in nutrient levels related to wind erosion of soil fine particles after the historical disturbance by livestock. Historical grazing may lead to changes in soil organic matter content including declines of 60-70% in surface minerals relative to never-grazed sites. Livestock grazing could have long-lasting effects on soil fertility of native grasslands in this part of southeastern Utah. Arid ecosystems are more vulnerable to soil impacts than mesic areas that historically supported grazers prior to human settlement. If grazing leads to disturbance of biological crusts, regeneration typically requires decades for initial colonization and hundreds of years for a crust lichen community to form (references). Native grasslands in the southwest are becoming increasingly rare due to shrub and tree encroachment and nonnative grass invasion. 20th century grazing has led to increase in shrub species in southcentral Utah. Loss of soil fine fraction due to erosion following disturbance appears to be an important mechanism leading to nutrient depletion in disturbed sites. Increased wind erosion in grazed vs. ungrazed areas. Crust cover on historically grazed sites is characterized by spotty distributions of cyanobacterium with little moss or lichenized crust development despite 30 years without livestock. Impacts of processes such as soil erosion can be irreversible on management timescales. Historic grazing in southwestern Utah was responsible for a period of soil depletion that continues to impact current soil biogeochemical characteristics 3 decades after grazing ended. Lower contents of soil fine particles in historically grazed sites leads to lower concentrations of many rock-derived minerals. Grazing triggers wind erosion and results in significant nutrient loss in semi-arid settings.

Large Exclosures

Bock, C.E., J.H. Bock, and H.M. Smith. 1993. Proposal for a system of federal livestock exclosures on public rangelands in the western United States (Conservation Biology 7(3):731-33)

Location: western US

Habitat types – broad diversity of ecosystem types

Exp. Design – overview/synthesis

Taxa/objects: none

Key findings: at least 212 million acres of federal land grazed by domestic livestock in 17 western states; most on BLM lands. Recommends exclosure program include 20% of each parcel of land; minimum size 2,500 acres, representative of major habitats. Provided 5 arguments for large exclosures. Most livestock exclosure studies suggest that livestock operate as keystone species – determine which species thrive and diminish. Some exclosures haven't changed following livestock removal because (a) certain grasslands have a very tight evolutionary association with native grazers (Great Plains); (b) they have been so altered historically by grazers that they cannot return to original condition (desert grasslands of southwest); (c) insufficient time for post-grazing changes; and (d) exclosures too small to pick up change or function as intact ecosystems. In general, livestock are highly destructive of many components of most grassland ecosystems. Grazing consequences appear to be an all or nothing phenomenon. **Within the broad range of “moderate” grazing, sensitive species always are reduced, while tolerant ones predominate, even if pastures are “rested” on a rotational basis. Range improvement efforts, like grazing itself, have been experiments without permanently ungrazed controls.**

Wildlife Studies

Krueper, D., J. Bart, and T.D. Rich 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (U.S.A.). Conservation Biology 17(2):607-615..

Location: San Pedro Riparian National Conservation Area (NCA), southeastern Arizona

Habitat types – riparian, mesquite grassland, and Chihuahuan desert-scrub

Exp. Design – monitored vegetation and birds from 1986-1990 following removal of cattle in 1987.

Taxa/objects: plants and birds

Key findings: density of herbaceous vegetation increased 4-6 fold in riparian and mesquite grassland; little change in herbaceous vegetation in desert scrub or in density of shrubs or trees in any of the communities. Of 61 bird species, mean detect/km increased for 42 species, 26 significantly, and decreased for 19 species, 8 significantly. Number of individuals increased each year with largest increase in riparian, open-cup nesters, neotropical migrants, and insectivores. Results suggest that removing cattle from riparian areas in sw US can have profound benefits for breeding birds. Removal of cattle was followed by increases in all groups of birds analyzed, including several species of concern and Partners In Flight species. Removal of cattle led to rapid and substantial recovery of riparian and mesquite vegetation and bird populations, including several species of high conservation concern.

Other: riparian areas support higher breeding diversity of birds than all other western habitats combined, including some of the highest non-colonial densities of breeding birds in NA (references given). Arguably, the single land use activity that has most affected western riparian systems and has led to the greatest change within western ecosystems in general has been livestock grazing (references provided). Grazing can change vegetation communities by: reducing plant density, changing species composition, decreasing plant vigor, decreasing seed and insect production, and eliminating vegetation recruitment (references provided). Additionally, trampling of soils may increase wind and water erosion, compact soils and prevent seedling establishment. Birds – depending on magnitude of use, these impacts can decrease avian reproductive success, lower food availability, increase predation on nests and adults, lower avian density and species diversity, and cause shifts in foraging techniques, distribution, and habitat use (references provided). Understory birds mostly affected by grazing; a small number of species that prefer open habitats or lower vegetation density may benefit from a shift in vegetation structure and composition brought on by grazing (references provided). Riparian vegetation can recover rapidly following cow removal (references provided). Most studies have concentrated on short-term effects on vegetation in mid to high elevation, or within small-scale livestock grazing exclosures. Fleischner (1994) suggested that exclosure studies do not accurately reflect the ecological potential of ecosystems – exclosures usually too small, have been in place only a short time, and typically have been grazed prior to exclosure. Saab et al. (1995) and Tewksbury et al. (2002) reviewed effects of cattle on birds in western NA. Among 68 species of neotrops, 46% decreased in abundance, 29% increased, 25% showed no clear response to grazing, and none were less abundant in ungrazed locations. Ground nesters mostly affected, followed by shrub-nesters and canopy nesters.

Stevenson, K.M. 2004. Ph.D. Dissertation – Conservation of plant and abiotic diversity in grazed and ungrazed meadows of the Sierra Nevada. University of California, Davis.

Location: Sierra Nevada, Kern Plateau, CA

Habitat types – wet meadows

Exp. Design – grazed vs. ungrazed (n=9 each)

Taxa/objects: plants

Key findings: grazed meadows had significantly higher channel width-to-depth ratio than ungrazed. Channel depth, channel width-to-depth ration, grazing, and year all significantly affect moisture class distribution. Cow/calf seasonal grazing is correlated with physical changes in meadow physiography, and these changes affect moisture class availability and habitat for meadow species. Megaforbs are especially susceptible to impacts of grazing in montane and sub-alpine meadows (from livestock consumption). Grazing should be controlled on overhanging banks and willow habitats, both important for infrequent (rare) species and species on the edges of their native ranges.

Earnst, S.L., J.A. Ballard, and D.S. Dobkin. 2004. Riparian songbird abundance a decade after cattle removal on Hart Mountain and Sheldon National Wildlife Refuges. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-191.

Location: Hart Mountain and Sheldon National Wildlife Refuges, eastern Oregon.

Habitat types – high desert riparian habitat

Exp. Design – monitored vegetation and birds from 2000-01 (with cows removed) compared to 1991-93 (with cows) on the refuge.

Taxa/objects: birds

Key findings: of 51 species, 71% exhibited positive trend in detections and 76% of species with significant change (either positive or negative) increased. Several species of concern in Columbia Plateau increased. Aspen and willow associates, but not meadow associates, exhibited significant increase. Detections of ground/low cup and high cup nesting species (but not cavity nesters) increased. Ground/understory foraging species, aerial, and overstory foragers increased but bark gleaners did not. These changes not related to regional (Breeding Bird Survey) changes.

Other: in the semi-arid West, riparian areas comprise only 1% of landscape but support a higher diversity of breeding songbirds than any other habitat (several additional references provided) and have been severely affected by agriculture, recreation, timber, water diversion, and particularly livestock grazing (several additional references provided). Cows deplete and sometimes eliminate riparian vegetation by grazing on herb layer and browsing on shrubs and young trees and they also cause compaction of soils, widening of channels, and lowering of water table (Platts 1991). Saab et al. (1995) reviewed 9 avian/grazing studies – species most affected were primarily ground or near-ground nesters and shrub nesting species. However, effects throughout avian community have also been documented where grazing severely impacted vegetation (several additional references provided). Dobkin (1994) found riparian vegetation (herb layer) increased by the 3rd year after cattle removal and this was associated with small increases in birds – exclosures had higher richness and abundance of birds and were dominated by wetland and riparian assoc. Other studies found community-wide effects of cattle removal – Krueper et al. (2003) found significant increases in both open cup and cavity nesters, residents and neotrops, all foraging guilds, and all species groups categorized by vertical strata. Tewksbury et al. 2002 compared grazed (>50 years) sites with ungrazed (>25 years) along Missouri River and found effects in both open-cup and cavity nesters, and low and high nesting species groups were equally affected. **It is generally accepted that species composition and structure of herbaceous and understory vegetation are affected by grazing, and, presumably, this change effects inverts.**

Baker, B.W., H.C. Ducharme, D.C.S. Mitchell, T.R. Stanley, and H.R. Peinetti. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. Ecological Applications 15(1):110-118.

Location: Rocky Mountain NP, Colorado

Habitat types – riparian

Exp. Design – compared standing crop of willow 3 years after simulated beaver cutting on paired plants with and without intense elk browsing.

Taxa/objects: beaver, elk, livestock

Key findings: simulated beaver cutting with intense elk browsing produced willow that was small and short with far fewer but longer shoots and a higher percentage of dead biomass. Simulated beaver cutting without elk browsing had the opposite effect – willow was large, tall and leafy with more shoots and lower percent dead biomass. Lack of willow suitable as winter food for beaver can cause beaver populations to decline creating a feedback mechanism that reduces beaver and willow populations. Populations

of beaver and willow have not thrived in riparian environments heavily browsed by livestock or ungulate such as elk. **Beaver and willow are mutualists. Beaver are keystone species. Willow is highly palatable and selected by livestock and ungulates. This new level of competition is unnatural to beaver-willow mutualisms, which probably evolved under relatively low herbivory in a more predator-rich environment. Beaver-willow community is likely to be stable if ungulate or livestock utilization of willow is absent or limited to the perimeter of the community and interior stems are mostly full height; declining if herbivory has penetrated the interior of the community and suppressed regrowth of beaver-cut stems; and recovering if interior or perimeter plants show evidence of previous hedging but include many unbrowsed leaders. Herding or hazing livestock away from riparian willow has been effective on western rangelands.**

Riparian Studies

Popolizio, C.A., H. Goetz, and P.L. Chapman. 1994. Short-term response of riparian vegetation to 4 grazing treatments. J. Range Manage. 47:48-53.

Location: Sheep Creek watershed of northcentral Colorado

Habitat types – montane riparian

Exp. Design – 4 grazing treatments: long-term grazing (G), protection from grazing since 1956 (P), recent protection following long-term grazing (P88), and recent livestock grazing following protection (G88)

Taxa/objects: plants

Key findings: long-term grazing and short-term grazing treatments were least similar. Long-term protection and short-term grazing were most similar. Plant cover differed significantly between grazed vs protected. Average percent grass cover increased under short-term protection after a history of long-term grazing. However, short-term (two years) grazing stimulated foliar cover of forbs, grasses, and sedges after more than 30 years of exclusion, however, other impacts were not assessed. **Differences resulting from grazing vs. protected treatments became more pronounced when less frequent and rare species were considered.**

Knapp, R.A., and K.R. Matthews. 1996. Livestock grazing, golden trout, and streams in the Golden Trout Wilderness, California: impacts and management implications. J. Fisheries Manage. 16:805-820.

Location: southern end of Sierra Range – eastern portion of wilderness area in the Inyo National Forest

Habitat types – riparian, meadows, stream morphology

Exp. Design – exclosures (ungrazed) vs. grazed stream sections; generated 1-tailed hypothesis regarding predicted changes in channel morphology and riparian vegetation.

Taxa/objects: physical riparian/stream measures, golden trout

Key findings: grazing is most widespread land use in western North America (references provided). Grazing affects 64 million ha of BLM and 53 million ha of USFS lands. Impacts on stream and riparian ecosystems are widespread (reviews provided) and are particularly acute in arid regions. At least 50% of riparian areas degraded in western NA by livestock. USGAO (1988) review concluded that most riparian areas are in need of

restoration (GAO 1988). Platts (1991) indicate that 15 of 19 studies showed stream-fish diminished by livestock grazing. All of Knapp and Matthews study sites showed marked differences in stream physical characteristics consistent with expected changes following removal of cattle. Ungrazed areas consistently had greater canopy shading, stream depths, and bank-full heights and smaller stream widths than grazed areas. Trout density and biomass significantly higher in ungrazed areas in 3 of 4 comparisons. Current levels of livestock grazing are degrading stream and riparian components of meadows to the detriment of threatened trout populations. Willow recruitment significantly impaired by grazing (this is a common result of livestock grazing in other studies as well). Vegetation changes were faster (ungrazed) than stream morphology changes following grazing. In general, meadows grazed by livestock are in poorer condition than areas inside exclosures and this degradation is negatively impacting trout. Restricting or eliminating grazing will increase meadow stability, improve habitat for trout, and enhance conditions for a wide range of other riparian species.

Kauffman, J.B., M. Mahrt, L.A. Mahrt, and W.D. Edge. 2001. Wildlife of riparian habitat. Pages 361-388 in D.H. Johnson and T.A. O'Neil (editors). Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis.

Location: WA/OR

Habitat types – riparian

Exp. Design – overview/synthesis/wildlife habitat relations book.

Taxa/objects: multi

Key findings: riparian areas occupy as little as 0.5-2% of the landscape, but contain more plant, mammals, bird, and amphibian species than do surrounding uplands. Riparian habitats considered most critical of wildlife habitats in rangelands of southeastern Oregon, the Blue Mountains, and western Oregon and Washington. Approximately 253 species of vertebrates use Westside and 265 species use eastside riparian areas. Out of 593 species in OR/WA, 319 (53%) use riparian (p. 365). Almost all productive floodplain riparian zones in central and eastern WA/OR have been converted to ag use. Degree of utilization depends on season of use, frequency of use, and inherent site characteristics such as species composition, soil textures, slope, and climate. Domestic cows prefer to be near water and on gentle topography. Where uplands are steep and arid, cattle congregate principally in riparian zones. For example, on a Blue Mountain, Oregon, grazing allotment, the riparian zone comprised only 2% of the area, yet accounted for 81% of all forage consumed by cattle. Cattle can degrade riparian areas through the effects of forage removal, soil compaction, streambank trampling, and introduction of exotics (p. 379 –additional references provided). Secondary effects include hydrologic influences ultimately resulting in losses of ecosystem structure and composition, particularly deciduous woodland riparian stands of cottonwood, alder, or willow. In the short term, canopy loss through heavy use of shrubs and saplings influences structure and wildlife habitat, particularly for avian nesting. Heavy grazing also decreases reproductive success of riparian willows and depression in root production. Combination of root loss and trampling weakens and collapses stream banks. Bank loss and resulting sediment loads contribute to downcutting, channel widening, and degradation of fish habitat. As channel downcuts, over-bank flows cease, and hyporheic connectivity

(subsurface stream/floodplain water exchange) is lost. Eliminates potential for gallery (riparian) forest to develop. Loss of shade results in increased stream temperatures.

Kauffman, B. A.S. Thorpe, and E.N. Jack Brookshire. 2004. Livestock exclusion and belowground ecosystem responses in riparian meadows of eastern Oregon (Ecol. Applications 14(6):1671-1679)

Location: mid fork John Day, e. Oregon

Habitat types – riparian/wet meadows

Exp. Design – 3 “sustainably” grazed areas vs. ungrazed (9-18 years)

Taxa/objects: soil, below ground processes

Key findings: 1) removal of livestock is an effective restoration of soil, hydrology, and vegetation properties that at landscape scales likely have great effects on stream channel structure, water quality, and aquatic biota; (2) profound differences in below ground properties of grazed vs. exclosed communities; (3) dry meadows – total belowground biomass was ~50% greater in exclosures; wet meadows the TBGB was 62% higher; (4) soil bulk density was significantly lower and soil pore space higher in exclosed sites of both meadow types; (5) mean infiltration rate in exclosed dry meadows was ~13 x greater than in grazed and in wet meadows, mean infiltration rate in exclosures was 233% greater than grazed; (6) exclosed wet meadows, rate of net potential nitrification was 149 x greater and rate of potential mineralization was 32 x greater when compared to grazed sites.

Other: In WA/OR ~70% of wildlife use riparian zones as habitat; riparian and wetland, however, cover only 1-2% of western forest and range landscapes. Livestock grazing has had widespread ecological effects, including loss of native species, changes in species compo, soil deterioration, degradation of fish habitat, and changes in ecosystem structure and function (several additional references provided). Alterations in below-ground structure and processes of riparian zones could potentially influence the adjacent stream ecosystems through changes in root mass, soil structure, infiltration rates, and N turnover rates. Many studies reported decreased soil bulk density and/or increased soil pore space in sites excluded from cattle. If the entire study area were excluded from livestock, the surface 10 cm of soil in the meadows alone could potential store 16.6×10^6 more water!

Allen-Diaz, B, R.D. Jackson, J.W. Bartolome, KW. Tate, and L.G. Oates. 2004. Long-term grazing study in spring-fed wetlands reveals management tradeoffs. California Agriculture 58(3):144-148.

Location: UC Sierra Foothill Research and Extension Center.

Habitat types – oak woodlands and wetlands

Exp. Design – tracked species composition and cover for more than a decade on rocky-type wetlands under three levels of grazing intensity – ungrazed, light grazed, moderate grazed. Used 10-year (long-term) and 3-year (paired-plot) experiments.

Taxa/objects: N/A

Key findings: spring-fed wetlands perform many important functions within oak-woodland landscapes and livestock grazing modifies these functions. Lightly and moderately grazed wetlands exhibited lower insect family richness than ungrazed springs. Plant cover was maintained for the first 7 years of grazing and plant diversity was not significantly affected. Removal of grazing decreased emissions of greenhouse gas

methane and increased nitrate levels in springs. Light grazing at springs appeared to be desirable for ecosystem functions. Literature – livestock grazing can affect the functioning of spring-fed wetlands by acting as nutrient filter and altering plant community composition (Jackson 2002). Species composition controlled by vagaries of climate and not by grazing intensities they studied. Lightly grazed wetlands maintained greater species evenness (herbaceous) and diversity relative to pretreatment values either ungrazed or moderately grazed. At creeks, moderately grazed plots maintained greater relative total species, evenness and diversity than lightly grazed and ungrazed. On marshy springs, decreased diversity was observed with grazing removed for 1 year (although no distinction was made between native and exotics – my comment). After 7 years, found no significant differences in herb cover among grazing intensities, however, by 2002 (10 years), moderate grazing resulted in significant decrease in plant cover. Sustained grazing at moderate or higher intensities is not desirable for these systems. Occasional moderate grazing didn't affect plant cover. No changes in channel morphology or water quality detected in short or long-term studies. Lightly and mod grazed wetlands exhibited lower family richness (aquatic insects) than ungrazed springs.

APPENDIX B2: BIBLIOGRAPHIC ENTRIES (for Chapter 2)

I. GRAZING AND PLANT COMMUNITY DYNAMICS

Allen-Diaz, B. 2004. Sierra Nevada grasslands: interactions between livestock grazing and ecosystem structure and function. Pp. 111-114 in: P. Stine, D. Graber and D. Murphy, eds., Proceedings from the Sierra Nevada Science Symposium, October 7-10, Kings Beach, CA. USDA Forest Service Pacific Southwest Research Station General Tech. Report PSW-GTR-193. Albany, CA.

Long-term research has been focusing on the effects of various controlled cattle grazing treatments on spring-fed wetlands of the Sierra Nevada foothills near Brown's Valley, CA. Treatment plots range from 0.75 to 1.2 ha and are enclosed with a 2-strand electric fence. Cattle numbers are controlled in order to achieve grazing treatment levels of 800-1,000 kg/ha (light grazing) or 500-600 kg/ha (moderate grazing) residual dry matter in the uplands. The third grazing treatment removes grazing animals from the plots. Researchers have tracked species composition, cover, channel morphology, water quality, and aquatic insects and examined carbon, nitrogen, and methane dynamics. Results show that plant composition can be manipulated with grazing and that lightly grazed sites maintain a greater diversity and evenness of plant species. Total plant cover did not differ between sites after 7 years, but after 10, moderately grazed sites showed significant decreases in cover. Spring-fed wetlands did not show any response to grazing treatments during the first 5 years of the study, but further studies showed that removing grazing from spring-fed wetlands resulted in increased nitrate concentrations in spring waters. Channel morphology did not vary with treatment, but the species richness of aquatic insects tended to decrease with moderate grazing. The effect of grazing on spring-fed wetlands is complex, but in a broad sense, these studies indicate that some level of grazing is probably desirable, particularly from the standpoint of species diversity and productivity. Appropriate management, including adjustments to the timing and intensity of grazing, should be used to maximize the health of these habitats and their benefit to the larger landscape.

Allen-Diaz, B., Barrett, R., Frost, W., Huntsinger, L., and Tate, K. 1999. Sierra Nevada Ecosystems in the presence of livestock. A report to the Pacific Southwest Station and Region. USDA Forest Service, Berkeley, CA.

This document was prepared by a group of scientists with expertise in California rangeland ecosystems. The group was asked to critically review the Sierra Nevada Ecosystem Project (SNEP 1996), Forest Service Sierra Nevada Science Team (SNST 1998) report, and other literature in order to provide an assessment of the current science base for addressing rangeland issues in the Sierra Nevada. Primary findings are summarized as follows: 1) Grazing is a polarized issue with some people arguing for removal of grazing based "science" and others supporting grazing based on "science." The evaluation of grazing effects is not so black and white. "Grazing" is most often treated as a yes or no proposition, but it really is a complex process where timing, frequency, duration, season of use, and intensity matter. 2) In many studies it is difficult to determine when "historic grazing" is being discussed versus "current grazing." Without detailed descriptions of grazing season, frequency, intensity, and system as well as a quantitative description of the range site, riparian type, or stream class it is difficult to interpret the work with regard to current livestock management in the Sierra Nevada. Unfortunately, this problem permeates much of the existing rangeland literature. 3) Much of the existing work on grazing continues to be conducted as case studies. Although lacking in statistical and experimental design rigor, case studies do serve to provide a wealth of applied information. The key to learning from the tremendous amount of case study work occurring is the development and use of standard pre-treatment and post-treatment monitoring, standard reporting of "grazing" management tested, standard reporting of ecosystem characteristics, and standard reporting of watershed history and characteristics. Such information would allow the resources management community to benefit from individual case study efforts. 4) A key problem with the grazing literature cited in SNEP is that the authors do not always differentiate between peer-reviewed original research, non-peer-reviewed proceedings, editorials, position statements, or informational pamphlets, etc. when supporting statements. In tracing statements back to their original source we found a tendency to extend research results far beyond their original findings. This limits the utility of the document for resource managers.

Amme, D. and J. Morris. 2004. Stewardship grazing: managing California's coastal prairie and foothill grasslands on public lands. In: Proceedings, Ecology and

Management of California Grasslands, April 2-3, 2004, Berkeley, CA. Available online at: <http://cbc.berkeley.edu/grass/Abstracts.htm>.

While it is universally accepted that the California grassland and savanna landscape evolved with and are shaped by the processes of grazing, rest, and fire, very little is known on how these processes can be applied to manage for restoration and conservation goals, especially for public open space lands. Without fire or periodic grazing to reduce and recycle the buildup of un-decomposed plant litter, the thatch can reach in excess of 20,000 lbs per acre, snuffing out grassland richness and diversity. More often than not, fire and mowing are costly and unrealistic options on public parks and open spaces. The only practical option available is grazing management, which controls the season, frequency, duration, and intensity of livestock grazing: a stewardship grazing program. This type of livestock management adds a level of sophistication typically not found in grazing practices in California. There are many impediments to grazing on public lands including the cost and design of badly needed infrastructure improvements, the cost and coordination of moving livestock between isolated grasslands often under different ownerships, public access and conflicts, and accurate monitoring needed for program adjustments.

Baker, H. G. 1978. Invasion and replacement in Californian and neotropical grasslands. Pages 368-384 in J. R. Wilson, editor. *Plant Relations in Pastures*. CSIRO, East Melbourne, Australia.

The replacement of the perennial bunchgrasses of California grasslands by weedy, annual Mediterranean grasses under livestock grazing within 200 years is outlined. Attention is paid to corresponding changes in predominant plant breeding systems from allogamy (sometimes with facultative apomixis) in the bunchgrasses to autogamy in the annuals. Studies of population structures of the grasses are reviewed. The deleterious effects on grass productivity of recently increased rates of tree removal from oak woodlands are considered. In the highlands of Mexico and Guatemala, perennial bunchgrasses have not been replaced by annuals, despite imposed grazing pressure, because of the climatic difference between these highlands and California, and the grazing preferences of sheep.

Bakker, J.D., S.D. Wilson, J.M. Christian, et al. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications* 13:137-153.

Semi-arid ecosystems such as grasslands are characterized by high temporal variability in abiotic factors, which has led to suggestions that management actions may be more effective in some years than others. Here we examine this hypothesis in the context of grassland restoration, which faces two major obstacles: the contingency of native grass establishment on unpredictable precipitation, and competition from introduced species. We established replicated restoration experiments over three years at two sites in the northern Great Plains in order to examine the extent to which the success of several restoration strategies varied between sites and among years. We worked in 50-yr-old stands of crested wheatgrass (*Agropyron cristatum*), an introduced perennial grass that has been planted on $>10 \times 10^6$ ha in western North America. Establishment of native grasses was highly contingent on local conditions, varying fourfold among years and threefold between sites. Survivorship also varied greatly and increased significantly with summer precipitation. No consistent differences were found between drilling and broadcasting in their effects on establishment, but survivorship was nearly threefold higher in broadcast plots. Plots without seed added, or with native hay added, had almost no seedlings of native grasses. In contrast, broadcasting the residue remaining after cleaning seeds from native hay produced the highest seedling densities of any treatment. Competition from *A. cristatum* was significantly and consistently reduced through annual application of a generalist herbicide (glyphosate), which increased native grass establishment and survivorship and the richness and total cover of native species. Herbicide decreased standing crop and increased soil moisture and available nitrogen. *A. cristatum* was controlled without suppressing native vegetation, both by spraying in early spring, which selectively killed the cool-season *A. cristatum*, and by application with a wick, which selectively killed the taller *A. cristatum*. *A. cristatum* persisted over four years, however, in spite of annual herbicide application. *A. cristatum* cover in control plots increased significantly with summer precipitation. In summary, broadcasting and drilling differed little in their effects on establishment, but broadcasting increased survivorship and will allow the emergence of plant-induced heterogeneity. Competition from introduced species can be reduced but not eliminated by continuing herbicide application. Lastly, the positive relationships between precipitation and both *A. cristatum* and native seedling survivorship suggest that management should focus on controlling *A. cristatum* during dry years and on introducing native species during wet years.

Barry, S. J. 2004. Opportunities for using livestock to restore and manage California's native grasslands. In: Proceedings, Ecology and Management of California Grasslands,

April 2-3, 2004, Berkeley, CA. Available online at:
<http://cbc.berkeley.edu/grass/Abstracts.htm>

A recent, comprehensive review of the literature on California's native grasslands found that few studies have examined the impact of livestock grazing on native plants and many of these studies lacked replication of treatment and controls for quantitative analysis (see D'Antonio et al. 2002). Although grazing studies are inherently difficult to design and conduct, additional studies should consider prescribed grazing strategies to achieve restoration and management goals. Current research using GIS collars on livestock is helping range animal scientist understand grazing patterns on California's grasslands. Similarly, recent research on diet preference is not only helping animal behaviorist predict which plants a grazing animal will consume but also how a grazing animal can be enticed to consume undesirable plants. Using the latest research on grazing animal behavior and management can a successful grazing strategy be developed and tested to work towards restoration and management of California's native grasslands? This paper presents a series of considerations for a successful grazing strategy, including 1) species and class of livestock to be used; 2) the season of use; 3) the intensity of use. Examples of how these grazing strategies are being applied for restoration and management of California's native grasslands are discussed.

Bartolome, J.W., J.S. Fehmi, R.D. Jackson and B. Allen-Diaz. 2004. Response of a native perennial grass stand to disturbance in California's Coast Range grassland. *Restoration Ecology* 12(2): 279-283.

To assess the potential for enhancing an existing stand of native perennial grasses on a California Coast Range Grassland site, we experimentally manipulated the seasonal timing and presence of grazing for 3 years (1994 through 1996) and of autumn burning for 2 years (1994 and 1995) and measured species cover for 6 years (1993 through 1998). We subjected the species matrix to classification (TWINSPAN) and ordination (CCA) and tested the ordination site scores as well as diversity indices with linear mixed effects models. Four distinct plant community groups emerged from the classification. Two of these were dominated by annual grasses and two by perennial grasses. No treatment effects were observed on diversity. For composition, temporal and spatial random effects were important mixed effects model parameters, as was the fixed effect covariate, pre-treatment CCA site score, indicating the importance of random environmental variation and initial starting conditions. Incorporation of these random effects and initial condition terms made for more powerful tests of the fixed effects, grazing season, and burning. We found no significant burning effects. Grazing removal imparted a shift in plant community from more annual-dominated toward more perennial-dominated vegetation. Individual perennial grass species responded differently according to genus and species. *Nassella pulchra* (purple needlegrass) increase was greatest under spring grazing and *N. lepida* (foothills needlegrass) was greatest with grazing removal. *Danthonia californica* (California oatgrass) had little response over time under seasonal grazing treatments, but increased with grazing removal. Under relatively mesic weather conditions it appears that grazing removal from Coast Range grasslands with existing native perennial grass populations can increase their cover. However if *N. pulchra* is the sole existing population, spring season-restricted grazing should be equally effective at enhancing cover of the native grass species.

Bartolome, J.W. 1979. Germination and seedling establishment in California annual grassland. *Journal of Ecology* 67: 273-281.

Data for plant density, germinable seed in the soil, and seed production in annual grassland were obtained at Hopland Field Station, California, in 1973 and 1974. The study combined indirect estimates of numbers of seed in the soil, germination in soil samples containing natural seed, and estimation of plant density. Autumn patterns of establishment differed significantly between the two study years. Plant density increased through the autumn, reaching peaks of 261.8 and 345.3 plants per dm² in the seventh week after germination began, in 1973 and 1974 respectively. The numbers of germinable seed in the top 6.4 cm of the soil prior to the start of the growing season were 670.5 per dm² in 1973 and 610.2 per dm² in 1974, and thus showed little difference between years. Comparison of depletion of the soil seed-bank in the soil and increase of plant density showed that seeds germinating in the first week of the growing season produced fewer established seedlings than seeds germinating in the second or third weeks. The few seeds remaining in the fifth and sixth weeks had a high probability for successful establishment. Six species-groups exhibiting contrasting strategies for germination and establishment are discussed in detail.

Bartolome, J.W. and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madrono* 28(3): 172-184.

We present information clarifying the past and present role of the native perennial grass *Stipa pulchra* in the California grassland. *Stipa pulchra* occupies a diverse array of habitats in northern and central California, as shown from information collected on more than 1500 plots by the State Cooperative-Soil-Vegetation Survey. *Stipa pulchra* did not

increase in density over a 20 year period in ungrazed areas on the Hopland Field Station in northern California and was replaced by other perennial grasses and annuals on some plots. *Stipa pulchra* germinated more slowly than associated annual plants and *S. pulchra* seedlings apparently did not survive the period of rapid spring growth in annual grassland. In pot trials fewer *S. pulchra* germinated and plants grew poorly when grown with high densities of *Bromus mollis* and *Festuca megalura*. High densities of *B. mollis* limited *S. pulchra* growth more dramatically than high densities of *F. megalura*. We suggest that *S. pulchra* is the most common California native grass not because the species dominated the original California grassland, but because it is favored by disturbances common now. Disturbances that reduce associated annuals are important for colonization by *S. pulchra*.

Bartolome, J.W. and M.P. McClaren. 1992. Composition and production of California oak savannah seasonally grazed by sheep. *Journal of Range Management* 45: 103-107.

Seasonal grazing trials, conducted over 3 years at the Hopland Field Station in Mendocino County, Calif., tested the effects of 2 seasonal grazing strategies on within- and between-year production and composition in blue oak (*Quercus douglasii*) savanna understory and adjacent open annual grassland. Moderate intensity summer-fall-winter and spring-summer sheep use had few within-year effects. In contrast, production and composition varied considerably between years in both treatments. Forbs (especially legumes) decreased in open grassland and oak understory between years within both seasonal grazing regimes. This change could not have been caused by selective grazing because there were no corresponding within-year patterns. Instead, between-year changes are more likely related to non-selective effects of stocking rate and/or weather. Results from this study suggest that seasonal grazing systems offer little potential for improvement of annual range composition.

Bedunah, D.J. 1992. The complex ecology of weeds, grazing, and wildlife. *Western Wildlands (summer)*: 6-11.

This article discusses the ecology of invading plant species in the Intermountain West, examines the role of grazing in the spread of exotic weeds and discusses the impacts of weeds on domestic livestock, wildlife and native flora. Livestock grazing is a form of disturbance that can significantly increase the amount of bare soil and reduce the ability of grazed plants to compete with ungrazed plants. Livestock also serve as an important vector for transporting weed seed. The success of exotic weeds has been attributed to allelopathy, their superior ability to get and use water and nutrients, and magnitude of reproduction. Once perennial exotics invade a site, they are often able to move into undisturbed stands of native vegetation. Weeds have dramatically changed native plant communities in the West, reducing native forage production, wildlife habitat and the value of these rangelands for livestock grazing. The effects of such changes on ecosystem function are largely unknown.

Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* 11:1261–1275.

Bromus tectorum is an exotic annual grass that currently dominates many western U.S. semi-arid ecosystems, and the effects of this grass on ecosystems in general, and soil biota specifically, are unknown. *Bromus* recently invaded two ungrazed and unburned perennial bunchgrass communities in southeastern Utah. This study compared the soil food-web structure of the two native grassland associations (*Stipa* [S] and *Hilaria* [H]), with and without the presence of *Bromus*. Perennial grass and total vascular-plant cover were higher in S than in H plots, while quantities of ground litter were similar. Distribution of live and dead plant material was highly clumped in S and fairly homogenous in H. Soil food-web structure was different between H and S, with lower trophic levels more abundant in H and higher trophic levels more abundant in S. In *Bromus*-invaded plots, the quantity of ground litter was 2.2 times higher in *Hilaria*-*Bromus* (HB) than in H plots, and 2.8 times higher in *Stipa*-*Bromus* (SB) than in S plots. Soil biota in HB generally responded to the *Bromus* invasion in an opposite manner than in SB, e.g., if a given component of the food web increased in one community, it generally decreased in the other. Active bacteria decreased in H vs. HB, while increasing in S vs. SB. Soil and live plant-infecting fungi were the exception, as they increased in both types of invaded plots relative to uninvaded plots. Dead-plant-infecting fungi decreased in H vs. HB and increased in S vs. SB. Most higher-trophic-level organisms increased in HB relative to H, while decreasing in SB relative to S. Given the mixed response to invasion, the structure of these soil food webs appears to be controlled by both plant inputs and internal dynamics between trophic levels. When compared to non-invaded sites, soil and soil food-web characteristics of the newly invaded sites included: (1) lower species richness and lower absolute numbers of fungi and invertebrates; (2) greater abundance of active bacteria; (3) similar species of bacteria and fungi as those found in soils invaded over 50 yr ago; (4) higher levels of silt (thus greater fertility and soil water-holding capacity); and (5) a more continuous cover of living and dead plant material (thus facilitating germination of the large-seeded *Bromus*). These results illustrate that (1) soil food-web structure can vary widely within what would generally be considered one vegetation type (semi-arid

grassland), depending on plant species composition within that type, and (2) addition of a common resource can evoke disparate responses from individual food-web compartments, depending on their original structure.

Belsky, A.J. and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. *Conservation Biology* 11(2):315-327

Many ponderosa pine and mixed-conifer forests of the western, interior United States have undergone substantial structural and compositional changes since settlement of the West by Euro-Americans. Historically, these forests consisted of widely spaced, fire-tolerant trees underlain by dense grass swards. Over the last 100 years they have developed into dense stands consisting of more fire-sensitive and disease susceptible species. These changes, sometimes referred to as a decline in "forest health," have been attributed primarily to two factors: active suppression of low-intensity fires (which formerly reduced tree recruitment, especially of fire-sensitive, shade-tolerant species), and selective logging of larger, more fire-tolerant trees. A third factor, livestock grazing, is seldom discussed, although it may be as important as the other two factors. Livestock alter forest dynamics by (1) reducing the biomass and density of understory grasses and sedges, which otherwise outcompete conifer seedlings and prevent dense tree recruitment, and (2) reducing the abundance of fine fuels, which formerly carried low intensity fires through forests. Grazing by domestic livestock has thereby contributed to increasingly dense western forests and to changes in tree species composition. In addition, exclosure studies have shown that livestock alter ecosystem processes by reducing the cover of herbaceous plants and litter, disturbing and compacting soils, reducing water infiltration rates, and increasing soil erosion.

Belsky, A.J., A. Matzke and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *J. Soil Water Conservation* 54: 419-431.

This paper summarizes the major effects of livestock grazing on stream and riparian ecosystems in the arid West. We focused primarily on results from peer reviewed, experimental studies, and secondarily on comparative studies of grazed vs. naturally or historically protected areas. Results were summarized in tabular form. Livestock grazing was found to negatively affect water quality and seasonal quantity, stream channel morphology, hydrology, riparian zone soils, instream and streambank vegetation, and aquatic and riparian wildlife. No positive environmental impacts were found. Livestock were also found to cause negative impacts at the landscape and regional levels. Although it is sometimes difficult to draw generalizations from the many studies, due in part to differences in methodology and environmental variability among study sites, most recent scientific studies document that livestock grazing continues to be detrimental to stream and riparian ecosystems in the West.

Biswell, H.H. 1956. Ecology of California grasslands. *Journal of Range Management* 9:19-24.

A number of protected areas have been studied in order to record changes in vegetation when such areas are not grazed. The rapidity of change depends on rate of accumulation of mulch, weather and other factors that affect general distribution and growth of plants. It has been hypothesized that native perennial grasses will take over under grazing protection. This happens occasionally but not always. In a protected area of fertile soil near Berkeley a stand of 65% purple needlegrass decreased to about 10% after several years of protection, being crowded out chiefly by ripgut grass which was growing three or four feet tall. In the foothills east of the San Joaquin Valley, pine bluegrass gradually decreased under protection from grazing. It appears that much of the change in species composition is caused by accumulation of mulch. If the mulch is removed by hand, the plant cover may be set back to the stage of forbs. Where mulch accumulates slowly the changes in plant cover are less rapid, and the vegetation may stay in a relatively low stage of succession for many years. The perennial grasses often increase, or can be maintained, under a system of grazing management that retards the growth and reproduction of annuals but favors that of the perennials. This happens where the annuals are closely grazed followed by complete protection to permit the perennials to grow flower stalks and mature seed.

Blumler, M. A. 1992. Some myths about California grasslands and grazers. *Fremontia* 20:22-27.

Several widespread beliefs about California grasslands are discussed that, from the author's perspective, have little or no scientific basis, and need critical re-examination. The commentary focuses on myths that determine how we look at the California grassland ecosystem and how we attempt to manage it. Primary points raised include the following: 1) despite the emphasis on "re-establishment" of bunchgrasses, there is no good evidence that perennial grasses ever dominated California grasslands except in the north Coast Ranges where climate is less seasonal. 2) Some exotic

species have the capacity to become established and displace native species even in the absence of human disturbance. Eurasian species from similar climates and environmental conditions have shown themselves to be better competitors than many native grassland species, particularly in the case of aggressive annuals over perennials. 3) Bunchgrasses are inherently less tolerant of grazing than sod-forming rhizomatous grasses, and the predominance of the latter in the Great Plains is due to the historical presence of bison. As a corollary, the great success of introduced Mediterranean species in California is due to the supposedly light grazing pressure that existed pre-historically. 4) Native bunchgrasses vary in their tolerance of grazing. Comparisons across fences separating grazed and ungrazed plots that otherwise are ecologically similar suggest that, in some areas, native perennials benefit only slightly from grazing exclusion. 5) Any management strategy that favors some natives will hurt others, while also benefiting and harming various alien plant species. Furthermore, the responses of each species to grazing is likely to vary with environmental conditions, which are highly variable over the total geographical range of widely distributed species such as many bunchgrasses. Under these circumstances, a diversity of grazing regimes, including exclusion of livestock, might be the best management strategy.

Botkin M. J. M, and L S. Y. Wu. 1981. How ecosystem processes are linked to large mammal population dynamics, p. 373-387. In: C. W. Fowler and T. D. Smith (eds.), *Dynamics of Large Mammal Populations*. John Wiley, New York.

No abstract or summary available.

Brady, W. W., M. R. Stromberg, E. F. Aldon, C. D. Bonham, and S. Henry. 1989. Response of a semi-desert grassland to 16 years of rest from grazing. *Journal of Range Management* 42 (4): 284-288

Grazing was eliminated from the Appleton-Whittell Research Ranch Sanctuary, located in south-central Arizona, in 1968. Long term changes in canopy cover of vegetation were evaluated between 1969 and 1984, and comparisons were made between ungrazed and grazed plant communities in 1969. Long-term changes included both increases in species richness (diversity) and significant increases in canopy cover for midgrass, shortgrass, shrub, and forb species groups. Total vegetation cover was not significantly different on the grazed and ungrazed areas, but cover of midgrasses was significantly different. Increased cover of pine lovegrass (*Eragrostis intermedia* Hitchc.) on the ungrazed pasture was largely responsible for this difference. No differences in cover existed for the shortgrass, shrub, or forb species groups. Observations suggest that long-term (perhaps cyclical) changes in vegetation are occurring in addition to short-term influences of herb ivory. Data do not support the hypothesis that continued animal impact is necessary to prevent ecosystem deterioration.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. *Journal of Applied Ecology* 40:601–614.

Rangeland ecologists have been debating the validity of two current paradigms for the evaluation of vegetation dynamics on rangelands. This debate frequently contrasts the conventional model of continuous and reversible vegetation dynamics (range model) with a more contemporary model that can accommodate discontinuous and non-reversible vegetation change (state-and-transition model). The range and the state-and-transition models are conceptually related to the equilibrium and non-equilibrium paradigms within ecology, respectively. The methodological dichotomy that has developed between the range and the state-and-transition models has fostered the perception that these two ecological paradigms are mutually exclusive. We challenge this perception and contend that both methodologies and their corresponding paradigms are non-exclusive. Equilibrium and non-equilibrium ecosystems are not distinguished on the basis of unique processes or functions, but rather by the evaluation of system dynamics at various temporal and spatial scales. Consequently, ecosystems may express both equilibrium and non-equilibrium dynamics. This confirms early interpretations that ecosystems are distributed along a continuum from equilibrium to non-equilibrium states. Although both equilibrium and non-equilibrium dynamics occur in numerous ecosystems, the empirical evidence is frequently confounded by (i) uncertainty regarding the appropriate evidence necessary to distinguish between paradigms; (ii) disproportionate responses among vegetation attributes to climate and grazing; (iii) comparisons among systems with varying degrees of managerial involvement; and (iv) the evaluation of vegetation dynamics at various spatial and temporal scales. This critique supports the conclusion that a paradigm shift has not taken place in rangeland ecology, but rather, the debate has forced a more comprehensive interpretation of vegetation dynamics along the entirety of the equilibrium–non-equilibrium continuum. Therefore, the rangeland debate should be redirected from the dichotomy between paradigms to one of paradigm integration.

Brown CS, Rice KJ. 2000. The mark of Zorro: Effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. *Restoration Ecology* 8:10-17.

Native perennial grasses were once common in California prairies that are now dominated by annual grasses introduced from Europe. Competition from exotics may be a principal impediment to reestablishment of native perennial grasses. Introduced annual grasses, such as *Vulpia myuros* (zorro fescue), are often included with native perennial species in revegetation seed mixtures used in California. To examine the potential suppressive effect of this graminoid, we evaluated the growth and performance of a mixture of California native perennial grasses and resident weeds when grown with varying densities of *V. myuros*. The annual fescue exhibited a strongly plastic growth response to plant density, producing similar amounts of above-ground biomass at all seeding densities. Perennial grass seedling survival and above-ground biomass decreased and individuals became thinner (i.e., reduced weight-to-height ratio) with increasing *V. myuros* seeding density. *V. myuros* also significantly suppressed above-ground biomass and densities of weeds and had a more negative effect on weed densities than on native perennial grass densities. Biomass of native grasses and weeds was not differentially affected by increasing densities of *V. myuros*. Overall, because *V. myuros* significantly reduced the survival and performance of the mixture of native perennial grasses and this effect increased with increasing *V. myuros* density, we conclude that including this exotic annual in native seed mixtures is counterproductive to restoration efforts.

Bugg, R.L., C.S. Brown and J.H. Anderson. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. *Restoration Ecology* 5: 214-228.

Along rural roadsides of the Sacramento Valley of California, we seeded native and non-native perennial grasses to gauge their potential value in roadside vegetation management programs. In trial I (polycultures), three seeded complexes and a control (resident vegetation only) were tested. Each seeded plant complex included a different mix of perennial grasses seeded into each of several roadside topographic zones. The seeded levels of plant complex were: native perennial grasses 1 (8 species); native perennial grasses 2 (13 species); and non-native perennial grasses (3 species). In trial II, plots were seeded to monocultural plots of 15 accessions of native Californian and three cultivars of non-native perennial grasses. Plots in both trials were seeded during January 1992 and evaluated for three successive years. In trial I polycultures during 1993, canopy cover by seeded species was not significantly different among the three seeded complexes. The three seeded complexes showed statistically equivalent reduction of canopy cover by resident plant species. Biomass of seeded perennial grasses was greater for non-native perennial grasses than for native perennial grasses 1 or native perennial grasses 2. Total biomass (seeded plus resident species) was greatest for non-native perennial grasses. In trial II monocultures during 1993, the non-native *Thinopyrum intermedium* ssp. *trichophorum* (pubescent wheatgrass) attained the greatest height, followed by the native species *Nassella (Stipa) cernua* (nodding needlegrass), *Nassella (Stipa) pulchra* (purple needlegrass), and *Elymus trachycaulus* var. *majus* (slender wheatgrass). By contrast, the non-native *Festuca ovina* (sheep fescue) and the native *Poa secunda* ssp. *secunda* (pine bluegrass) were particularly short. *N. cernua*, *N. pulchra*, *E. trachycaulus*, and *T. intermedium* ssp. *trichophorum* showed particularly great canopy cover, whereas particularly low values of canopy cover were obtained for *F. ovina* and *P. secunda* ssp. *secunda*. A highly significant inverse linear relationship was obtained by regression analysis when canopy cover for seeded perennial grasses was used to predict canopy cover for resident plant species ($p < 0.0001$, $r^2 = 0.297$, slope 520.336 , intercept 539.442). In 1994, the following native perennial grasses showed substantial canopy cover in trial II monocultures and appear promising for use in Sacramento Valley rights-of-way: *Bromus carinatus* (California brome), *Elymus glaucus* (blue wildrye), *E. trachycaulus*, all accessions of *Hordeum brachyantherum* ssp. *brachyantherum* (meadow barley), a prostrate accession of *Hordeum brachyantherum* ssp. *californicum* (California barley), *N. cernua*, and *N. pulchra*. In addition, the non-native *T. intermedium* ssp. *trichophorum* performed well. By contrast, virtual failure of stands was observed for the non-native *F. ovina* and the following native species: *Elymus multisetus* (squirreltail), two accessions of *Festuca idahoensis* (Idaho fescue), *Festuca rubra* (creeping red fescue), and *P. secunda* ssp. *secunda*.

Burcham, L.T., 1957. California rangeland: an historic-ecological study of the range resource of California. California Department of Natural Resources, Division of Forestry, Sacramento, CA.

The range resource of California has been profoundly affected by use during nearly two centuries that domestic animals have been grazed upon it. The change has been detrimental in that productive capacity has been lowered and perhaps permanently damaged. Results of range use cannot be measured with any degree of precision, because no adequate base for measurement was established before use began. What was the original condition of the native ranges and probable carrying capacity for domestic livestock at the beginning of the Spanish colonization? To what extent has the range resource deteriorated and how is this deterioration related to grazing and other kinds of land use? What steps are

being taken to reverse the trend of declining range productivity? This report examines these questions in the light of available documentary evidence and of conditions which may be observed on the range today. Throughout this discussion principal emphasis will be placed on developments in the grassland, woodland and chaparral plant associations, both in "Spanish California" and the foothills of the Sierra Nevada and the North Coast Ranges.

Campbell, C.G. and B. Allen-Diaz. 1997. Livestock grazing and riparian habitat water quality: an examination of oak woodland springs in the Sierra foothills of California. Pp. 339-345 in: Proceedings of the symposium on oak woodlands: ecology, management and urban interface issues. USDA Forest Service Pacific Southwest Research Station, Gen. Tech. Report PSW-GTR-160. Berkeley, CA.

Studies throughout the western United States have shown that livestock can degrade riparian vegetation and stream channels and produce sediment, pathogen, and nutrient loading. This study at the Sierra Foothill Research and Extension Center is the first to focus on effects of livestock grazing on hardwood rangeland springs and associated riparian resources. Cattle grazing treatments at three intensities were applied in 1- to 2.5 ha pastures, which included a spring and ephemeral creek. Over a 5-year period we monitored nitrate, orthophosphate, dissolved oxygen, temperature and pH. Results show no significant differences in measured parameters among treatments. Sites were the source of some significant differences. This study indicates that moderate livestock grazing intensities do not detrimentally affect water quality at springs or ephemeral creeks in the oak woodlands of California.

Carlsen, T.M., J.W. Menke and B.M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology* 8: 18-29.

Populations of the rare annual forb *Amsinckia grandiflora* may be declining because of competitive suppression by exotic annual grasses, and may perform better in a matrix of native perennial bunchgrasses. We conducted a field competition experiment in which *Amsinckia* seedlings were transplanted into forty 0.64-m² experimental plots of exotic annual grassland or restored perennial grassland. The perennial grassland plots were restored using mature 3 cm-diameter plants of the native perennial bunchgrass *Poa secunda* planted in three densities. The exotic annual grassland plots were established in four densities through manual removal of existing plants. Both grass types reduced soil water potential with increasing biomass, but this reduction was not significantly different between grass types. Both grass types significantly reduced the production of *Amsinckia* inflorescences. At low and intermediate densities (dry biomass per unit area of 20–80 g/m²), the exotic annual grasses reduced *Amsinckia* inflorescence number to a greater extent than did *Poa*, although at high densities (>90 g/m²) both grass types reduced the number of *Amsinckia* inflorescences to the same extent. The response of *Amsinckia* inflorescence number to *Poa* biomass was linear, whereas the same response to the annual grass biomass is logarithmic, and appeared to be related to graminoid cover. This may be because of the different growth forms exhibited by the two grass types. Results of this research suggest that restored native perennial grasslands at intermediate densities have a high habitat value for the potential establishment of the native annual *A. grandiflora*.

Corbin, J.C., C.M. D'Antonio and S.J. Bainbridge. 2004. Tipping the balance in the restoration of native plants: Experimental approaches to changing the exotic:native ratio in California grassland. Pp. 154-179 in: M. Gordon and L. Bartol, editors. *Experimental Approaches to Conservation Biology*. University of California Press, Los Angeles, CA.

As exotic species increasingly threaten native biodiversity, habitat managers have turned to a variety of tools designed to increase the efficiency of plant restoration projects. These efforts include eliminating exotic competitors through mechanical removal, herbicide application, livestock grazing, prescribed burning, or biological control. In this chapter, we evaluate the ability of experimental tests of these techniques to favor native species in California grassland ecosystems. Overall, the existing data are insufficient to conclusively discern a relationship between livestock grazing and California's native grassland plants, or to evaluate the potential of grazing to enhance native-species richness and cover. Grazing has been shown to benefit native species in some individual studies, but its effects do not appear to be generalizable among studies or among years. Studies such as those of Stromberg and Griffin (1996) and Safford and Harrison (2001) suggest that grazing does not have as strong an effect on native species as has previously been suspected, but more research is needed to explore the generality of such conclusions. We found no evidence that any of the strategies consistently favored native species relative to exotic species. Outcomes were highly case specific and likely varied with biotic and abiotic conditions in the experimental systems. Several studies suggest that these

techniques are more successful in reducing specific invasive plant species in California grasslands rather than in increasing the success of native revegetation.

Corbin, J.D. and C.M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85(5): 1273-1283.

Though established populations of invasive species can exert substantial competitive effects on native populations, exotic propagules may require disturbances that decrease competitive interference by resident species in order to become established. We compared the relative competitiveness of native perennial and exotic annual grasses in a California coastal prairie grassland to test whether the introduction of exotic propagules to coastal grasslands in the 19th century was likely to have been sufficient to shift community composition from native perennial to exotic annual grasses. Under experimental field conditions, we compared the above-ground productivity of native species alone to native species competing with exotics, and exotic species alone to exotic species competing with natives. Over the course of the four-year experiment, native grasses became increasingly dominant in the mixed-assemblage plots containing natives and exotics. Although the competitive interactions in the first growing season favored the exotics, over time the native grasses significantly reduced the productivity of exotic grasses. The number of exotic seedlings emerging and the biomass of dicot seedlings removed during weeding were also significantly lower in plots containing natives as compared to plots that did not contain natives. If interactions between native perennial and exotic annual grasses follow a similar pattern in other grassland habitats, then the introduction of exotic grass propagules alone without changes in land use or climate, or both, was likely insufficient to convert the region's grasslands.

D'Antonio, C. Bainbridge, S. Kennedy, C. Bartolome, J. Reynolds, S. 2002. Ecology and restoration of California grasslands with special emphasis on the influence of fire and grazing on native grassland species. Study funded by the David and Lucille Packard Foundation and the University of California, Berkeley.

We reviewed livestock-grazing studies from throughout California in an attempt to quantitatively evaluate the use of grazing as a tool to reduce exotic species cover and promote native biological diversity. Our initial goal was to conduct a meta-analysis of the size and direction of grazing effects on native and exotic plants using all the available published and unpublished data sets from California. Meta-analysis is a statistical way of synthesizing results from different studies on a common topic (Gurevitch and Hedges 1993). We calculated an "effect size" in each study for each response variable (e.g., native forb cover) based on the ratio of the variable in the treated area (grazed) compared to the control (ungrazed). We assessed the effect of grazing on the measured response variables across studies using the mean of the pooled effect sizes. We found that most studies lacked adequate controls, lacked replication, or had no available measurement of among-plot variability and hence were not useable for meta-analysis. A summary of the six studies that fit the meta-analysis criteria demonstrated that livestock grazing was associated with an increase in the cover of native perennial grasses for those sites. Contrary to the claims of others (Thomsen et al. 1993; Kephart 2001), these studies showed a slight negative effect of livestock grazing on native-forb abundance and a positive effect of grazing on the abundance of exotic forbs. However, the results should be interpreted with caution because this small number of studies is inadequate for a true meta-analysis, and the addition of just a few studies could reverse the overall outcome. In addition, these studies represent a small subset of the California grassland and may not be representative of the state as a whole. The often heated debates over the impact of livestock grazing and the role, if any, that grazing should play in grassland restoration are likely to continue until many additional careful quantitative studies are conducted across the full range of grassland habitats in the state.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.

This paper focuses on the potentially devastating global consequences of exotic grass invasions. In the introduction, the authors list three ways that biological invasions can affect ecosystems: by altering (1) the system-level rates of resource supply, (2) trophic structure, or (3) disturbance regimes in the invaded area. After describing global geographic patterns of alien grass invasions, they outline the potential effects on ecosystems that occur via competition for light, nutrients, and water. Such changes can lead to the slowing or altering of plant succession and may increase the proportion of the Earth's surface that remains in an early successional stage. In addition, grasses can also alter geomorphological processes and microclimate. Finally, the authors discuss the interactions between grass invasions and fire (which they view as the most significant effect of alien grasses on ecosystems) and some potential global consequences of this interaction.

Dahlgren, R.A., M.J. Singer and X. Huang. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. *Biogeochemistry* 39: 45-64.

There is great interest in understanding how rangeland management practices affect the long-term sustainability of California oak woodland ecosystems through their influence on nutrient cycling. This study examines the effects of oak trees and how to moderate intensity grazing on soil properties and nutrient pools in a blue oak (*Quercus douglasii*) woodland in the Sierra Nevada foothills of northern California. Four combinations of vegetation and management were investigated: oak with grazing, oak without grazing, open grasslands with grazing, and open grasslands without grazing. Results indicate that oak trees create islands of enhanced fertility through organic matter incorporation and nutrient cycling. Compared to adjacent grasslands, soils beneath the oak canopy have a lower bulk density, higher pH, and greater concentrations of organic carbon, nitrogen, total and available P, and exchangeable Ca, Mg, and K, especially in the upper soil horizons (0–35 cm). In contrast, the light grazing utilized at this site had minimal effects on soil properties which included an increase in the bulk density of the surface horizon and an increase in available P throughout the entire soil profile. While low to moderate intensity grazing has little effect at this study site, there could be much larger impacts under the more intensive grazing practices utilized on many rangelands. The lack of oak regeneration and oak tree removal to enhance forage production may eventually lead to large losses of nutrients and soil fertility from these ecosystems. Results of this study have important implications for predicting how management practices may potentially affect oak regeneration, water quality, and ecosystem sustainability.

Dennis, A. 1989. Effects of defoliation on three native perennial grasses in the California annual grassland. Dissertation, University of California, Berkeley, CA.

In grasslands of California's Mediterranean climate zone, remnant populations of native perennial grasses occur within dense stands of introduced annuals. Growth of the native perennials under grazing is influenced both by the direct effects of defoliation on individual plants, and by changes in the physical and competitive environment which accompany grazing of the surrounding annual vegetation. I conducted experiments on planted and naturally established populations of three native grass species (*Poa scabrella* (Thurb.) Benth. ex Vasey, *Melica californica* Scribn., and *Koeleria cristata* (L.) Pers.) to determine the magnitude of these direct and indirect grazing effects on growth of species representing a range of phenological characteristics. *Stipa pulchra* Hitchc. was also included in the field experiments. Field experiment treatments included clipping of subject plants and surrounding vegetation at one of three dates, and removal of surrounding vegetation. Garden experiments, conducted separately for seedlings and established plants, included combinations of clipping at one of three dates and presence or absence of *Bromus mollis* L. Plant response was inferred from number of tillers, foliage height, weight of shoots, and number of flowering culms in the year following treatment. The perennial species differed phenologically, but all produced 50-90% of their net tiller production and foliage height growth for the season by late December. The annual vegetation, in contrast, carried out most of its growth during March and April. Removal of annual vegetation enhanced growth primarily during winter and early spring. Water and light competition do not appear to be the major mechanisms through which the annual vegetation reduces growth of the perennials. All species except *Stipa pulchra* responded negatively to clipping while foliage was green, whether annual vegetation was present or not. Clipping after senescence enhanced growth of *Poa scabrella* and *Melica californica*. Further research is needed to determine if phenologically similar treatments would enhance growth of the other species. Results suggest that December grazing would result in considerable reduction of *Poa scabrella* and *Melica californica*, while producing considerable enhancement of *Stipa pulchra*.

Dwire, K.A. 1984. What happens to native grasses when grazing stops? *Fremontia* 12: 23-25.

Livestock were removed from the coastal grassland prairies at Sea Ranch, a residential development in northern Sonoma County in the mid-1960s. Prior to development, the area was grazed continuously over a one hundred year period, mostly by sheep and to a lesser extent by cattle and horses. This article summarizes on-going investigation of plant succession and response of different grass species, including native, following the cessation of grazing. Since the study began in 1979, authors have observed a marked increase in the abundance of two introduced perennial grasses, sweet vernal grass (*Anthoxanthum odoratum*) and velvet grass (*Holcus lanatus*) invading mixed grassland meadows. There has also been increased seed production, growth, and number of plants of California oatgrass (*Danthonia californica*), purple needlegrass (*Stipa pulchra*) and blue wildrye (*Elymus glaucus*) since the cessation of grazing. There has also been a steady decline in hairgrass (*Deschampsia caespitosa* var. *holeiformis*), while the abundance of reedgrass (*Calamagrostis nutkaensis*) remains unchanged in more mesic habitats. The climate at Sea Ranch, where summer fog reduces seasonal drought stress, has probably contributed to this success, and plays an important role in reducing any advantage annuals may have over perennials in drier habitats.

Duncan, D.A. and W.J. Clawson. 1980. Livestock utilization of California's oak woodlands. Pp. 306-313 in: T.R. Plumb, ed. Proceedings of the symposium on the ecology, management, and utilization of California's oaks. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-44. Berkeley, CA.

No abstract or summary available.

Dwire, K. A., B. A. McIntosh, and J. B. Kauffman. 1999. Ecological influences of the introduction of livestock on Pacific Northwest ecosystems. Pages 313–335 in D. D. Gobel and P. W. Hirt, editors. *Northwest Lands, Northwest Peoples: Readings in Environmental History*. University of Washington Press, Seattle, Washington, USA.

As the most pervasive land use, livestock grazing has had widespread and dramatic ecological impacts, including loss of native species, changes in species composition, soil deterioration, degradation of fish and wildlife habitat, and changes in ecosystem structure and function. This essay describes the ecological changes resulting from livestock grazing that have occurred in the interior Pacific Northwest (that is, east of the Cascades Mountains) over the past 150 years. The authors review the history of livestock grazing, describe a simple model of the primary, secondary, and tertiary influences of livestock grazing, and discuss ecological changes that have occurred in forested, grassland, riparian and stream environments.

Dyer, A.R. 2003. Burning and grazing management in a California grassland: growth, mortality, and recruitment of *Nassella pulchra*. *Restoration Ecology* 11(3): 291-297.

Annual grasslands in California are often managed with seasonal grazing and prescribed burning on the assumption that such practices have long-term benefits for native species. Mature native perennial bunchgrasses, particularly *Nassella pulchra* (purple needlegrass), are often the focal species, although very little is known about responses at different life history stages. Thus, important questions remain about long-term population dynamics of both mature plants and seedling recruitment. In plots receiving repeated grazing and burning events over 7 years, mortality of mature plants was threefold higher on mounds than on intermounds and likely reflected increased competition intensity associated with increased resource availability in deeper soil. Burning and grazing treatments had strong positive effects on basal area of mature *N. pulchra*. However, plants in grazed plots that were not burned contained considerable standing dead biomass. Topographic location strongly influenced growth as intermound plants grew relatively more than mound plants, but the effects on growth of burning and grazing did not vary with topographic location. In mapped plots *N. pulchra* recruitment was very low, and overall density dropped an average of 31%. However, a significant time-by-burning effect indicated that survival was significantly higher in burned plots. After 7 years of repeated treatments, effects of burning and grazing management on mature *N. pulchra* were positive but not for all phenological stages. Understanding long-term influence of management on bunchgrass populations may not be easy to determine because short-term results may not reflect long-term responses and some life cycle dynamics may be observed only over very long periods.

Dyer, A.R. 2002. Burning and grazing management in a California grassland: effect on bunchgrass seed viability. *Restoration Ecology* 10: 107-111.

Prescribed fire is an important management tool for reducing the dominance of non-native species in annual grasslands; both annual and perennial native species show strong vegetative responses in the subsequent growing season. However, although the post-fire contribution of native species to the seed bank is assumed to be larger than in pretreatment years, the effects on seed quality, particularly viability and longevity, are not well understood. In this study, I germinated *Nassella pulchra* (purple needlegrass) seed that had been stored for 10 years after collection from target plants receiving treatment combinations of summer burning and grazing by sheep. Seeds from burned plants were larger and had higher germinability than seed from unburned plants. Seeds from plants that were both burned and grazed had the highest germination. The strong relationship between long-term viability and seed size suggests greater maternal provisioning and increased seed quality subsequent to burning and grazing. I conclude that managing for seed quality may be a useful approach for conservation of native species in California's critically endangered grassland habitats.

Dyer, A. R., H. C. Fossum, and J.W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madrono* 43:316–333.

We tested the hypothesis that prescribed burning and intense, short-duration grazing of the California annual grassland by sheep would increase emergence and survival of perennial bunchgrass seedlings at the Jepson Prairie Preserve in Solano County, California. Seeds of *Nassella pulchra*, either from a bulk seed collection or in three weight classes, were planted along paired transects on two topographic locations with differing soil depth. Treatment combinations that included burning or spring grazing produced higher rates of emergence than other treatments, but only in the first season after the burn. Very few seedlings (0.01%) survived in any treatment to the end of the fourth growing season. Although burning, grazing, and topography influenced the emergence of seedlings, survival to a mature stage appeared to be more strongly influenced by factors not manipulated or monitored in this study. Based on these data, we suggest that recruitment into the *N. pulchra* population may be strongly influenced by climatic variables and that the effectiveness of management techniques may be dependent on annual climatic variation. Management techniques for increasing *N. pulchra* populations must account for numerous and potentially specific habitat requirements of seedlings.

Dyer, A. R., and K. J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* 7:484–492.

In inland California grasslands, the high densities of alien annual species have altered the growing environment for native perennial grasses. Using variable-density plots, we measured the influence of intraspecific competition (conspecifics only) and diffuse competition (mixed-composition neighborhoods that include conspecifics) on growth and survival of *Nassella pulchra*, purple needlegrass. We assessed the effects of intraspecific and diffuse competition in weeded plots and unweeded plots, respectively, across a density gradient of *N. pulchra* plants (16–356 plants/m²). We used summer fire and spring sheep grazing to reduce diffuse competition in unweeded plots. The potential effect of rooting volume on competitive interactions was explored by establishing plots on two sites of different soil depth. Diffuse competition had an overriding influence on *N. pulchra* growth in all treatments. Intraspecific competitive effects were apparent only in the absence of diffuse competition. The effects of grazing and soil depth on growth were only short-lived interactions with the burning treatment. Burning was a longer-lived interaction, but only in weeded plots. Plant mortality was significantly increased by diffuse competition. Overall, *N. pulchra* survival was greatest in weeded plots, in grazed plots, and in deeper soil plots. The growth of *N. pulchra* individuals was negatively affected by alien annual species in all treatment combinations. Our data indicate that recruitment of *N. pulchra* within inland California grasslands is reduced by the adverse environment created by high densities of alien annual species. Successful attempts to increase populations of *N. pulchra* through management of the grassland community must involve significant modification of the biotic environment.

Dyer, A.R., and Rice, K.J. 1999. Effects of competition on resource availability and growth of California bunchgrass. *Ecology* 80:2697-2710.

In California, little is known about the sensitivity of native bunchgrasses to competition or to changes in resource availability. We investigated the effect of non-native annual vegetation on resource availability and growth of a native bunchgrass, *Nassella pulchra*, in a pair of factorial field experiments that incorporated effects of both interspecific and intraspecific competition as well as variation in soil depth. Plots of differing target densities and neighborhoods were used to assess changes in above-ground (light) and below-ground (water) resource availability over multiple seasons in two sites with differing soil depth. *N. pulchra* grown without interspecific competitors grew larger and produced more culms at all planting densities compared to plants in plots with interspecific competitors. Intraspecific competition significantly influenced growth only in the absence of interspecific competition. Reproductive effort, as measured by flowering culm production, was more sensitive than vegetative growth to both forms of competition. Light availability and variability at the soil surface was greatly reduced by the non-native annual neighborhood. As expected, soil moisture was rapidly depleted by annuals to 30 cm in all plots. In deep-soil plots, soil moisture was reduced at 60–150 cm depths only when annual vegetation was removed, and depletion was correlated with *N. pulchra* basal area. This result suggests that the interspecific neighborhood reduced root growth in *N. pulchra* and its subsequent ability to use deep moisture. Within California's inland grasslands, non-native annual vegetation has changed seasonal patterns of resource availability. We conclude that (1) increased competition for light during the spring, when growth of annuals is most rapid, suppresses growth and reproduction of *N. pulchra*; (2) by suppressing bunchgrass growth, annual grasses reduce access to belowground resources by competitive interference; and (3) the loss of perennial grasses in California grasslands and the general dominance by non-native annual species results in the relative underutilization of deep soil resources. These conclusions suggest that the dominance of California grasslands by non-native annual vegetation has shifted the primary limiting resource from soil moisture to light and the timing of resource limitation from summer to winter and spring.

Edwards, S.W. 1995. Notes on grazing and native plants in central California. The Four Seasons (Journal of the Regional Parks Botanical Garden) Volume 10(1): 5-34.

Control of brush encroachment and reduction of competition from exotic herbaceous plants are indirect benefits of grazing, browsing, and trampling by livestock to grassland native grasses and wildflowers in California. Control of within-bunch residue is a possible direct benefit that has been demonstrated experimentally elsewhere, but that requires investigation in California. Mismanaged grazing or overgrazing has caused widespread destruction of native biodiversity in California, and it continues to do so. Cultivation has caused more severe depletion in many places, and its extent in the landscape has probably been underestimated. Much of the original loss of native biodiversity that has been attributed to grazing may have been caused by plowing. The sheer ability of exotic super-competitors to eliminate native plants, especially in excluded terrains, is a dominant factor in central California. Well-managed livestock grazing, integrated over the landscape with appropriate exclusions, can be an excellent tool with which to address all these problems. The paleontological record shows that California's native vegetation and flora evolved in the context of intensive grazing, browsing and trampling by an array of medium to large mammals. The biology of native plants cannot be understood without considering this pre-history.

Ellison, L. 1960. Influence of grazing management on plant succession of rangelands. *Botanical Review* 26: 1-78.

No abstract or summary available.

Fernandez, A. R. *et al.* 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science* 4: 313–322.

Morphological (size and shape) and functional (growth, reproduction and phenology) attributes are used to characterize 42 annual species of Mediterranean grasslands according to their strategy. Principal components analysis of the matrix of 42 species x 9 attributes shows that the main trend of variation is related to plant size. Larger species have larger seeds, lower relative growth rates and lower reproductive output. The second and third trends of variation are related to plant shape. Ordination of species shows differences in shape between taxa and growth forms (grasses, legumes, forbs). The relative abundance of species with different attributes vary with the level of stress (water and nutrient availability) and disturbance (grazing and ploughing). Size is related to stress, with larger plants dominating in productive habitats and smaller ones in the most unproductive. Disturbance is related to shape and phenology, since grazing favors species with low canopies and ploughing favors species with shorter life cycles that are usually small in size. Relations between plant attributes and habitat characteristics are examined within the more general framework of plant strategy theory.

Fleischner, T.L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8: 629-644.

Livestock grazing is the most widespread land management practice in western North America. Seventy percent of the western United States is grazed, including wilderness areas, wildlife refuges, national forests, and even some national parks. The ecological costs of this nearly ubiquitous form of land use can be dramatic. Examples of such costs include loss of biodiversity; lowering of population densities for a wide variety of taxa; disruption of ecosystem functions, including nutrient cycling and succession; change in community organization; and change in the physical characteristics of both terrestrial and aquatic habitats. Because livestock congregate in riparian ecosystems, which are among the biologically richest habitats in arid and semiarid regions, the ecological costs of grazing are magnified in these sites. Range science has traditionally been laden with economic assumptions favoring resource use. Conservation biologists are encouraged to contribute to the ongoing social and scientific dialogue on grazing issues.

Fleischner, T.L. 1998. Grazing practices. Pp. 319-320 in P. Calow, ed. *The Encyclopedia of Ecology and Environmental Management*. Blackwell Science, London, UK.

No abstract or summary available.

Fleischner, T.L., D.E. Brown, A.Y. Cooperrider, W.B. Kessler, and E. L. Painter. 1994. Society for Conservation Biology position statement: livestock grazing on public lands in the United States of America. *Society for Conservation Biology Newsletter* 1(4): 2-3.

This position statement, adopted by the Board of Governors of the Society for Conservation Biology, asserts that livestock grazing as it is currently practiced in the western U.S. is responsible for a host of negative ecological effects on native ecosystems. Specifically, grazing often results in declines in native species biomass and abundance, reduced

biodiversity, aids the spread of invasive species, interrupts ecological succession, impedes the cycling of the most important limiting nutrient (nitrogen), disrupts community organization and food webs, and degrades the structure and function of riparian habitats. The Society for Conservation Biology asks the public land management agencies to: 1) evaluate the ecological costs and appropriateness of livestock grazing on an ecosystem basis, 2) remove livestock immediately from damaged areas, except where it can be shown that grazing provides benefits, 3) allow livestock grazing only where, and in such a manner, that it serves positive ecological roles, 4) help society make informed choices, 5) establish a network of significant areas where livestock are excluded, to serve as benchmarks for scientific evaluation of the ecological effects of grazing, and 6) eliminate grazing on public lands where it is accompanied by widespread control of native predators.

Foin, T. C., and M. M. Hektner. 1986. Secondary succession and the fate of native species in a California coastal prairie community. *Madroño* 33:189-206.

Secondary succession in former sheep pastures in the northern California coastal prairie favors community dominance by perennials, especially grasses. Studies of secondary succession at Sea Ranch, Sonoma County, show that the relative cover is dominated increasingly by *Anthoxanthum odoratum*, an introduced perennial grass. Native species are not successful at increasing their cover during succession and are unlikely to regain cover dominance in the coastal prairie.

Fossum, H.C. 1990. Effects of prescribed burning and grazing on *Stipa pulchra* seedling emergence and survival. Thesis, University of California-Davis, Davis, CA.

The hypothesis that prescribed burning and short-duration time-controlled grazing treatments benefit perennial bunchgrass seedling establishment and survival was tested in a 16 month study at Jepson Prairie Preserve, Solano County, CA. A total of 4320 purple needlegrass (*Stipa pulchra*) seeds were planted on matched transects in the fall of both 1988 and 1989 on mound (M) and intermound (IM) sites to study the effects of treatments (experiment 1) and seed size (experiment 2) on seedling establishment and survival. Treatments were randomly assigned within each block and were prescribed, including 3 levels of grazing (early spring grazed – ESG, summer grazed – SG, and ungrazed – UG) and 2 levels of burning (burned – B and unburned – UB). Emergence of seedlings by January 1989 and March 1989 was lowest for UG or SG treatments alone and highest for ESG/B treatments. By March 1990, survivorship of January 1989-emerged seedlings was highest for ESG/B or UB and B alone, and lowest for SG/B. The total number of seedling survivors recorded in March 1990 was highest for B in combination with ESG and UG and lowest for SG/UB. ESG/B significantly increased the density of exotic forbs, native grasses and bare ground cover, and reduced the density of exotic grasses (on M sites), litter cover and average height of the vegetation compared to no management. The density of neighbor species surrounding surviving *S. pulchra* seedlings in ESG/B was comprised of significantly less exotic grasses, higher litter cover and higher average sward height, and significantly less litter cover in UG/UB compared to density in the surrounding grassland community.

Franklin, J.F. and C.T. Dyrness. 1988. Grasslands of the interior valleys of western Oregon. Pp. 119-129 in: *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR.

Grasslands occupied extensive areas of the interior valleys of western Oregon before they were settled and continue to do so today. Almost all grassland areas have been heavily grazed by domestic livestock – cattle, sheep, or goats – and are extensively used as unimproved pastureland today. The nature of the original grassland communities is conjectural, since grazing and introduction of alien species have altered all stands to some degree. Several authors have suggested these grasslands probably looked similar to parts of the “California annual-type grassland” with *Danthonia californica* and *Stipa* spp. as typical dominant species. Other species on well-drained sites included *Agrostis hallii*, *Agropyron caninum*, *Bromus carinatus*, *B. vulgaris*, *Elymus glaucus*, *Festuca octoflora*, *F. californica*, *F. rubra*, *F. occidentalis*, *Melica subulata*, *Poa scabrella*, *Sitanion jubatum* and *Stipa lemmonii*. There are few descriptive data for existing valley grasslands of the Umpqua and Rogue Valleys, most of which are dominated by introduced species, especially annual grasses. One of these, *Taeniatherum caput-medusae*, is an extremely undesirable species which now dominates many stands.

Freilich, J.E. et al. 2003. Ecological effects of ranching: A six-point critique. *Bioscience* 53(8): 759-763.

Ranching is the dominant land use in much of the American West. Although a copious literature has examined the effects of various grazing practices on native ecosystems, we present here the idea that ranching has important impacts on the land independent of those caused by grazing itself. If biological conservation is to be successful on the western grasslands and shrublands, ranchers must be central to any plan. Focusing on the Great Plains of the United States, and

on Wyoming in particular, we raise six points of concern that must be addressed before we can hope to restore or maintain native ecosystems on the range: 1) persecution of “problem animals” 2) truncation of the food web 3) fencing, roads and fragmentation 4) exotic weeds and the chemicals used to control them 5) alteration of fire regimes and 6) impacts to water supplies and riparian areas.

Frost, W.E., J.W. Bartolome and J.M. Connor. 1997. Understory-canopy relationships in oak woodlands and savannas. Pp. 183-189 in: Proceedings of the symposium on oak woodlands: ecology, management and urban interface issues. USDA Forest Service Pacific Southwest Research Station, Gen. Tech. Report PSW-GTR-160. Berkeley, CA.

We summarize available information about the relationships between oak overstory and understory plants for major California rangeland types. Understory biomass, productivity, and plant species composition vary considerably because of geographic location, overstory species composition, and overstory density and distribution. Deciduous oak canopies in areas with less than 50 cm annual precipitation generally have either no effect or enhance understory productivity compared to adjacent grassland. Dense canopies in areas with more than 50 cm annual precipitation generally suppress understory productivity. Forage management implications are summarized for different woodland types around the state.

Fuhlendorf, S.D. and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51(8): 625-632.

Traditional rangeland management promotes homogeneity through uniform distribution of livestock grazing across the landscape, and favoring the most productive, most palatable forage species for domestic cattle. The results of traditional management are uniform utilization among plants and areas and a reduction of inherent landscape heterogeneity, which may have a critical impact on biodiversity and wildlife habitat. Alternative management approaches can facilitate patch heterogeneity. In the Great Plains of North America, heterogeneity can be promoted through fire and grazing disturbances of focal points within landscapes in which focal patches shift through time, producing a shifting mosaic that can enhance biodiversity and enrich wildlife habitat in grasslands with a long evolutionary history of grazing.

Galbraith, W.A. and E.W. Anderson. 1991. Grazing history of the Northwest. *Rangelands* 13(5): 213-218.

The history of grazing seems to have followed a similar pattern throughout the world. First, an abundance of native forage, then deterioration or loss of this resource, followed by efforts for rehabilitation. This paper summarizes the livestock grazing history of Oregon, Washington and British Columbia.

Garcia-Crespo, D. 1983. Multiple treatments to renovate depleted bunchgrass (*Muhlenbergia rigens* and *Stipa pulchra*) range sites in southern California. Dissertation. Loma Linda University, Loma Linda, CA.

No abstract or summary available.

Gelbard, J.L. and S. Harrison. 2003. Roadless habitats as refuges for native grassland diversity: interactions with soil type, aspect and grazing. *Ecological Applications* 12: 404-415.

The idea that roadless habitats act as refuges for native-plant diversity against exotic-plant invasion has seldom been tested. We examined the effect of distance from roads and its interactions with soil type, aspect, and livestock grazing on native- and exotic plant diversity in a 130 000-ha inland California (USA) foothill grassland landscape. During spring 2000 and 2001, we measured the numbers of and cover by native and exotic plant species in 92 sites stratified by distance from roads (10 m, 100 m, and 1000 m), soil type (nonserpentine and serpentine), and aspect (cool, warm, and neutral slopes). In nonserpentine grasslands, native cover was greatest in sites .1000 m from roads (23%) and least in sites 10 m from roads (9%), and the percentage of species that were native was significantly greatest in sites .1000 m from roads (44%) and least in those 10 m from roads (32%). In addition, the most distant sites had the largest number of native grass species and the fewest exotic forb species. In serpentine grasslands there was no significant effect of distance from roads on the numbers of and cover by native and exotic species. On both soils, two exotic species

(*Centaurea solstitialis* and *Aegilops triuncialis*) were at their lowest frequencies, while a native bunchgrass, *Nassella pulchra*, was at its highest frequency, in sites 1000 m from roads. On nonserpentine soils only, the exotics, *Convolvulus arvensis* and *Polypogon monspeliensis*, were at their lowest frequency, while a native bunchgrass, *Poa secunda*, was at its highest frequency in the most distant sites. Native species were more abundant on serpentine than nonserpentine soils; on serpentine, natives were more abundant on slopes than flat sites, while on nonserpentine, natives were least abundant on warm, south-facing slopes. Grazing, soil type, and aspect all significantly interacted in their effects on native and exotic richness and cover. Grazing negatively affected the number of native grass species, but not the number of native forb species on nonserpentine, and positively affected the number of native forb species, but not the number of native grass species on serpentine. Roadless areas are significant refuges for native species. However, to protect these habitats from the continued threat of invasion, land managers should consider means of preventing construction of new roads, limiting off-highway vehicle access into grasslands with low road densities, identifying a regime of livestock grazing that favors the persistence of natives over the spread of exotics, and monitoring recreational trails and grazing allotments within roadless areas to detect and eradicate new infestations.

George, M.R., J.R. Brown and W.J. Clawson. 1992. Application of nonequilibrium ecology to management of Mediterranean grasslands. *Journal of Range Management* 45:436-440.

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

Gerlach, J., A. Dyer and K. Rice. 1998. Grassland and foothill woodland ecosystems of the central valley. *Fremontia* 26: 39-43.

Central Valley grassland and foothill woodland ecosystems have been dramatically altered by exotic plant invasions and by serial changes in ecosystem management practices. In some areas as much as 95% of the herbaceous biomass is produced by a handful of Mediterranean annual species. The distribution and extent of woody species also have been dramatically altered. Unfortunately, no historic records exist that adequately describe either the pre-invasion condition of the ecosystem or the invasion process and resulting ecosystem changes. However, we do know that many of the changes were driven by reasonably well-documented changes in land management practices. Recent experiments have shown that the resulting ecosystem changes are significant, and that many species of native plants are poorly adapted to the modified environments. These environments are being further degraded by an invasion of longer-lived annual dicots, such as yellow star thistle (*Centaurea solstitialis*). This new invasion is modifying significant ecosystem properties and threatens adult native plants as well as seedlings.

Gordon, D.R. et al. 1989. Competition for soil water between annual plants and blue oak seedlings. *Oecologia* 79: 533-541.

We examined the competitive effects of two annual species on soil water potential and blue oak (*Quercus douglasii* Hook & Arn.) seedling growth and water relations. Two densities of the annual grass *Bromus diandrus* (Roth.) (100/dm², 3.6/dm²) and one density of the annual forb *Erodium botrys* (Cav.) (3.6/dm²) comprised plant neighborhoods around the oak seedlings grown in 1 m deep boxes. Rates of soil water depletion differed among neighborhoods. Soil in the *Erodium* neighborhoods dried significantly more slowly than did soil in the *Bromus* neighborhoods at either density. Differences in the rates of soil water depletion were correlated both with the 30% lower root biomass developed by *Erodium*, and the lower water extraction rates of *Erodium* relative to *Bromus* roots at constant root biomass. These results suggest that the annual species are not equivalent competitors for water: fibrous grass roots had greater competitive effect than did forb tap-roots. In a control container without an annual neighborhood, soil water potentials remained high for the duration of the experiment. Oak seedling emergence and growth responses were significantly affected by annual plant density. High density of annual plants suppressed oak root growth and shoot emergence. Only 20% of the acorns planted in high density *Bromus* neighborhoods showed aboveground shoot growth; 56% of those planted in low density *Bromus* or *Erodium* emerged. Ninety percent emerged in the control box. Relative growth rates of oak seedling roots and shoots were directly dependent on soil water potentials. Soil water was also closely correlated with oak seedling predawn water potentials and gas conductance measurements. Higher soil water potentials greater dry weights, and longer growing seasons were found for oak seedlings in the *Erodium* neighborhood and the container with no annuals than in *Bromus* neighborhoods of either density. These results suggest that

competition for soil water with introduced annual species contributes to the increased rate of blue oak seedling mortality currently observed in California woodland systems.

Griggs, F. T. 2000. Vina Plains Preserve: Eighteen years of adaptive management. *Fremontia* 28(1): 48-51.

This article summarizes 18 years of vegetation monitoring data (1982-2000) associated with testing various approaches to rotational grazing and livestock removal from the 4,600 acre Vina Plains Preserve, located in Butte and Tehama Counties, near the north end of the Sacramento Valley. Livestock removal was found to benefit several species of rare vernal pool plants and native perennials, however, non-native weeds – particularly medusahead (*Taeniatherum caput-medusae*) and yellow starthistle (*Centaurea solstitialis*) also increased. When conducted under carefully controlled conditions, grazing was found to be an effective management tool for reducing the impacts of non-native weeds and increasing the relative abundance of native plants in this vernal pool grassland complex.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121: 518–526.

Little is known about the potential for coexistence between native and non-native plants after large-scale biological invasions. Using the example of native perennial bunchgrasses and non-native annual grasses in California grasslands, we sought to determine the effects of interference from non-native grasses on the different life stages of the native perennial bunchgrass *Nassella pulchra*. Further, we asked whether *N. pulchra* interferes with non-native annual grasses, and whether competition for water is an important component of these interspecific interactions in this water-limited system. In a series of field and greenhouse experiments employing neighbor removals and additions of water, we found that seedling recruitment of *N. pulchra* was strongly seed-limited. In both field and greenhouse, natural recruitment of *N. pulchra* seedlings from grassland soil was extremely low. In field plots where we added seeds, addition of water to field plots increased density of *N. pulchra* seedlings by 88% and increased total aboveground *N. pulchra* seedling biomass by almost 90%, suggesting that water was the primary limiting resource. In the greenhouse, simulated drought early in the growing season had a greater negative effect on the biomass of annual seedlings than on the seedlings of *N. pulchra*. In the field, presence of annuals reduced growth and seed production of all sizes of *N. pulchra*, and these effects did not decrease as *N. pulchra* individuals increased in size. These negative effects appeared to be due to competition for water, because *N. pulchra* plants showed less negative pre-dawn leaf water potentials when annual neighbors were removed. Also, simply adding water caused the same increases in above-ground biomass and seed production of *N. pulchra* plants as removing all annual neighbors. We found no evidence that established *N. pulchra* plants were able to suppress non-native annual grasses. Removing large *N. pulchra* individuals did not affect peak biomass per unit area of annuals. We conclude that effects of interference from non-native annuals are important through all life stages of the native perennial *N. pulchra*. Our results suggest that persistence of native bunchgrasses may be enhanced by greater mortality of annual than perennial seedlings during drought, and possibly by reduced competition for water in wet years because of increased resource availability.

Hamilton, J.G. 1997. Changing perceptions of pre-European grasslands in California. *Madrono* 44:311-333.

The grasslands of California are dominated by non-native annual grasses primarily of Mediterranean origin. Because replacement of native species occurred before extensive botanical study, the original extent and composition of native vegetation is unknown. In 1920, the influential ecologist F.E. Clements concluded that widely scattered patches of perennial bunchgrasses were 'relicts' of a once vast perennial grassland. He proposed that the pre-European vegetation of the Central Valley, the valleys of southern California, and many areas of the Coast Ranges were originally dominated by the perennial grass *Nassella pulchra*. Although this hypothesis has become widely accepted, analysis of the data indicates that, especially for central and southern California, this hypothesis is probably incorrect. Clements made a number of mistakes, including misidentification of important taxa, over-reliance on his putative 'relicts', misunderstanding of the role of fire in grassland communities, and taking other people's work out of context. Alternative hypothesis have existed for almost as long as Clements' original hypothesis, but these have been generally ignored both by Clements and by many subsequent researchers in the field. There is a growing body of evidence to suggest that many of the areas dominated today by non-native annual grasses may formerly have been dominated by different vegetation types such as oak woodland, chaparral or coastal scrub.

Hamilton, J.G., J.R. Griffin and M. Stromberg. 2002. Long-term population dynamics of native *Nassella* (Poaceae) bunchgrasses in central California. *Madrono* 49: 274-284.

California bunchgrass communities are one of the most endangered ecosystem types in the United States. In this study, we sought to determine long-term (52+ years) changes in populations of native bunchgrasses, *Nassella pulchra* (A. Hitchc.) Barkworth and *Nassella cernua* (Stebb. & Love) Barkworth, in unmanaged stands. At the landscape scale, *Nassella* has increased. However, population dynamics of individual stands appeared related to land-use history. Non-native annuals, by themselves, did not seem to cause decline of *Nassella* stands, but light grazing did cause reduction of *Nassella* basal cover. Areas that were historically cultivated supported *Nassella* stands with lower basal cover and size distributions qualitatively different from areas that were never cultivated. Mortality of *Nassella* was concentrated in small plants. Interspecific interference probably was important in limiting seedling recruitment in stands with low *Nassella* basal cover, and intraspecific interference appeared to become important as *Nassella* basal cover increased. Even in the presence of non-native annuals, *Nassella* stands in areas that have not been disturbed by cultivation do not appear to require management for maintenance. New individuals are recruiting into populations, and conservative estimate of longevity of large individuals of *Nassella* is 100 years. However, in areas that have been cultivated, active management may be required to increase the abundance of *Nassella*.

Hanley, T.H. and J.L. Page. 1981. Differential effects of livestock use on habitat structure and rodent populations. California Fish and Game 68: 160-173.

Effects of livestock grazing on habitat structure, measured in terms of relative composition of plant life forms (trees, shrubs, forbs, graminoids), were assessed for 26 Great Basin habitat types in northeastern California and northwestern Nevada. Livestock grazing impact was quantified by comparison of "present" plant life form composition of each habitat type (determined by sampling 132 stands of vegetation) with estimates of "potential" plant life form composition based on U.S. Soil Conservation Service range site descriptions and other synecologic literature. Rodent populations were surveyed in livestock-grazed and -ungrazed communities of seven representative habitat types. Livestock grazing resulted in decreased relative abundance of herbaceous vegetation, particularly perennial bunchgrasses, in the study area. This had the effect of decreasing diversity of plant life forms in the more xeric habitats and increasing diversity of plant life forms in the more mesic habitats. Microtine rodents were consistently found in lower abundance in livestock-grazed than -ungrazed communities. Other species (*Eutamias minimus*, *Perognathus parvus*, and *Peromyscus maniculatus*) appeared to act as "decreasers" in xeric habitats and "increasers" in mesic habitats. Percentage change (from "potential" to "present" conditions) in rodent community diversity was positively correlated with percentage change in plant life form diversity. Change in plant life form diversity accounted for 79% of the variation in change in rodent species diversity.

Harris, G. A. and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. Ecology 51:530-534.

Rapidly elongating *Bromus tectorum* and *Taeniatherum asperum* roots penetrated the soil ahead of *Agropyron spicatum* roots and used available moisture. In contrast, *Agropyron desertorum* roots penetrated the soil almost as rapidly as *B. tectorum* and *T. asperum* and remained in favorable moisture. These differences in root penetration resulted in lower leaf water potentials and poorer survival in *A. desertorum*. The results suggest that in areas where root growth occurs at low temperatures and where lands are infested with *B. tectorum* and *T. asperum*, seedlings of *A. desertorum* would be more successful than seedlings of *A. spicatum*.

Harrison, S. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. Oecologia 121:99-106.

Serpentine meadows in Northern California supported higher species richness at the 1-m² scale than adjacent nonserpentine meadows, and had a considerably higher proportion of native species. Within each soil type, total species richness (natives plus aliens) was unrelated to biomass, cover, soil depth, or soil characteristics (N, P, Ca⁺⁺, Mg⁺⁺, water-holding capacity). However, the proportion of native species on serpentine was higher in meadows with lower levels of phosphorus and a lower calcium/magnesium ratio; the proportion of native species in nonserpentine meadows was higher on cool (north to northeast facing) slopes. At a regional scale, some of these effects were partly reversed; the rate at which new species accumulated with the addition of new sites, or beta diversity, was highest for native plant species in nonserpentine meadows. All of the above effects were independent of whether grazing by cattle was absent (removed 13 years ago) or present. The status of low-productivity serpentine soils as a refuge for native grassland species appears to be the result of their abiotic resistance to alien species, but not of a negative relationship between productivity and total species richness.

Harrison, S., B.D. Inouye and H.D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* 17: 837-845.

Grazing and fire are major forces shaping patterns of native and exotic species diversity in many grasslands, yet both of these disturbances have notoriously variable effects. Few studies have examined how landscape-level heterogeneity in grassland characteristics, such as soil-based variation in biomass and species composition, may contribute to variation in the effects of fire or grazing. We studied the effects of livestock grazing and fire in a mosaic of serpentine and non-serpentine soils in California, where most grasslands are dominated by exotic annuals and serpentine soil is the major refuge for native grassland species. We predicted that the effects of disturbance would be proportional to productivity and therefore would be greater on non-serpentine than serpentine soils. We measured species composition at 80–100 grazed or ungrazed sites for 2 years before (1998–1999) and 2 years after (2000–2001) an autumn wildfire. Both disturbances increased total species richness on both soils. However, fire enhanced total and exotic species richness more on non-serpentine soils and enhanced native species richness more on serpentine soils. Grazing increased native species richness on serpentine soils but not on non-serpentine soils. These soil-disturbance interactions suggest that the use of fire and grazing to manage native species diversity in wildlands must be done with careful attention to background ecological heterogeneity.

Hart, R.H. 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. *Plant Ecology* 155:111-118.

Shortgrass steppe rangeland near Nunn, Colorado, USA, has been lightly, moderately, or heavily grazed by cattle, or protected from grazing in exclosures, for 55 years. Plant species biodiversity and evenness were greatest in lightly- and moderately-grazed pastures. Both pastures were dominated by the warm-season shortgrass *Bouteloua gracilis*, but the cool-season midgrasses *Pascopyrum smithii* and *Stipa comata* contributed significantly to biomass production on the lightly-grazed pasture, as they did in the exclosures. Diversity was least in the exclosures, which were strongly dominated by the cactus *Opuntia polyacantha*. *Buchloë dactyloides*, another warm-season shortgrass, and *Bouteloua gracilis* were co-dominants under heavy grazing, and diversity was intermediate. Plant community structure and diversity were controlled by selective grazing by cattle and soil disturbance by cattle and rodents. Shortgrass steppe moderately or heavily grazed by cattle was similar to and probably as sustainable as steppe grazed for millennia by bison and other wild ungulates.

Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* 7:376-381.

We tested the effects of fall burning and protection from livestock grazing as management to enhance native grasses on a coastal grassland in central California. Plants from the Mediterranean, introduced beginning in the late 1700s, have invaded and now dominate most of California's grasslands. Coastal grasslands are generally less degraded than those inland and have higher potential for restoration and conservation. Productivity of the experimental plots varied annually and declined over the course of the study because of rainfall patterns. Foliar cover of the native *Danthonia californica* (California oatgrass) increased more under grazing than grazing exclusion and did not respond to burning. Two other natives, *Nassella pulchra* (purple needlegrass) and *Nassella lepida* (foothill needlegrass), responded variably to treatments. The response of *N. pulchra* differed from that reported on more inland sites in California. Restoring these grasslands is complicated by differing responses of target species to protection from grazing and burning. The current practice of managing to enhance single species of native plants (e.g., *N. pulchra*) may be detrimental to other equally important native species.

Hatch, D.A., J.W. Bartolome, and D.S. Hillyard. 1991. Testing a management strategy for restoration of California's native grasslands. Pp. 343-349 In Yosemite Centennial Symposium Proceedings: Natural Areas Conference with the Yosemite Centennial Celebration, October 13-20, 1990, Davis, California. National Park Service, Branch of Publications and Graphic Design, Denver Service Center, Denver, CO.

No abstract or summary available.

Hatch, D.A., J.W. Bartolome, J.S. Fehmi, and D.S. Hillyard 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* 7:376-381.

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Hayes, G. and Holl, K. 2003. Site-specific responses of native and exotic species to disturbance in a mesic grassland community. *Applied Vegetation Science* 6: 235(44).

Grassland communities are increasingly recognized as disturbance-dependent ecosystems, yet there are few replicated, multi-site studies documenting vegetation responses to varying frequencies and types of grassland disturbance. Even so, land managers frequently manipulate disturbance regimes in an attempt to favor native grassland plants over exotic species. We conducted a factorial experiment testing three frequencies of clipping combined with litter accumulation, litter removal, and soil disturbance within the highly threatened California coastal prairie plant community. We monitored the response of native/exotic, grass/forb plant guilds once a year for four years. More frequent clipping reduced cover of exotic grasses and favored exotic forbs, whereas native species were largely unaffected by clipping frequency. Litter accumulation, litter removal, and soil disturbance did not affect vegetation composition. Effects of litter accumulation may take longer than our experiment allowed, and soil disturbance due to our treatments was not sufficiently strong to show consistent effects relative to mammalian soil disturbance. Treatment response of some plant guilds differed among sites, highlighting the importance of replicating experiments at several sites before recommending conservation management practices.

Hayes, G. F. and K.D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* 17 (6): 1694-1702

Livestock grazing represents a major human alteration of natural disturbance regimes in grasslands throughout the world, and its impacts on plant communities have been highly debated. We investigated the impact of cattle grazing on the California coastal prairie plant community with a focus on native annual forbs, a number of which are of conservation concern. In spring 2000 and 2001, we surveyed the vegetation community composition, vegetation structure, and soil chemical parameters at 25 paired grazed and ungrazed sites over a 670-km range of the ecosystem. Native annual forb species richness and cover were higher in grazed sites, and this effect was concomitant with decreased vegetation height and litter depth. Soil properties explained less of the variation. Exotic annual grass and forb cover were higher in grazed sites. Native grass cover and species richness did not differ in grazed and ungrazed sites, but cover and species richness of native perennial forbs were higher in ungrazed sites. Our results suggest that cattle grazing may be a valuable management tool with which to conserve native annual forbs in the ecosystem we studied but that grazing differentially affects the various life-history guilds. Therefore, land managers must focus on creating a matrix of disturbance regimes to maintain the suite of species native to these mesic grasslands. The results of this and other studies highlight the importance of considering the adaptation of vegetation communities to disturbance in making recommendations for grazing management.

Hayes, G. F. and K.D. Holl. 2004. The effects of cattle grazing disturbance and implications for the conservation of native plants in California coastal prairie. In: *Proceedings, Ecology and Management of California Grasslands, April 2-3, 2004*, Berkeley, CA. Available online at: <http://cbc.berkeley.edu/grass/Abstracts.htm>.

Over the last 250 years, cattle became a dominant component of disturbance regimes in coastal prairie, while exotic plants proliferated. To investigate the impact of cattle grazing on the native plant community, we combined manipulative experiments examining grazing-related disturbances with field surveys of grazed and ungrazed coastal prairie sites. We conducted a factorial experiment in winter 1999 through spring 2003 at three coastal prairie sites near Santa Cruz, testing a combination of clipping frequencies and secondary disturbances (litter removal and soil disturbance) on the abundance of native and exotic plant guilds. While secondary treatments had no effect, increased clipping frequency tended to increase native grass and decrease exotic grass and exotic forb abundance, although the effects were site-specific. During a 2-year field survey, we surveyed cattle grazing impacts in 25 paired grazed/ungrazed sites spanning a 670-km range of coastal prairie plant community, focusing on native annual dicots. Results suggest native annual dicot species richness and cover was higher at grazed sites, concomitant with decreased litter depth and vegetation height. Conversely, native perennial forbs decreased and exotic annual species increased in

grazed sites. These results implicate the need for landscape-level planning to target disturbance regime restoration to maintain different guilds of native plants.

Heady H.F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. *Ecology* 37:798-812.

Amounts and position of natural mulch were manipulated according to 8 treatments and 8 replications for a period of 4 years. Yearly production of herbage was on oven-dry weight basis determined by sampling square foot plots. Botanical composition, ground coverage and height of plant materials were determined by the point system. A total of 46 species were found in the study area. Sixteen of them were alien and 40 were annual. Six species that were both alien and annual contributed between 67 and 84% of the composition during the 4 years of the study. A perennial bunchgrass, *Stipa pulchra*, increased in numbers from none to 612 plants within the enclosure between 1952 and 1955. Amounts of mulch in the different treatments varied between zero and nearly 5,000 pounds on an acre basis. Not all of the mulch decomposed each year so there was a gradual accumulation from 1952 to 1955. The percentage increase was relatively greater where a larger proportion of current growth was left on the plots than where small amounts remained. The increase in percentage of the soil surface covered with mulch in each April from 1953 to 1955 also indicated accumulation of mulch. With increasing amounts of mulch on the soil immediately before the fall rains, there was an increase in herbage production the following spring. This relationship is expressed by the regression equation $Y = 1214 + 0.354X$ for production within the 1,200 to 2,400 pound range. *Baeria chrysostoma* responded quickly to the mulch treatment and after 1953 it was very abundant with no mulch and absent where mulch was the heaviest. *Aira caryophylla* reacted in a similar fashion except it did not show significant differences between treatments until 1954 and the trend was still developing in 1955. Several other grasses and broadleaved herbs followed these same trends although to a much lesser degree. *Bromus mollis* was the only plant that increased a significant amount of percentage composition with the heaviest mulch treatments. It is the species which contributed most to the high production. Studies on the natural vegetation in the California annual type should include a measure of the variation resulting from different yearly environments.

Heady, H. F. 1958. Vegetation changes in the California annual type. *Ecology* 39:402–416.

Changes in the California annual grassland type were studied on three sites during the five successive growing seasons, 1951 to 1956. The sites were located on the Hopland Field Station in Mendocino County. The field data were collected by counting the number of plants by species on quadrats of one square inch in size. The three sites were characterized by distinctly different combinations of annual plants throughout the study. The seasonal growth pattern proceeds from germination, usually in November, through a short period of moderate growth, then a longer winter period when growth is slow, and finally ends with about a month of fast growth in April and May. Average number of plants per square inch varied between 3.3 and 35.0 with different situations. All species decreased in numbers per unit of area from December to June. *Bromus mollis*, *Bromus rigidus* and *Erodium botrys* decreased less in numbers per unit of area than the others, and thus, increased in percentage botanical composition. The numbers of plants per unit of area varied greatly between years as also did the various species. For example, 1953 was a year when the grasses clearly dominated the vegetation. *Erodium botrys* constituted a larger proportion of the vegetation in 1955 than in the other years. The patterns of seasonal and yearly change were recorded on the three sites, with different combinations of the botanical composition of the annual species. Changes in the annual type vegetation due to such items as grazing, seeding, fertilization, and fire are reviewed and the influence of mulch on percentage botanical composition is illustrated. Data and observations indicate that most of the germination occurs in a short period after the first fall rains of 0.5 to 1 inch. Cause for the differences in total numbers of plants between years was not found. The changes were examined in relation to the patterns of rainfall and temperatures and to grazing. The results are discussed as illustrations of seasonal, annual and successional changes in vegetation.

Heady, H. F. 1995. Valley grassland. Pages 491-514 in: M. G. Barbour and J. Major, editors. *Terrestrial Vegetation of California* (4th edition). California Native Plant Society, publication Number 9, Sacramento, CA.

The author describes the (presumed) historic and contemporary composition of grassland plant communities in the Central Valley and foothills of California; plant succession tended toward perennial bunchgrass dominants on nearly all well-drained upland sites, asserts that numerous annual species were present, and they dominated intermediate and early successional stages. Permanent alteration of the native grasslands began when Europeans first reached California. These changes resulted from a combination of 1) invasion by alien plant species, 2) overgrazing by domestic livestock, 3) agricultural cultivation, and 4) fire. Introduced annual plants are relatively resistant to grazing and in the presence of disturbance, exhibit a number of competitive advantages over native perennial grasses. Complete absence of livestock

is about the only situation that sometimes permits the reinvasion of perennial grasses. Removal of livestock now may be as disruptive to pristine conditions as the presence of too many livestock. Exotic annual grasses now dominate most if not all sites and cannot be eliminated under any known rangeland management practice.

Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and M. C. Stroud. 1988a. The California prairie. Pages 313-335 in R. T. Coupland, editor. *Natural Grasslands: Introduction and Western Hemisphere*. Elsevier, New York, NY.

Based on the present distribution of species, the floristic composition of relict areas, and the responses of vegetation in areas ungrazed and seasonally grazed by livestock, several conclusions may be drawn concerning the nature of the pre-settlement vegetation in California grasslands: 1) the original vegetation was mostly dominated by perennial bunchgrasses, reflecting the absence of heavy grazing pressure by large ungulates. Evolutionary changes in the native California bunchgrasses tended toward tolerance of light grazing and dry-season fires, but not heavy grazing use. 2) The floristic composition of the pristine grassland varied with location, as did the relative dominance of perennial and annual components. Perennial forbs and grasses dominated the more northern coastal areas, but were widely scattered in drier inland sites. Perennial species mentioned as abundant in early accounts include *Calamagrostis nutkaensis*, *Danthonia californica*, *Deschampsia caespitosa*, *Festuca idahoensis* and *Festuca rubra*. 4) When protected from grazing, perennial grasses often increase in annual grassland, although many communities remain dominated by annuals. 5) Introduced annuals are now generally present everywhere, preventing the return of natives to their former abundance.

Hektner, M.M. and T.C. Foin. 1977. Vegetation analysis of a northern California Coastal prairie: Sea Ranch, Sonoma County, California. *Madrono* 21:83-103.

No abstract or summary available.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.

Ecosystem ecologists traditionally have focused their attention on direct interactions among species, particularly those interactions that control flows of energy and materials among trophic levels. Emerging evidence suggests that indirect interactions may be more important than direct ones in determining ecosystem patterns and processes. Here I review indirect effects of ungulates on nutrient cycling, net primary production and disturbance regimes in terrestrial ecosystems. Ungulates influence the nitrogen (N) cycle by changing litter quality, thereby affecting conditions for N mineralization, and by adding readily available N to upper levels of the soil in urine and feces. As a result of these additions, natural heterogeneity in the spatial distribution of N within landscapes is amplified by ungulate selection of habitats and patches. The magnitude of returns of plant N to the soil in urine and feces is a function of animal body mass and characteristics of the diet, particularly N content and levels of tannin. Effects of N cycling can cascade throughout the ecosystem, and can stabilize or destabilize the composition of plant communities. Net primary production can increase or decline in response to ungulate grazing. The direction of this response depends on the intensity of grazing or browsing, the evolutionary history of the ecosystem, and the opportunity for regrowth. Opportunity for regrowth is determined by physiological and morphological characteristics of the plant as well as environmental conditions, particularly the extent and timing of moisture availability. Ungulates influence fire regimes by altering the quality and quantity of fuels available for combustion. In grasslands, ungulates often reduce the extent, frequency and intensity of fires, while in shrublands and forests, their effects can increase the likelihood of crown fires, while reducing the likelihood of surface fires. I develop the case that the way that ungulates influence ecosystem process is contingent on historical context, in particular the long-term context provided by plant-animal coevolution and soil development and the short-term context created by climate and weather. I show that ungulates are important agents of change in ecosystems, acting to create spatial heterogeneity, modulate successional processes, and control the switching of ecosystems between alternative states.

Hobbs, R.J. 2001. Synergisms among habitat fragmentation, livestock grazing and biotic invasion in southwestern Australia. *Conservation Biology* 15: 1522-1528.

The agricultural development of southern Australia over the past 200 years has resulted in extensively fragmented systems, often with only small, isolated remnants of native vegetation remaining. Grazing by sheep and cattle has affected both the remaining fragments and the surrounding matrix, and non-native plant and animal species have had dramatic effects on the native biota. Invasive plant species have the potential to significantly alter ecosystem composition and functioning, and invasive animals, particularly rabbits (*Oryctolagus cuniculatus*), foxes (*Vulpes vulpes*) and cats (*Felis catus*) effectively alter habitat and drive native fauna to local extinction. These different

influences often interact. For instance, smaller fragments are often more prone to plant invasion and are more likely to have been grazed in the past. Invasion of plant species is often linked with livestock grazing or rabbit invasion, and other higher-order interactions are also apparent. Classical fragmentation studies that concentrate on parameters such as habitat area and isolation but ignore changes in habitat condition brought about by livestock and invasive species are unlikely to yield meaningful results. Similarly, management of fragmented ecosystems must account for not only the spatial characteristics of the remaining habitat but also the importance of other influences, particularly those that impinge on fragments from the surrounding matrix.

Holmes, T.H. 1990. Botanical trends in northern California oak woodland. *Rangelands* 12(1):3-7.

Over the past two centuries human activity has markedly affected the oak woodland communities of northern California, spurring many shifts in its physiognomy and composition. This article focuses on these shifts, describing general historical trends and causes. Livestock grazing, woodcutting, fire, urban sprawl and alien plant invasions have all played a significant role in altering vegetation patterns and species composition. Most agree that the pre-invasion community consisted of perennial grasses such as purple stipa, pine bluegrass, blue wildrye, California brome, prairie junegrass and California oatgrass; plentiful perennial forbs such as *Brodiaea* and a principal contribution from various native legumes. These natives were displaced by alien annuals from Europe and Asia. In comparison to native perennial grasses, aliens have greater climatic adaptability, more rapid germination in the presence of sufficient moisture, more rapid growth to maturity, more prolific seed production, greater seed viability, and broader effectiveness in competing for scarce resources. In addition, alien species were often better adapted to domestic grazing and thrived in the many sites disturbed by cultivation.

Holmes, T. H., and K. J. Rice. 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Annals of Botany* 78: 233–243.

In western California, exotic cool-season annuals appear to have widely replaced native perennial bunchgrasses as the herbaceous community dominants in grasslands, oak savannas, and oak woodlands. We argue that because these two herbaceous plant types possess very different life histories, this invasion may have correspondingly altered seasonal patterns of soil-water availability. To begin to assess this hypothesis, in this study we compared exotic cool-season annuals and native perennial bunchgrasses in terms of growth, biomass allocation, rooting distribution, root morphology, and soil-water utilization. Exotic cool-season annuals completed their life cycle early in the dry season through rapid growth apparently made possible by a high proportional allocation to shoots in combination with the efficient production of roots of high specific root length. Further, annuals tended to concentrate root growth and soil-water utilization in the upper soil profile. In contrast, native perennial bunchgrasses allocated a high proportion of their biomass to the production of a deep root system, which allowed them to continue soil-water utilization well into the dry season and contribute to the formation of a very dry soil profile. Taken together, these contrasting patterns suggest that the invasion of exotic cool-season annuals might have produced a corresponding increase in the amount of water present at depth in the soil profile during the dry season.

Holstein, G. 2001. Pre-agricultural grassland in central California. *Madroño* 48:253-264.

An increasingly dogmatic paradigm maintains that central California's pre-agricultural grasslands were once entirely dominated by the bunchgrass *Nassella pulchra*. Evidence from early records and current relict vegetation, however, indicates they were spatially diverse. In moderate precipitation areas, *Nassella pulchra* frequently dominated grasslands in foothills and occasionally also on sandy valley floors, but grassland on heavier soils in valleys and on many hill slopes was dominated by the rhizomatous graminoids *Leymus triticoides*, *Carex barbarae*, and *C. praegracilis*. Dominance shifted to spring-active annual forbs in low precipitation areas and probably to summer-active annual forbs (tarweeds) on infertile old terrace soils.

Huddleston, R.T. and T.P. Young. 2004. Spacing and competition between planted grass plugs in pre-existing perennial grasses in a restoration site in Oregon. *Restoration Ecology* 12(4): 546-

Planting native species into restoration settings where other natives already occur is a common practice. However, the competitive consequences of such plantings are rarely studied. Planting density also affects restoration costs. Here we examined the effects of established individuals of Lemmon's needlegrass (*Achnatherum lemmonii*) on plugs of bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*) in a restoration site in Oregon. All three of these grasses are local native perennials. Plugs were planted at 6, 12, and 18 cm from established A.

lemmonii bunchgrasses and also in plots without *A. lemmonii* neighbors. Plug survival was uniformly high, averaging more than 98%. Plugs planted at 6 cm from established grasses showed significantly lower growth and reproduction than plugs planted at 18 cm, which had similar values to plugs not planted in the vicinity of *A. lemmonii*. These results suggest that interplanting distances of as little as 18 cm were sufficient to greatly reduce competitive effects on newly planted plugs, at least in early establishment at this site.

Huenneke, L. F., and H. A. Mooney. 1989. The California annual grassland: an overview. Pages 213-218 in: L. F. Huenneke and H. Mooney, editors. *Grassland Structure and Function: California Annual Grassland*. Kluwer Academic Publishers, Dordrecht, Netherlands.

Several themes developed in other chapters of this book are summarized in this paper. These include: references to patchiness and heterogeneity within the California grassland, despite the wide geographic ranges of most of its dominant species; the conspicuous and tight links between physical environmental factors, particularly climate, and the species composition and productivity of the system in any particular place and time; the importance of biotic interactions and of individual species' characteristics in determining resource availabilities, community structure, and system production. Most important, though, is the system's unique history as the site of successful invasion by Mediterranean Basin annual grasses and of displacement of native grassland species.

Jackson, R.D. and B. Allen-Diaz. 1998. *Quercus garryana* stand structure in areas with different grazing histories. *Madrono* 45(4): 275-282.

We estimated seedling, sapling and mature tree densities for two historically defined grazed-classes (low and high) of the Mad River Ranger District, Six Rivers National Forest, CA. Using *Quercus garryana* vegetation coverages on a geographic information system and a variable probability sampling scheme, 9 oak stands were randomly selected from each grazed-class. We employed a second sampling stage by selecting 3 simple random samples of 100-m² quadrants from each of the 18 oak stands selected in the first sampling stage. We found greater seedling and mature tree densities for the high grazed-class and greater sapling densities for the low grazed-class. Sapling densities were roughly double and seedling densities about 5 times mature tree densities regardless of grazed-class. We suggest that increased grazing intensity creates favorable environments for seedling survival, but may ultimately reduce the number of seedlings transitioning to the sapling size-class. Our results showing roughly 2:1 sapling to mature tree ratios indicate the *Q. garryana* regeneration is occurring on these rangelands.

Jackson, L.E. and J.W. Bartolome. 2002. A state-transition approach to understanding non-equilibrium plant community dynamics of California grasslands. *Plant Ecology* 162: 49-65.

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

Jackson, L. E., and J. Roy. 1986. Growth patterns of Mediterranean annual and perennial grasses under simulated rainfall regimes of southern France and California. *Acta Oecologia/Oecologia Plantarum* 7:191–212.

Phenology, growth and biomass allocation were studied in three annual grasses (with French and Californian populations of each species) and four perennial grasses (two French and two Californian) to suggest reasons for the different roles of annual and perennial grasses under the Mediterranean-type climates of France and California. We tested the hypothesis that the earlier and longer summer drought in California may be a factor in preventing the successional replacement of the non-native annuals by native perennials. The annuals (*Avena barbata*, *Bromus mollis* and *B. madritensis*) had similar phenologies characterized by the completion of their life cycle before the date of the onset of summer drought typical for southern France. The reproductive phenology of the perennials (*Dactylis glomerata*, *Bromus erectus*, *Stipa pulchra* and *Poa scabrella*) was delayed one month compared to the annuals. Due to higher allocation to leaves and lower sensitivity to winter temperatures, annuals had higher growth rates; they were an order of magnitude larger through the winter and by June annual plants were twice as large as the perennials. In autumn and winter, annuals allocated approximately 50% of their biomass to leaves and 30% to roots, while perennials allocated 30% and 50% to leaves and roots, respectively. The biomass allocated to sexual reproduction was approximately 60% in the annuals and 40% in the perennials. The switch from vegetative to reproductive growth was rapid and sudden in the annuals and more gradual in the perennials. The annuals had similar growth and reproductive output when grown under the simulated summer drought regimes of southern France and California, but perennials had fewer leaves and tillers under the earlier drought (Californian) regime. *S. pulchra* had less reproductive output, and all perennials (except *P. scabrella* which did not break its summer dormancy) had reduced autumn regrowth when the length of the summer drought increased. Californian populations of the annuals had earlier spring reproductive phenologies, but did not grow larger or have different reproductive outputs than the French populations when subjected to the California rainfall regime. Since production and yield in the perennials were increased by shorter summer drought, different rainfall patterns in southern France and California may partially explain the contrasting roles of perennial grasses in the two regions. Annual grasses appear to be phenologically adapted to set seed before summer drought begins, pre-adapting them to the earlier drought in California.

Jackson, L. E., and J. Roy. 1989. Comparative ecology of annual grasses: native versus Californian habitats and populations. Pp. 81-91 in: L. F. Huenneke and H. Mooney, editors. *Grassland Structure and Function: California Annual Grassland*. Kluwer Academic Publishers, Dordrecht, Netherlands.

We combined biogeographical and experimental information to identify factors that may be important in maintaining the dominance of Mediterranean annual grasses in the California grasslands. In California, annual grasslands are found in the interior valleys. Oak savannas in the Coast Range and Sierra Nevada have an annual grassland understory. Also, annual grassland dominates the first stage of succession following fire in coastal and Sierran foothill brushlands. Stands of annual grasses are dense mixtures of many species native to the Mediterranean Basin. In the Mediterranean Basin, annual grasses mainly occur in open, recently disturbed habitats. In northwestern areas (e.g. southern France), where summer drought is short, annuals are rapidly replaced by perennials. In areas to the south (e.g. Tunisia) with very arid climates, annual grasses do not form dominant communities. Only in the eastern Mediterranean Basin, where the climate is most similar to California, are annual grasses both ruderal and present in later successional communities. However, they do not form stable climax grassland communities as they do in California. We conducted a field experiment to determine the effect of the timing of summer drought on the growth of annual grasses from California and from southern France. Drought imposed in late April did not affect growth or biomass allocation in *Bromus mollis*, *Bromus madritensis* or *Avena barbata* compared to watered plants. *B. madritensis* had similar growth rates, as well as leaf and tiller production. However in the French populations, inflorescence emergence was later by one to two weeks and above-ground biomass continued to increase later in the season, than in the California populations. We discuss how dominance of annual grasses may be related to community structure and the timing and duration of drought. The different roles of annuals in the two regions cannot be attributed to different growth patterns and drought responses of regional populations. Instead, availability of perennial seeds and the response of perennials to drought may be important factors determining community structure and successional patterns in the two areas.

Jansen, H.C., R.R. Snow, G.A. Treber and F.L. Bell. 1997. Effects of livestock grazing on blue oak saplings. Pp. 313-319 in: Proceedings of the symposium on oak woodlands: ecology, management and urban interface issues. USDA Forest Service Pacific Southwest Research Station, Gen. Tech. Report PSW-GTR-160. Berkeley, CA.

Effects of two systems of livestock grazing and no grazing on the growth of blue oak (*Quercus douglasii*) saplings were examined over a 4-year period in western Colusa County, California. In grazed plots, base and height growth and moisture stress of saplings were less, while soil bulk density was mostly higher. Residual dry matter increased in non-grazed plots but not in grazed plots. Effects of the two grazing systems on sapling and plot variables did not differ significantly except for browse utilization which was significantly higher under high-intensity, short-duration grazing than under traditional, moderate grazing in 3 out of 4 years.

Jimerson, T.M., J.W. Menke, S.K. Carothers, M.P. Murray, V. VanSickle and K. Heffner-McClellan. 2000. A field guide to the rangeland vegetation types of the northern California province: Klamath, Mendocino, Shasta-Trinity and Six Rivers National Forests. USDA Forest Service Pacific Southwest Research Station, R5-ECOL-TP-014. San Francisco, CA.

This field guide describes an ecological classification for rangeland plant communities – both existing and potential natural – on Forest Service lands in northern California province, including the Klamath, Mendocino, Shasta-Trinity and Six Rivers National Forests. The classification is based on data collected from a series of 0.1 acre plots subjectively located in grasslands, oak woodlands, meadows, and chaparral and conifer forests with rangeland potential. A number of rangeland vegetation types are described and summary statistics are presented on physical and biological environment, species diversity and dominance, soils, geographic distribution, and management implications. Indicator species are provided for each vegetation type. The authors discuss the history and ecological dynamics of rangelands in northwest California, and the impacts of various land management practices including livestock grazing.

Jimerson, T.M. and S.K. Carothers. 2002. Northwest California oak woodlands: environment, species composition and ecological status. Pp. 705-717 in: Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-184. Berkeley, CA.

This paper describes the oak woodland plant communities of northwest California and their ecological status using data from 446 ecology plots collected on federal lands in Humboldt, Trinity, Siskiyou, Mendocino, Tehama, Glenn, Colusa and Lake Counties. Geographically, oak woodlands lie between the coastal mixed evergreen forests and the valley grasslands of the Central Valley. They were found in small patches nested within a mosaic of annual grasslands and conifer forests, and hence contain species common to both of these vegetation types. The oak woodlands of northwest California were primarily included in three vegetation series: Oregon white oak (*Quercus garryana*), black oak (*Quercus kelloggii*) and blue oak (*Quercus douglasii*). Valley oak (*Quercus lobata*) was also found in the study area, but because of its limited extent and insufficient samples, it will not be described here. Due to their history of livestock grazing and their proximity to annual grasslands, many of northwest California's oak woodlands contained high cover of non-native species. In some types, non-native grass and/or forb cover far exceeded that of native species. Oak woodlands had a significantly lower cover of invasive weeds when compared to annual grasslands, which is likely related to continued disturbance from cattle grazing. Oak woodland sites containing noxious and invasive weeds had significantly higher bare ground ($p = .05$), higher surface gravel and rock cover (indicative of disturbed soil surfaces, $p = .009$), thinner A soil horizons ($p = .017$), lower available water holding capacity ($p = .05$), as well as lower canopy cover ($p = .001$) and higher cover of early seral grass species ($p = .002$). These attributes increase the potential for successful noxious weed encroachment. Management that maintains high litter cover or limits the creation of bare soil will likely reduce the potential for new infestation sites. In reference areas, where disturbance was primarily natural and cattle grazing was absent, the grass seral status was often dominated by cover in the late-seral category (e.g. perennial grasses). Based on these findings, specific threats to oak woodlands include: 1) potential loss in biodiversity as a result of competition from invasive non-native species and understory invasion by conifers, 2) potential soil productivity loss as a result of surface disturbance from livestock grazing and non-native grass invasion, 3) increased cover of noxious weeds in conjunction with #2 above, and 4) potential negative impacts on ecological processes through altered fire regimes.

Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: A quantitative review. *Western North American Naturalist* 60: 155-164.

A quantitative review was conducted of the effects of cattle grazing in arid systems on 16 response variables ranging from soil bulk density to total vegetative cover to rodent species diversity. Using various studies from North American arid environments that used similar measures for assessing grazing effects on the same response variables, each study was assigned to serve as a single data point in paired comparisons of grazed versus ungrazed sites. All analyses tested the one-tailed null hypothesis that grazing has no effect on the measured variable. Eleven of 16 analyses (69%) revealed significant detrimental effects of cattle grazing, suggesting that cattle can have a negative impact on North American xeric ecosystems. Soil-related variables were most negatively impacted by grazing (3 of 4 categories tested were significantly impacted), followed by litter cover and biomass (2 of 2 categories tested), and rodent diversity and richness (2 of 2 categories tested). Vegetative variables showed more variability in terms of quantifiable grazing

effects, with 4 of 8 categories testing significantly. Overall, these findings could shed light on which suites of variables may be effectively used by land managers to measure ecosystem integrity and rangeland health in grazed systems.

Jones, A. 2001. Review and analysis of cattle grazing effects in the arid West, with implications for BLM grazing management in southern Utah. Wild Utah Project. Salt Lake City, UT. Available online at: <http://rangenet.org/directory/jonesa/litrev.html%20>

This report includes an extensive review of the ecological literature in examining the evidence that livestock grazing can impede the Bureau of Land Management from meeting adopted standards and guidelines for healthy rangelands. The majority of literature included in this review comes from studies conducted in the Colorado Plateau and Intermountain West, with particular emphasis on lower elevation sites such as those generally administered by the BLM in Utah. In addition to a review of the scientific literature, the authors examine livestock management in southern Utah as a case study to evaluate BLM grazing management in light of the findings of this review.

Keeley, J. E. 1990. The California valley grassland. Pp. 2-23 in A.A. Schoenherr (ed.), *Endangered Plant Communities of Southern California*. California State University, Fullerton. Southern California Botanists, Special Publication No. 3.

In the foothill grasslands and savannas of California, non-native grasses and forbs dominate due to a history of over-grazing coupled with extreme droughts. These ecosystems have already been so heavily invaded by non-native grasses and forbs that present livestock grazing at low to moderate stocking densities is not tied to shifts in the native/non-native dominance. However, our research in the southern Sierra Nevada shows that grazing by different types of livestock in foothill woodlands may alter species composition and distribution of plant functional types or growth forms.

Keeley, J. E. 1993. Native grassland restoration: the initial stage-assessing suitable sites. Pp. 277-281 in J.E. Keeley (ed.), *Interface between Ecology and Land Development in California*. Southern California Academy of Sciences, Los Angeles.

No abstract or summary available.

Keeley, J.E., D. Lubin and C.J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13(5): 1355–1374.

Patterns of native and alien plant diversity in response to disturbance were examined along an elevational gradient in blue oak savanna, chaparral, and coniferous forests. Total species richness, alien species richness, and alien cover declined with elevation, at scales from 1 to 1000 m². Blue oak savannas were heavily dominated by alien species and consistently had more alien than native species at the 1-m² scale. All of these aliens are annuals, and it is widely thought that they have displaced native bunchgrasses. If true, this means that aliens have greatly increased species richness. Alternatively, there is a rich regional flora of native annual forbs that could have dominated these grasslands prior to displacement by alien grasses. On our sites, livestock grazing increased the number of alien species and alien cover only slightly over that of sites free of livestock grazing for more than a century, indicating some level of permanency to this invasion. Blue oak savannas are an important propagule source for alien species because they maintain permanent populations of all alien species encountered in post-fire chaparral, and because the vegetation mosaic in this region places them in close proximity.

Kie, J.G. and J.F. Lehmkuhl. 2001. Herbivory by wild and domestic ungulates in the Intermountain West. *Northwest Science* 75 (special issue):55-61.

Management of ungulates is seldom undertaken with a focus on the effects on forest health and productivity but rather focusing on populations of the ungulates and their habitat needs. Consequently, only limited research has examined grazing and browsing by ungulates in coniferous forests as a chronic disturbance factor affecting nutrient turnovers, competitive interactions among plant species, and rate and trajectories of successional pathways. Local effects are quite variable and depend on ecosystem productivity. Grazing can have mixed effects on species richness and the spread of exotic plants at the landscape scale. Grazing can also affect nitrogen fixation and rate of nitrogen mineralization. Ungulate density relative to carrying capacity of the site largely determines the effects of herbivory. High population densities of ungulates have been shown to change plant species composition, growth of trees, and to damage

regeneration. Grazing also reduces accumulation of fine fuels on the forest floor, which formerly carried low-intensity, high-frequency ground fires. Effects of wild ungulates can be controlled by hunting regulations, and in some cases, by artificial contraception. Effects of grazing by livestock can be controlled through management actions such as changes in livestock numbers, changes in timing and duration of grazing, altering livestock distribution with fencing and placement of salt and supplemental feed, and specialized rotational grazing systems such as deferred and rest rotation.

Kinney, W.C. 1996. Condition of rangelands before 1905. Pp. 31-45 in: Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II. Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources. Davis, CA.

Historical accounts indicate that highly productive and diverse rangelands existed when Europeans arrived in the Sierra Nevada. Large ungulate populations were present, and perennial grasses dominated foothill rangelands. Numerous observers reported severe overgrazing by livestock in the late 1800s, due in part to a lack of regulation of the common rangelands. Livestock management contributed to annual grassland conversion on the west side and to juniper woodland expansion on the east side of the range. The abundance of a diverse assemblage of large grazing mammals at the end of the Pleistocene indicates that Sierra Nevada rangelands were highly adapted to intense grazing pressure and that animal disturbance was an integral part of this highly productive system. This evidence argues for a recognition that well-managed animal disturbance is as vital as well-managed fire to ecosystem health and sustainability.

Krueger, W.C. and A.H. Winward. 1974. Influence of cattle and big game grazing on understory structure of a Douglas-fir – ponderosa pine – Kentucky bluegrass community. *Journal of Range Management* 27(6): 450-453.

A Douglas-fir-ponderosa pine-Kentucky bluegrass community was studied 14 years after grazing by cattle and big game, by big game, and no cattle or big game grazing. Heavy season-long use by cattle and big game resulted in apparent retrogression. The herbaceous component of the community was substantially changed by cattle and big game grazing but not by big game grazing alone. Grazing by cattle and big game and big game only had similar effects on the browse components of the community.

Landsberg, J. *et al.* 1999. The impacts of livestock grazing on biodiversity in natural ecosystems. Pp. 752-777 in: Jury, G. and Fahey, G. C. (eds), *Nutritional Ecology of Herbivores*. Proc. of the 5th International Symp. of the Nutrition of Herbivores, American Society of Animal Science, Savoy, IL.

Many different models have been proposed to explain or predict the impacts of livestock on biodiversity, but their success in informing management decisions has been mixed. In part this is because of the complexities of the interactions, and the large disparities in the scales at which impacts and management occur. In this paper, we consider impacts at a hierarchy of scales ranging from individual plants and animals through to differences between regions and ecosystems, and discuss herbivory models in terms of their relevance at various levels in the hierarchy. Major points: 1) Livestock grazing inevitably impacts on bio-diversity in natural ecosystems that have not previously been grazed by livestock. The nature and extent of the impact is hugely variable, however. 2) The impact is most extreme when natural ecosystems are converted to fertilized, exotic pastures to support livestock. The impacts of ancillary activities such as water provision, fencing, fire management, and pest control also lead to major shifts in the abundance and distribution of many native biota. Numerous examples from Australia and South Africa of local and regional extinctions of some species, and incursions by others, attest to the magnitude of the changes wrought by ancillary activities associated with livestock management. 3) Most nutritional theory remains focused at the finer scale of animal-plant interactions, where generalizations are few. Promising areas of conceptual development include the characterization of plant traits associated with grazing sensitivity and resistance, and the identification of key habitat characteristics for sensitive fauna. 4) Concepts related to focal species and species' functional identity are important for linking local animal-plant interactions with processes that occur across landscapes. 5) At bioregional scales, concepts that relate grazing impacts to their evolutionary context have proven helpful for understanding the constraints under which different systems operate: why some ecosystems tolerate or even benefit from livestock grazing, while others are more sensitive. 6) An understanding of the impacts of livestock grazing on biodiversity should take cognizance of differences among systems, not only in the capacities and sensitivities of natural systems, but also in the cultures, expectations, and needs of their managers.

Langstroth, R.P. 1991. Fire and grazing ecology of *Stipa pulchra* grassland: a field study at Jepson Prairie, California. Thesis, University of California-Davis, Davis, CA.

Individual *Stipa pulchra* target plants were permanently marked on mound and intermound sites in the field and subjected to six combinations of prescribed burning, fire suppression, short-duration early spring grazing, short-duration summer grazing, and protection from grazing by domestic sheep. Average and maximum foliage height, live crown cover, fragmentation, basal area and perimeter, and ramet densities were measured. Average and maximum foliage heights were reduced by fire for at least two seasons after the burn. Grazing reduced the height of the next season's regrowth relative to no grazing. Mound plants were generally taller than intermound plants. Live crown cover was reduced by fire overall the first post-burn season, however, by the second season burned plants experienced new tillering and often had more live cover than unburned plants. Live tiller distribution patterns became more dispersed for all target plants under all treatments over time, except for ungrazed burned intermound plants, where the solid growth pattern increased. Fragmentation was enhanced significantly by fire and to a lesser degree by early spring grazing. Basal area was reduced by fire overall, although intermound plants tended to increase with or without burning. Intermound plants increased in basal perimeter (especially when burned), while mound plants did not change significantly overall. Area/perimeter ratios, except for unburned intermound plants, tended to decrease under all treatments. Ramet density was increased by burning on mounds and by early spring grazing on both mound and intermound locations.

Laudenslayer, W.F. et al. 1989. Historical effects of forest management practices in eastside pine communities in northeastern California. Pp. 26-34 in: A. Tecele, W. Covington and R.H. Hamre, eds. Multi-resource management of ponderosa pine forests; Nov. 14-16, 1989, Flagstaff, AZ. USDA Forest Service Rocky Mountain Research Station Gen. Tech. Report RM-185. Fort Collins, CO.

The eastside pine region of northeastern California, characterized by stands of ponderosa (*Pinus ponderosa*) and Jeffrey pines (*P. jeffreyi*), have long been influenced by timber harvest, livestock grazing and fire exclusion. Intensive, unmanaged grazing of the eastside pine forests and adjacent rangelands resulted in the decline of perennial bunchgrasses and increase of the invasive cheatgrass (*Bromus tectorum*) as well as shrubs and small trees. At the time of the first settlements in the area, extensive acreages of bunchgrass had little or no junipers or sagebrush. However, junipers and sagebrush increased substantially in the period during and after unmanaged grazing, especially of sheep. The increase in woody vegetation is also related to fire exclusion, and the removal of fine fuels by livestock. These activities have substantially altered the overstory and undergrowth of eastside pine stands, and will affect options for management in the future.

Laycock, W.A. 1994. Implications of grazing vs. no grazing on today's rangelands. Pp. 250-280 in: Vavra, M., W.A. Laycock and R.D. Pieper, eds. 1994. ***Ecological Implications of Livestock Herbivory in the West***. Society of Range Management, Denver, CO.

Grazing by livestock affects different rangeland communities in different ways. In general, more mesic communities that evolved under grazing may be rather resistant to deterioration caused by grazing. However, if they do become degraded they usually improve rather quickly when grazing is reduced or stopped. This predictable response fits the present conceptual range condition model reasonably well. On many arid and semi-arid rangeland communities, grazing too heavily can cause rapid degradation. However, improvement in range condition when grazing is reduced or removed often is extremely slow or absent. The current conceptual model used to determine range condition does not take into account this lack of response to a release from grazing. Examples are given of apparent "stable states" of range condition for many arid and semi-arid vegetation types, including a number of shrub-dominated communities. In these situations, even complete removal of livestock grazing results in little or no improvement in range condition for many years or even decades. This lack of conformity to the present range condition model for many vegetation types is not very well understood by managers and often leads to inappropriate conclusions about proper management strategies to improve range condition. Examples of possible alternative conceptual models, including the "stable state" and "threshold" concepts are presented.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119: 757-773.

The morphology of rhizomatous and caespitose grasses reflects the two extremes to which perennial grasses have evolved at least in partial response to continuous high versus low selection pressure by large congregating mammals. In

North America steppe of the *Bouteloua* Province east of the Rockies dominated by a mix of mainly rhizomatous C₃ and C₄ grasses which have long been associated with large herds of bison and more recently with cattle. Introduction of cattle into these grasslands had much less effect on community structure than did livestock introduction into steppe of the *Agropyron* Province west of the Rockies which lacked large herds of mammals throughout the Holocene (and perhaps earlier). The underlying cause of native ungulate sparseness may have been related to the moisture cycle of the Prevailing westerlies, which may have largely excluded C₄ species, thereby severely controlling bison numbers. In these communities both the dominant C₃ caespitose grasses and the prominent cryptogam layer were soon destroyed by domestic ungulates and replaced largely by alien winter annuals. The relative changes in these two Provinces over the past 200 years illustrate the importance in plants of herbivore-adapted traits in generating the overall physiognomy of some steppes and the resiliency of those grasslands to the introduction of novel selection pressure.

Marty, J.T., S.K. Collinge and K.J. Rice. 2005. Responses of a remnant California native bunchgrass population to grazing, burning and climatic variation. *Plant Ecology* 181: 101-112.

This study examined the interactive effects of grazing intensity and burning on a remnant population of the California native bunchgrass *Nassella pulchra*. We measured growth, reproduction and mortality of permanently marked bunchgrasses and measured bunchgrass seedling recruitment and density in permanent quadrats. We burned half of the treatment plots in late spring 1998. Grazing treatments were implemented in 1998, 1999 and 2000 at four different intensities: ungrazed, light rotational grazing (31% average biomass removal), heavy rotational grazing (42% average biomass removal), and continuously grazed. Both burning and grazing affected the bunchgrass population. Bunchgrass mortality was 10% higher in burned vs. unburned plots but was not significantly different among grazing treatments. Seedling density was 100% higher in burned vs. unburned plots 2 years after the burn, however seedling densities never attained preburn levels. Seedling densities did not differ significantly among grazing treatments, but grazing reduced the height and reproduction of the mature bunchgrasses. Adult bunchgrass density did not differ significantly in any of the treatments but experienced a five-fold decrease over the 4 years of the experiment. Although the continuous grazing treatment reduced the number of culms produced per plant by 75% from the baseline year, the effect on culm production in the continuous grazing treatment was not consistently greater than the rotational grazing treatments. The interaction of grazing and burning had no significant impacts on the *N. pulchra* populations except on the diameter of adult bunchgrasses which was highest in the lightly grazed, unburned treatments 2 years following the burn. All response variables except bunchgrass height followed a similar pattern in time over the 4 years of the experiment regardless of treatment, peaking in 1998 and then declining in 1999 and 2000. We believe the above average rainfall and below average temperatures experienced late in the growing season in 1998 provided conditions that favored the native bunchgrasses. Overall, we found few interactive effects of grazing and burning but the separate treatments did affect bunchgrass growth, reproduction and mortality, and these effects were modulated by the ubiquitous effects of climatic fluctuations.

Marty, J.T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands of California. *Conservation Biology* 19 (5): 1626-1632.

Cattle are usually thought of as a threat to biodiversity. In regions threatened by exotic species invasion and lacking native wild grazers, however, cattle may produce the type of disturbance that helps maintain diverse communities. Across 72 vernal pools, I examined the effect of different grazing treatments (ungrazed, continuously grazed, wet-season grazed and dry-season grazed) on vernal-pool plant and aquatic faunal diversity in the Central Valley of California. After 3 years of treatment, ungrazed pools had 88% higher cover of exotic annual grasses and 47% lower relative cover of native species than pools grazed at historical levels (continuously grazed). Species richness of native plants declined by 25% and aquatic invertebrate richness was 28% lower in the ungrazed compared with the continuously grazed treatments. Release from grazing reduced pool inundation period by 50 to 80%, making it difficult for some vernal-pool endemic species to complete their life cycle. My results show that one should not assume livestock and ranching operations are necessarily damaging to native communities. In my central California study site, grazing helped maintain native plant and aquatic diversity in vernal pools.

Maslovat, C. 2002. Historical jigsaw puzzles: piecing together the understory of Garry oak (*Quercus garryana*) ecosystems and the implications of restoration. Pp. 141-149 in: Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-184. Berkeley, CA.

Ecosystem restoration requires a set of reference vegetation conditions which are difficult to find for Garry oak (*Quercus garryana*) ecosystems in Canada because contemporary sites have been drastically altered. A survey of historical information provides only limited clues about the original understory vegetation. Although there is considerable variation in the soils, climate and successional status of current ecosystems, an exploration of the ecology of contemporary, native grass species existing in association with Garry oaks can point to which species may have been adapted to the historical disturbance regimes of pre-European contact ecosystems. Both California oatgrass (*Danthonia californica*) and *Acnatherum* sp., such as Lemmon's needle grass (*A. lemmonii*), have ecological characteristics that suggest they are adapted to the disturbance regimes of fire and camas digging. These characteristics include dormancy, hygroscopic awns, and self-pollinated cleistogenes.

Mason, L. and S. Mazer. 2004. Effects of cattle grazing on three native California perennial grass species: seedling growth, reproduction and survivorship. In: Proceedings, Ecology and Management of California Grasslands, April 2-3, 2004, Berkeley, CA. Available online at: <http://cbc.berkeley.edu/grass/Abstracts.htm>.

We monitored the responses of three native perennial bunchgrasses to cattle grazing in order to determine whether there are consistent effects of grazing on seedling performance that could help to inform a management strategy for grassland sustainability and restoration in serpentine-derived soils at Vandenberg Air Force Base (VAFB) in Santa Barbara County, California. We evaluated the effects of grazing on growth, reproduction, and survivorship of *Bromus carinatus*, *Hordeum brachyantherum*, and *Nassella pulchra* over two growing seasons, 2000-2001. Grazing promoted the highest mean seedling growth in all three species relative to complete protection from large herbivores. Increased competition and standing litter in ungrazed treatments suppressed seedling growth more than did the temporary reduction of biomass. There was, however, significant spatial variation in the magnitude and significance of grazing effects on seedling performance. Under some conditions (lighter grazing in richer soils), grazing appeared to promote reproduction by *B. carinatus* and *H. brachyantherum* seedlings. In contrast to the apparent positive effects of grazing on seedling growth and reproduction, grazing reduced seedling survivorship. Our results suggest that grazing combined with rest-rotation may be an effective tool to help maintain populations of native perennial bunchgrasses at Vandenberg Air Force Base. We recommend enforcing a grazing regime in which seedlings are protected during their early growth in winter and early spring, and in which seedlings are permitted to reach a threshold size before exposure to grazing.

MacDougall, A. 2002. Invasive perennial grasses in *Quercus garryana* meadows of southwestern British Columbia: prospects for restoration. Pp. 159-168 in: Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-184. Berkeley, CA

Garry oak (*Quercus garryana*) meadows of the Pacific Northwest are heavily invaded by non-native species but the dynamics surrounding this ecosystem transformation are poorly understood. Of particular uncertainty is the role of the invasive species in structuring the community, and the potential stability of this invasive-dominated system when disturbed. Clarifying such issues is central to restoration success for Garry oak meadows, one of the most endangered terrestrial ecosystems [in British Columbia]. This paper examines the competitive inter-relationships among exotic and native flora, and how these inter-relationships are modified by a series of disturbance treatments (burning, mowing, and selective removal of invasives). Recruitment dynamics are also described. Pre-treatment surveys of vascular plant taxa identified 80 species within the study area located near Duncan, British Columbia. Thirty-nine of the species were non-native. Two of the invasives – Kentucky bluegrass and orchard grass – were dominant, averaging a combined 80% of total cover in all plots. Disturbance treatments, regardless of type or intensity, caused significant decreases in total percent cover of the exotic dominant grasses, and significant increases in ground level light, total species richness and total percent cover of native flora. A combination of disturbance and native seed additions revealed that native plant recruitment is limited primarily by dispersal, though the dense invasive sward probably restricts recruitment success also. These results indicate that the invasive sward could be de-stabilized by disturbance treatments, though supplemental recruitment measures are also needed to restore native species dominance to these meadows.

MacDougall, A.S. and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology* 92: 422–434

Invasive species dominate many ecosystems but the competitive strategies underlying this dominance are unclear. Are invasive species generalist competitors, or do they only thrive in certain environments? Do they occur mainly post-

disturbance or can they persist throughout succession? We tested the relative importance of resource acquisition (competitive suppression ability) and the ability to tolerate reduced resource levels (competitive tolerance ability) among four C3 perennial grass species in an invaded oak savanna. Two species (*Poa pratensis* and *Dactylis glomerata*) are exotic invaders and are thought to have replaced the two native species (*Bromus carinatus* and *Elymus glaucus*) as dominants. Using glasshouse and field experiments we tested whether the two strategies were maintained with changing resource levels and successional conditions, and their relative roles in explaining exotic dominance. The relative importance of suppression- and tolerance-based competition shifted with neighbor density, burning and planting order. Further, the relative importance of particular plant traits changed depending on the imposed conditions, and the exotic dominants were only competitively superior under certain circumstances. Competitive suppression ability was maintained with changing resource levels but was confined to post-disturbance conditions. When planting of neighbors was delayed, the early establishing targets were dominant regardless of species, fertility and neighbor density. Competitive tolerance ability determined long-term patterns of relative abundance and coexistence, but only under the current field conditions of low fertility and limited disturbance. Alteration of these conditions changed the relative abundance of the four grasses, and would probably reconfigure species patterns in the oak savanna community generally. Exotic dominance is presently determined by tolerance-based competitive traits interacting with the long-term absence of disturbance. Dominance is therefore contingent on the interaction of competitive strategies, resource availability and disturbance history rather than any one factor alone. Exotic flora dominate all stages of succession in this savanna because there exists both early (suppression) and late (tolerance) successional specialists. The identity of the dominant changes with succession based on the competitive strategy it employs. This result highlights the importance of examining the historical context of invaded communities and tracking their successional status over time.

McIntyre, S. et al. 1995. Plant life history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* 83: 31–44.

Species composition and disturbance state (level of soil disturbance, grazing and water addition) were recorded for 120 (30-m²) plots in temperate grassland of the New England Tablelands (Australia). Three different classificatory schemes were used, based on a) life form (sensu Raunkiaer); b) dispersal unit morphology and c) vegetative reproduction. We analyzed the effects of the different disturbance types and intensities on number and proportion of species belonging to these groups. The results were used to describe the spectrum of life-histories likely to be present at sites in different states of exogenous disturbance. Soil-disturbed sites had proportionately more therophytes, versatile/flat rosettes and wind-dispersed species. Two features are likely to lead to success in soil-disturbed site: ability to colonize open space (e.g. therophytes, wind dispersal) and capacity to capture resources effectively (e.g. flat architecture of rosettes). Non-disturbed sites had more geophytes, chamaephytes, phanerophytes, proto-hemicryptophytes and erect rosettes, with greater numbers of vegetatively reproducing species. Heavily grazed sites had higher proportions of therophytes and versatile/flat rosettes and species with mobile seeds than sites with light grazing. Moderately grazed sites had increased proportions of versatile and erect rosettes and more species with adhesive seeds (mainly grasses). Lightly grazed sites had a greater diversity in terms of evenness of all life-forms, dispersal morphologies and reproductive modes. Of the three attributes examined, life-form was most useful in characterizing community response to different disturbance types. Traits related to regeneration (seed morphology and capacity of vegetative reproduction) were relevant to soil disturbance only. Our results support the use of such classifications for monitoring the effects of disturbance.

McLean, A. and E.W. Tisdale. 1972. Recovery rate of depleted range sites under protection from grazing. *Journal of Range Management* 25: 178-184.

It is estimated to take from 20 to 40 years for overgrazed ranges in the rough fescue and ponderosa pine zones to recover to excellent range condition when fully rested. Little change in plant composition took place inside exclosures, placed on poor condition range, in less than 10 years following fencing. It took longer for the sites to progress from poor to fair condition than from fair to good condition. The main plants to increase with protection were bluebunch wheatgrass and rough fescue. The main species to decrease were Sandberg bluegrass, low pussytoes, and rabbitbrush.

McNaughton S.J. 1968. Structure and function in California grasslands. *Ecology* 49:962-972.

Functional and floristic properties of annual grasslands on serpentine and sandstone soils at an elevation of 180 m on Stanford University's Jasper Ridge were determined along an intuitive habitat gradient from northeast to southwest exposures. The most frequent species contributed the most to peak standing crop in only half the stands. *Stipa pulchra*, the only native species among the important species, was more important on serpentine than on sandstone sites. *Bromus mollis*, the other consistently important species, increased in importance with decreasing moisture supply on both soils. The sandstone grasslands sustained a greater biomass, were more productive, and were less diverse than serpentine

grasslands. Within the grasslands as a whole, productivity was inversely related to diversity and positively related to dominance. Stability, however, was related to neither productivity, diversity nor dominance. Thus productivity may increase in such a system with no sacrifice in stability. Properties of sandstone grasslands were clearly related to the habitat gradient from cool, moist sites to warm, dry sites. There was no such relationship in serpentine grasslands. Dominance-diversity curves generally fit previously described models, except on southwestern serpentine exposures. The annual grassland vegetation is a mosaic of floristic composition and ecological properties, shifting in response to habitat patterns but without abrupt discontinuities.

Mawdsley, K. F. 2000. Jepson Prairie Preserve today. *Fremontia* 27:52-55.

This article summarizes results of a multi-year, multi-season study on the effects of fire and grazing on native purple needlegrass (*Nassella pulchra*) and the invasive annual grasses at the Jepson Prairie preserve, located in southern Solano County, CA. Researchers found that late-spring burning reduced thatch density and absolute cover of non-native annual species such as medusahead (*Taeniatherum caput-medusae*), while increasing cover of native grasses and forbs. The preserve has adopted a regulated grazing program to control the build-up of biomass from exotic annual grasses. The timing and intensity of grazing are managed to promote recovery of native bunchgrasses.

Menke, J.W., C. Davis and P. Beesley. 1996. Rangeland assessment. Pp. 901-972 in: Sierra Nevada Ecosystem Project, Final Report to Congress, vol. III. Assessments, commissioned reports and background information. University of California, Centers for Water and Wildland Resources. Davis, CA.

This public rangeland/livestock grazing assessment includes a post-1905 history of livestock use on 10 national forests of the Sierra Nevada and Modoc Plateau, a compilation of plant species indicators of livestock grazing effects, an assessment of grazing effects on sagebrush steppe and mountain meadow rangelands, and a case study on correlation of meadow and riparian conditions in the Sierra Nevada. While this assessment spans five decades of monitoring, it is important to recognize that although substantial reductions in livestock grazing intensity have occurred, most ranges were stocked above carrying capacity until very recently. A key indicator of improved conditions that we have observed is an increase in native perennial grass composition on some upland sagebrush steppe rangelands. A key indicator of declining condition is the continued cheatgrass invasion of many uplands. Based on the historical evidence of abuse of California mountain meadows during the post gold-rush era, the recolonization by native plants, low abundance of non-native weeds, and the soil protection being provided by herbaceous vegetation as indicated by 4-5 decades of range monitoring data is significant. Considering past heavy grazing in northeastern California, the eastern Sierra, and lands of the Mother Lode nearest Sacramento, it is not surprising that the Modoc, Plumas, Tahoe, Eldorado and Toiyabe Forests are continuing to lag a bit in recovery since their meadows were probably most impacted during the early days following settlement. The declining abundance of grass species on mountain meadows of the Sierra National Forest and the low abundance of grass species on mountain meadows of the Sequoia National Forest during the 4-5 decade monitoring period is a biodiversity concern. In a case study we investigated the potential for using long-term condition and trend monitoring data to indicate nearby riparian stream functionality. Using aggregated Parker transect data to the genus level, the life form categories of grasses, legumes, sedges, rushes, and forbs, and the raw data of bare soil exposure, litter and non-native species present currently and over the last 5 decades, we were able to predict 11-12 of 13 functioning at-risk riparian/stream trend directions correctly. As used in the assessments developed here, variable dynamics indicating sedge to grass ratio changes without compensation of rushes, invasion or retreat of weedy forbs, reductions in abundance of late-seral grasses such as *Deschampsia* and *Glyceria* species, radical fluctuation in clover composition, and "red flag" indicators like more than 7-10% bare soil exposure sometime in the meadow's 40-50 year history, were adequate to make the predictions.

Menke, J.W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20: 22-25.

Introduced, alien annual grasses native to southern Europe present a formidable obstacle to restoration and enhancement of native perennial grass populations in California foothill and valley grasslands. These alien competitors evolved during thousands of years of heavy grazing and periodic drought, and thus have many adaptations to compete successfully against our native perennials under present grassland conditions in California. This article discusses some potential approaches for reducing the competitive edge of alien annual species in California grasslands. If planned and implemented carefully, prescribed grazing and burning regimes can be useful tools to restore or maintain the abundance of native perennial grasses, where remnant populations are present, where managers take the long-term view, and where large acreages are involved.

Menke, J. 1989. Management controls on productivity. Pp. 173-200 in: L. F. Huenneke, and H. A. Mooney, editors. *Grassland Structure and Function: California Annual Grassland*. Kluwer Academic, Dordrecht, The Netherlands.

Replacement of the native perennial flora of California grasslands by alien annual plants has had a major impact on management options available to stewards of the grasslands. The tenacity of highly competitive annuals has made it difficult to control productivity for the purpose of improving performance of domestic livestock. On the other hand, the resilience of annual vegetation forgives abusive practices time and time again. Eight vegetation management technologies have been used to increase grassland productivity. Prescribed fire is used to reduce litter accumulations of undesirable weed species and to remove competing shrubs and trees of low forage value. Annual legumes and perennial grasses are seeded to increase the seasonal availability of high quality forages. Fertilizers are used alone or as part of a legume-based pasture improvement program. Irrigation has been used to lengthen the growing season of annual species. Some annual grasslands subject to soil compaction problems and also suitable for farming are used in a dual fashion for dryland grain farming and livestock grazing on a rotational basis. Until recently, herbicides were used in an array of different ways to make other improvements possible. Lack of response of the annual plants to season and intensity of grazing has resulted in little application of grazing systems but new systems are being investigated. Serious questions remain about the sustainability and cumulative effects of our grassland management practices. Grassland weed problems and lack of regeneration of deciduous savanna and woodland communities are problems needing greater attention.

Merelander, A.M., K.L. Heise, J.W. Bartolome and B.H. Allen-Diaz. 2001. Monitoring shows vegetation change at multiple scales. *California Agriculture* 55: 42-46.

Several historical data sets from the UC Hopland Research and Extension Center (HREC) provide valuable information on vegetation dynamics at multiple spatial and temporal scales. An early botanical survey by Harold Heady and Al Murphy provides a baseline for examining landscape-level changes in species richness and distribution over 50 years. We conducted a floristic survey between 1995 and 1999 and found gains and losses of native and non-native species abundance across the field station. On two sites where sheep were removed in 1958, permanent transects provide valuable information about plant community responses to protection from livestock grazing; in the oak understory, native perennial blue wildrye increased steadily, while in grasslands native purple needlegrass was less abundant after 43 years. On a cleared watershed, originally diverse in hardwood species, we found that only interior live oak and coast live oak were significantly reestablished after 30 years.

Meyer, M. D. and P. M. Schiffman. 1999. Fire season and mulch reduction in a California grassland: a comparison of restoration strategies. *Madrono* 46:25-37.

Prescribed burning and mulch reduction via grazing are two restoration strategies employed for the enhancement of native flora in California grasslands. However, the effectiveness of these methods to restore native species and suppress alien species is poorly understood. In particular, the effectiveness of different seasons of burning to restore native vegetation has been attributed to several factors, including plant phenology patterns (phenology hypothesis), fire intensities (intensity hypothesis), and accumulated mulch biomass (mulch hypothesis). In order to test these hypotheses and compare the efficacy of burning and grazing as restoration tools, the short-term effects of fire season and mulch reduction on grassland vegetation were evaluated in the Carrizo Plain Natural Area (San Luis Obispo Co, CA). Warm-season (late-spring and fall) burning significantly increased the cover and diversity of native vegetation and decreased the cover and seed viability of alien grasses relative to control treatments. Winter burning and mulch reduction did not increase the cover or diversity of native plants and grazing was only moderately effective at reducing alien plant cover. Seed germination data showed that the seeds of one common native plant species, *Phacelia ciliata* Benth, responded positively to fire. These results indicated that fire season is a significant factor in grassland restoration, and that the success of different fire seasons for restoration is determined by plant phenology patterns, season-specific fire intensities, and potentially the removal of all mulch biomass. Warm-season prescribed burning and not grazing or cool-season burning is the most effective strategy for restoring native vegetation to California grasslands.

Micallef, S.B. 1998. Grazing effects on the grassland vegetation of Mount Diablo State Park, California. Thesis, San Francisco State University, San Francisco, CA.

No abstract or summary available.

Milchunas, D.G. and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327-366.

Multiple regression analyses were performed on a worldwide 236—site data set compiled from studies that compared species composition, aboveground net primary production (ANPP), root biomass, and soil nutrients of grazed vs. protected, ungrazed sites. The objective was to quantitatively assess factors relating to differential sensitivities of ecosystems to grazing by large herbivores. A key question in this assessment was: Do empirically based, broad—scale relationships correspond to ecological theories of plant—animal interactions and conceptual frameworks for management of the world's grazing lands? Changes in species composition with grazing were primarily a function of ANPP and the evolutionary history of grazing of the site, with level of consumption third in importance. Changes in species composition increased with increasing productivity and with longer, more intense evolutionary histories of grazing. These three variables explained >50% of the variance in the species response of grasslands or grasslands—plus—shrublands to grazing, even though methods of measurement and grazing systems varied among studies. Years of protection from grazing was a significant variable only in the model for shrublands. Similar variables entered models of change in the dominant species with grazing. As with species composition, sensitivities of change in dominant species were greater to varying ecosystem—environmental variables than to varying grazing variables, from low to high values. Increase of the dominant species under grazing were predicted under some conditions, and decreases were more likely among bunch grasses than other life—forms and more likely among perennials than annuals. The response of shrublands was different from that of grasslands, both in terms of species composition and the dominant species. Our analyses support the perception of grazing as a factor in the conversion of grasslands to less desirable shrublands, but also suggest that we may be inadvertently grazing shrublands more intensively than grasslands. Percentage differences in ANPP between grazed and ungrazed sites decreased with increasingly long evolutionary histories of grazing and increased with increasing ANPP, levels of consumption, or years of treatment. Although most effects of grazing on ANPP were negative, some were not, and the statistical models predicted increases in ANPP with grazing under conditions of long evolutionary history, low consumption, few years of treatment, and low ANPP for grasslands—plus—shrublands. The data and the models support the controversial hypothesis that grazing can increase ANPP in some situations. Similar to species variables, percentage differences in ANPP between grazed and ungrazed treatments were more sensitive to varying ecosystem—environmental variables than to varying grazing variables. Within levels not considered to be abusive "overgrazing," the geographical location where grazing occurs may be more important than how many animals are grazed or how intensively an area is grazed. Counter to the commonly held view that grazing negatively impacts root systems, there was no relationship between difference in ANPP with grazing and difference in root mass; as many positive as negative differences occurred, even though most ANPP differences were negative. Further, there was a weak relationship between change in species composition and change in ANPP, and no relationship with root mass, soil organic matter, or soil nitrogen. All three belowground variables displayed both positive and negative values in response to grazing. Current management of much of the world's grazing lands based on species composition criteria may lead to erroneous conclusions concerning the long—term ability of a system to sustain productivity.

Milchunas, D.G., W.K. Lauenroth, and I.C. Burke. 1998. Livestock grazing: Animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* 38:65-74

We synthesized published and unpublished data from long-term grazing treatments in North American shortgrass steppe on diversity and abundance of plants, lagomorphs, rodents, birds, aboveground and belowground macroarthropods, microarthropods, and nematodes. The relatively small response of the plant community to grazing provides an opportunity to address some broad questions concerning relationships among responses of structural and functional aspects of systems in general. Are there consistencies in diversity and abundance responses to prating among groups of organisms? Are some groups more sensitive than others, or do responses mirror that of vegetation? Are the responses in terms of biodiversity related to ecosystem-level functional responses? Diversity, abundance, dominance, and dissimilarity responses to long-term grazing were highly variable across classes of organisms. Some groups of consumers displayed large differences among treatments even though differences in plant community attributes were relatively minor. Some responses were large even when comparing ungrazed to lightly or lightly to moderately grazed treatments. Birds appear to be particularly responsive to grazing. Differences among treatments in richness within groups other than plants and birds were relatively minor, especially when compared to large declines in abundance of some groups with increasing grazing intensity. For the well-studied groups (plants and birds), shifts in species in terms of 'quality' factors, such as exotic, endemic, and rare, generally suggest that livestock grazing may be more similar to conditions in recent evolutionary time in this particular system than would conditions resulting from the removal of the exotic, domestic grazers that appear to functionally serve as a surrogate to bison. Trophic structure composition did not vary greatly across grazing treatments. Further, large effects of grazing on some consumer groups did not translate into similarly large effects on ecosystem processes such as primary production or soil nutrient pools and cycling rates.

Miller, J. 2003. Cattle grazing and the loss of biodiversity in the East Bay. Center for Biological Diversity. Berkeley, CA.

The Center for Biological Diversity provides extensive documentation and scientific research papers to East Bay Regional Parks Department (EPRPD) as part of a review of their grazing management. These included a reference list of over 150 scientific, peer-reviewed research papers and articles detailing the environmental impacts of livestock grazing in the western U. S., and a 13 page summary of livestock grazing impacts on soil, stream, wildlife, and ecosystem function from peer-reviewed, scientific studies, with references. Also included was a comprehensive Survey of Livestock Influences on Stream and Riparian Ecosystems in the Western United States (Belsky et al. 1999).

Monsen, S.B. and S.G. Kitchen, eds. 1994. Proceedings: ecology and management of annual rangelands; 1992 May 18-22; Boise, ID. USDA Forest Service Intermountain Research Station Gen. Tech. Report INT-GTR-313.

No abstract or summary available.

Murphy, D.D., and P. R. Ehrlich. 1989. Conservation biology of California's remnant native grasslands. Pages 201–211 in L. F. Huenneke, and H. A. Mooney, editors. *Grassland Structure and Function: California Annual Grassland*. Kluwer Academic, Dordrecht, The Netherlands.

“The remnants of California's native grassland are threatened. Fortunately, even relatively small parcels seem able to preserve a fair sampling of the plant diversity; thus the situation is not as bleak as perusal of a map of remaining habitat might make it seem. The best hope for protection of remaining sites would seem to be working through the Endangered Species Act to protect threatened herbivorous invertebrates that are tied to that flora”.

Murphy, A.H. 1980. Oak trees and livestock: management options. Pp. 329-332 in: Plumb, T.R., ed. Proceedings of the symposium on the ecology, management and utilization of California oaks. USDA Forest Service Pacific Southwest Research Station, Gen. Tech. Report PSW-44. Berkeley, CA.

No abstract or summary available.

Noy-Meir, I. *et al.* 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77: 290–310.

Differences in plant species' abundances in response to cattle grazing and protection were measured across fences at fifteen sites in productive semi-natural mediterranean grasslands. The results were tested for the consistency of species' responses to grazing intensity and for their association with plant attributes expected to be involved in the grazing response. Of the seventy-three most common species, forty-nine showed responses that were largely consistent over sites, being either significantly more abundant on the more protected side, significantly more abundant on the more grazed side, or not significantly different. The remaining twenty-four species were inconsistent, being significantly more abundant on the protected side in some sites and on the grazed side in others. Of the inconsistent species, fourteen showed a pattern of responses over sites that could be explained by a unimodal response to grazing intensity, with an optimum at intensities between the extremes of complete protection and very heavy continuous grazing represented in the study. Species response to grazing was not significantly associated with family, which inferred chemical palatability, nor with spininess. Perennial species with long growing seasons were somewhat more frequent among protection increasers, and their total cover greater in protected grassland. Grazing response was strongly and significantly associated with plant growth form: protection increasers were mostly tall erect plants; grazing increasers mostly small, prostrate or rosette plants; and species with intermediate response mostly erect plants of medium height. Ungrazed grassland was dominated (60-80% cover) by tall perennials and tall, annual grasses. Under light to moderate grazing their cover decreased to the benefit of annuals of a wide range of growth forms and families; of those, under heavy grazing, small and prostrate annuals, rosette crucifers and thistles remained abundant. The observed responses to grazing from none to light and moderate intensity can be explained best by the opening of establishment gaps in the closed sward of foliage and mulch maintained by the dominants. At moderate to heavy grazing the vertical differential defoliation gradient imposed by cattle, particularly early in the growing season, becomes the major mechanism of grassland change.

Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *J. of Vegetation Science* 6(5): 701-710.

The separate and combined effects of fire and cattle grazing on structure and diversity of productive Mediterranean grasslands in northern Israel were examined within a set of climatically and edaphically similar sites. Cover and height of green and dry plants in winter, and species richness and diversity in spring, were measured in paired transects on both sides of cattle fences, and on both sides of boundaries of both incidental and experimentally lit fires. Early in the first growing season after a fire, plant cover as well as height of green plants were reduced, compared to unburned grassland. These structural effects of fire were similar to the effects of grazing, but they were greater in ungrazed than in grazed grasslands, indicating a fire-grazing interaction. The effects of fire were considerably attenuated in the second growing season after the fire. Species richness and diversity tended to be higher in grazed than in adjacent ungrazed grasslands. Richness consistently increased after a fire only in grazed grasslands with a strong perennial component. In ungrazed grasslands, and in predominantly annual grasslands, fires reduced species richness and diversity at least as often as they increased it. Fire and grazing should be regarded as two agents with distinct and interactive effects on the community, rather than as two alternative mechanisms of a general disturbance factor.

Noss, R.F and A.Y. Cooperider. 1994. Managing rangelands. In: *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press, Washington, D.C.

This chapter represents an attempt to develop recommendations on how to manage rangelands in the western United States for protecting and restoring native biodiversity, using extrapolation of existing data and extension of knowledge from other ecosystems. The authors assert that livestock grazing is the most insidious and pervasive threat to biodiversity on rangelands, resulting in vast changes on individual plants or species, plant communities, soils and watersheds, and native animals. In addition each of these effects have secondary or ecosystem-level effects. Each of these impacts is summarized, followed by a discussion of the effects of fencing, water development, predator control, vegetation conversion and other activities associated with livestock production. Lastly, a set of recommendations is presented for managing rangelands in areas that are to be managed primarily for biodiversity conservation (e.g. reserves), in multiple-use lands, and in areas where the primary objective is ecological restoration.

O'Leary J.F. and W.E. Westman 1988. Regional disturbance effects on herb succession patterns in coastal sage scrub. *Journal of Biogeography*. 15:775-786.

A prolonged grazing history and higher summer air pollution loads in the basin inland of Los Angeles may be acting in concert to eliminate native perennial grasses there; such grasses comprise a significant part of the post-fire herb flora in coastal sites of the coastal sage scrub. In addition, low resprouting vigor of subshrubs inland after fire permits a higher level of herb cover, initially of forbs, and later of non-native annual grasses. The divergent successional patterns of the post-fire herb stratum at the coast versus inland appear to result from subtle interactions between natural and anthropogenic forces in the region. Strict "fire annuals" – species that exhibit high cover in the first post-burn year and disappear thereafter – were not found in the study sites. Annuals that were present in large numbers in the first year persisted to varying degrees in the 4 years subsequent.

Odion, D., T. Dudley, C. D'Antonio. 1988. Cattle grazing in southeastern Sierran meadows: Ecosystem change and prospects for recovery. Pp. 277-292 in: C.A. Hall and V. Doyle-Jones, eds., *Plant Biology of Eastern California*.

Extensive, degraded (now sagebrush dominated) subalpine meadows occur in the southeastern Sierra Nevada in the Golden Trout Wilderness, where grazing reached its zenith in the late 1800's and persists at a moderate level now. We have been monitoring vegetation change in two of these meadows inside and outside cattle exclosures installed in 1984 as part of a restoration effort. Livestock trampling and defoliation break down protective sod, allowing streams that have sufficient energy to erode rapidly into the organic deposits, producing a gullied meadow and lowering the water table. The altered system is invaded by xerophytes. Natural recovery from this degradation is unassured in meadows that lie within the geomorphic domain of unstable meadows. Protection from grazing allows significantly more pioneer species to colonize areas bare from fluvial disturbance and higher survival of planted willows. Meadow vegetation will only return naturally—or survive if planted—where the water table is close to the surface. Meadows can best be rehabilitated by combining fencing with water-table raising procedures rather than undertaking these as single procedures. In addition to the more site-intensive restoration, we recommend that a stratigraphic study be undertaken to determine the pre-disturbance vegetation so that restoration can be directed towards recreating the natural habitat of these unique resources.

Ogle S.M., Reiners W.A., Gerow K.G. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* 149:46-58.

Annual brome grasses, *Bromus japonicus* and *B. tectorum*, are common exotic plants in the northern mixed prairies of North America. As annuals, bromes die following seed set in late spring, creating a functional difference between them and native perennial grasses because perennials continue to maintain live shoots into the summer and root systems throughout the year. Our objective was to investigate how the functional difference alters ecosystem properties over the growing season, including soil moisture content, quantity of plant biomass, litter accumulation and aboveground litter decomposition. We conducted an experiment in which the annual bromes were removed from treatment plots to compare with adjacent reference plots. While this experiment served as a direct test from brome impacts, observational plots also were sampled to determine if impacts were apparent in an unmanipulated system. A litter bag experiment was conducted to evaluate impacts of brome grasses on decomposition. Experimental removal of brome grasses led to more biomass both above- and belowground at the end of the growing season, and high brome observational plots averaged 28% less aboveground biomass and 40% less belowground biomass than the low brome plots. In contrast, removal of brome grasses did not produce a consistent impact on soil moisture content between sites or among months, and none of the measurable impacts from the removal experiment were significant in the observational study. Bromes slowed decomposition of aboveground litter at both sites. However, the overall impact on litter accumulation was only significant at one site, where brome removal reduced surface litter in the latter half of the growing season and high brome observational plots averaged 36% more litter than low brome plots. This study demonstrates how the brome functional type alters several properties in an ecosystem traditionally dominated by perennial grasses.

Painter, E.L. 1995. Threats to the California flora: ungulate grazers and browsers. *Madrono* 42: 180-188.

While herbivory probably is a natural part of all terrestrial ecosystems, livestock herbivory is not a natural part of California's natural ecosystems. In California, mammalian herbivores can range in size from small rodents to large ungulates. However, the potential of threats is greater from ungulates, which include native taxa (e.g. tule, Roosevelt, and Rocky Mountain elk, mule deer, pronghorn antelope) and alien livestock (cattle, horses, burros, sheep, goats). Impacts of the native ungulates are not well studied. There are few, if any, types of plant communities in California that are unimpacted by livestock. Livestock herbivory is a threat to some rare plant taxa. Livestock impacts can include alterations in species composition of plant communities, in ecosystem function, and in ecosystem structure. Although the impacts can be severe, in terms of negative impacts on native plants, carefully managed livestock herbivory may not be the most destructive land use practice.

Pantis, J.D., and T.A. Mardiris. 1992. The effects of grazing and fire on degradation processes of Mediterranean ecosystems. *Israel Journal of Botany* 41:233-242.

No abstract or summary available.

Peart, D.R. 1989. Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. *Journal of Ecology* 77: 267-289.

In a perennial grassland undergoing succession after the removal of domestic grazers, three natural processes could disrupt the canopy, and thus affect colonization. These are: canopy gap formation due to the death of individual bunchgrasses; soil disturbance by gophers; and grazing by native animals. Species' abilities to colonize canopy gaps and gopher mounds were assessed in the field, with seed introduction experiments, for the five most cover-dominant grass species: *Anthoxanthum odoratum*, *Holcus lanatus*, *Deschampsia holciformis*, *Rytidosperma pilosum* (all perennial bunchgrasses) and *Vulpia bromoides* (an annual grass). The effects of native grazers on colonization by the most abundant species, *Anthoxanthum*, were assessed, using grazer exclosures and seed introductions in annual-dominated vegetation, where grazing activity was highest. Colonization success was quantified as total leaf area, number of survivors and seed production, in sites where seeds of the colonist either fell naturally, or were introduced at natural densities. The formation of canopy gaps by the death of individual bunchgrasses and soil disturbances by gophers strongly affected colonization success. The best colonizers were *Anthoxanthum* and *Holcus*, whose colonization success was increased 6-2,500-fold by canopy gap formation, and 10-200-fold by the formation of gopher mounds. Few, small seedlings of *Deschampsia* and *Rytidosperma* survived in canopy gaps or on gopher mounds. Unlike *Anthoxanthum* and *Holcus*, *Deschampsia* and *Rytidosperma* did not reproduce in gaps or on mounds over a two-year period. *Vulpia* colonists had higher seed production on mounds than the four perennials. *Vulpia* also colonized canopy gaps, but was excluded by perennial vegetation in the second year of growth in the gaps. In annual-dominated vegetation, neither above-ground biomass nor colonization by *Anthoxanthum* was affected by excluding grazers.

However, exclusion of grazers led to an increase in the cover of forbs after two years. Clipping aboveground vegetation allowed *Rytidosperra* to achieve dominance in sites where, under undisturbed conditions, it existed only as a suppressed understory. All other perennials were negatively affected by clipping. The species with the highest natural densities of seed rain also had the greatest per seed colonization success, even though negative density-dependent effects must have been strongest for those species. Seed size was positively correlated with survivorship on mounds, but was unrelated to the sizes of individual colonists in gaps or on mounds. Overall, canopy gaps and gopher mounds favored the same species that colonized well in undisturbed sites. Both types of disturbance increased colonization by perennials in annual-dominated vegetation, and canopy gaps were required for changes in species dominance in perennial vegetation.

Pieper, R.D. 1994. Ecological implications of livestock grazing. Pp. 177-211 in: Vavra, M., W.A. Laycock and R.D. Pieper, eds. 1994. *Ecological Implications of Livestock Herbivory in the West*. Society of Range Management, Denver, CO.

In the western U.S. domestic livestock were introduced into some rangeland ecosystems where large ungulates were not abundant before settlement by Europeans. Grazing by introduced livestock probably has had much larger impacts on vegetation of the Intermountain region, Great Basin, and the Southwest than the Great Plains where livestock replaced bison as the dominant herbivore. Destructive livestock grazing in the west occurred primarily in the late 1800s and early 1900s, but was largely arrested after WWII when more intensive management was applied to most rangelands. Unfortunately, excessive grazing still occurs in some riparian and upland situations. Removing livestock from rangelands is unlikely to return these ecosystems to their pristine condition. Many other changes including climatic shifts, increases in woody plant species, reduction in fire frequency and intensity, introduction of alien plant species and other human activities have occurred, resulting in undetermined impacts on the native vegetation. Livestock grazing has played a role in reducing the amount of fuel for wildfires, altering nutrient distribution, acting to create patchiness at landscape levels in the environment for many animal species, and disrupting cryptogamic crusts. Nevertheless, domestic livestock grazing at conservative levels appears to be sustainable, even on sensitive western rangelands.

Pitt, M.D. and H.F. Heady. 1979. The effects of grazing intensity on annual vegetation. *Journal of Range Management* 32: 109-114.

Pastures grazed by sheep at moderate and 1%, 2-, and 2% times the moderate stocking rate from 1969-1973 were analyzed for relative changes in cover, herbage productivity, and botanical composition. All four pastures were less productive in 1973 than in 1969, but exhibited similar trends in cover and botanical composition regardless of grazing intensity. Only grazing at 2 1/2 times the moderate stocking rate produced a residual decline in productivity following 1 year of rest from the grazing treatment. However, this decline in productivity was managerially negligible compared to other stocking rates, and would probably disappear within 2-3 years in response to the overriding influence of annual weather, especially precipitation, patterns.

Pollak, O. and T. Kan. 1998. The use of prescribed fire to control invasive exotic weeds at Jepson Prairie Preserve. Pages 241-249 in Witham, C. W., E. T. Bauder, D. Belk, W. R. Ferren Jr., and R. Ornduff, editors. *Ecology, conservation, and management of vernal pool ecosystems – proceedings from a 1996 conference*. California Native Plant Society, Sacramento, CA.

Jepson Prairie in Solano County, an outstanding example of remnant California Central Valley vernal pool and grassland habitats, is threatened by invasive exotic species. This paper describes the results of a 200-acre late-spring prescribed fire conducted at Jepson Prairie in June of 1995 and aimed at reducing the cover of an extensive infestation of medusahead (*Taeniatherum caput-medusae*). Burned and unburned control plots are compared with respect to changes in community composition within three habitat types. The habitat types - mound, intermound, and swale - correspond to three topographic/hydrologic regimes within vernal pool complexes. Ocular estimates of percent cover (using Daubenmire cover classes) were recorded for six species guilds: native grasses, exotic grasses, native early forbs, exotic early forbs, native late forbs, and exotic late forbs. Cover of thatch, bare ground and residual dry matter was also measured. Results show significant decreases in the cover of exotic annual grasses (including medusahead) and thatch in burned mound and intermound habitats. Cover of native grasses and native early forbs increased on burned mound and intermound habitats. However, exotic early forbs also increased on burned mounds and intermounds, due mainly to an increase in cover of *Erodium* spp. The results provide strong evidence that late-spring burning reduces the cover of non-native annual grasses, such as medusahead, while increasing the dominance of native species and the cover of native grasses and forbs. Prescriptions for management of vernal pool and grassland habitats in

California should include late-spring prescribed fire in areas that have heavy infestations of medusahead or an accumulated thatch layer.

Pyke, C.R. and J. Marty. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. *Conservation Biology* 19(5): 1619-1625.

Climate change impacts depend in large part on land-management decisions; interactions between global changes and local resource management, however, rarely have been quantified. We used a combination of experimental manipulations and simulation modeling to investigate the effects of interactions between cattle grazing and regional climate change on vernal pool communities. Data from a grazing exclosure study indicated that 3 years after the removal of grazing, ungrazed vernal pools dried an average of 50 days per year earlier than grazed control pools. Modeling showed that regional climate change could also alter vernal pool hydrology. Increased temperatures and winter precipitation were predicted to increase periods of inundation. We evaluated the ecological implications of interactions between grazing and climate change for branchiopods and the California tiger salamander (*Ambystoma californiense*) at four sites spanning a latitudinal climate gradient. Grazing played an important role in maintaining the suitability of vernal pool hydrological conditions for fairy shrimp and salamander reproduction. The ecological importance of the interaction varied nonlinearly across the region. Our results show that grazing can confound hydrologic changes driven by climate change and play a critical role in maintaining the hydrologic suitability of vernal pools for endangered aquatic invertebrates and amphibians. These observations suggest an important limitation of impact assessments of climate change based on experiments in unmanaged ecosystems. The biophysical impacts of land management may be critical for understanding the vulnerability of ecological systems to climate change.

Ratliff, R.D. 1985. Meadows in the Sierra Nevada of California: state of knowledge. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-84. Berkeley, CA.

This report summarizes available information concerning the history, ecology and management of meadow communities in the Sierra Nevada of California – how meadows are classified, the development of meadow soils, meadow productivity, management issues and ways to evaluate range conditions and trends. The need to have some herbage ungrazed has long been recognized. For meadow sites in the Sierra Nevada, the rule of “graze half, leave half” is unsafe. Use of very wet or dry meadow sites should not exceed 35%; 45% use of more mesic sites is satisfactory. Some of the more common conditions that can adversely affect meadows are: 1) Defoliation of meadow plants. If too severe, frequent and at the wrong time, defoliation can deteriorate meadows, 2) Preferential grazing. This major cause of range deterioration is caused when animals and humans use specific areas about the same time each season, and a treatment that favors one species may eliminate another from the stand. Breaking the use pattern by modifying frequency and timing of use is the only effective way to counter the harmful effects of preferential grazing, 3) Trampling. This condition compacts the soil and cuts the sod. Even when the sod is not cut, trampling may lower the pH of the soil solution, 4) Redistribution of nutrients. Livestock redistribute nutrients within and among meadows and closely associated ecosystems. Short-term effects of nutrient redistribution are evident as dung pats and urine spots. Long-term effects gradually become evident as changes in species composition, 5) Rodent activities. Although rodent activities can markedly affect species composition and may induce erosion by channeling water, cultivation of the soil by rodents is beneficial. Overgrazing exacerbates the negative effects of rodents, but rodents inflict little harm to meadows in good condition, 6) Invasion by lodgepole pine. This autogenic process is both aided and hindered by livestock disturbance, and 7) Erosion. This condition occurs naturally and also as a result of overgrazing. Maintaining or restoring hydrologic characteristics is essential to maintaining a meadow.

Rice, K.J. 1989. Competitive interactions in California annual grasslands. Pp. 59-72 in: L. F. Huenneke, and H. A. Mooney, editors. ***Grassland Structure and Function: California Annual Grassland***. Kluwer Academic, Dordrecht, The Netherlands.

This paper examines the usefulness of a hierarchical approach in describing the influence of plant competition on variation in species diversity at within- and between-habitat spatial scales in California’s annual grassland ecosystem. High species diversity within California annual grasslands seems to reflect an underlying diversity of species interactions. At the interface of two species assemblages, soil heterogeneity, grazing, and competition may act in concert to maintain the floristic distinctiveness of each assemblage. Similarly, resource partitioning may complement competitive indeterminacy in promoting competitive coexistence within assemblages. Experimental studies of competitive interactions in annual grasslands should use designs that can detect both the direct and interactive effects of various causal agents acting simultaneously. The relative importance of equilibrational and nonequilibrational mechanisms of coexistence in natural populations is unclear because relevant field experiments are lacking. However, some characteristics of annual grasslands suggest that nonequilibrational coexistence mechanisms may be especially important. In

annual grasslands, autumnal rainfall is highly unpredictable in amount and distribution. As a result, germination can vary widely among years and locales. Experiments showing the importance of germination timing and early seedling environment on competitive success argue for the importance of competitive indeterminacy as a force promoting coexistence in such an environment.

Rice, K.J. and E.S. Nagy. 2000. Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. *American Journal of Botany* 87:1699-1706

Within the oak woodlands of California there is often a distinct shift in the botanical composition between the open grassland and the herbaceous understory beneath oak canopy. Botanical sampling at two woodland sites indicated that the annual grass *Bromus diandrus* was dominant under deciduous blue oak canopy, while a congener, *Bromus hordeaceus*, was dominant in open grassland. We examined the relative importance of congeneric competition and edaphic factors in creating these differences in species distribution in two separate field experiments that manipulated both congeneric and intraspecific competition, as well as soil type. We used the demographic measure of relative reproductive rate as an index of population growth. In general, demographic performance correctly predicted the distribution of the two annual grasses in the field. Our results indicate that reduced abundance of *B. hordeaceus* under canopy reflects the negative effects of competition with *B. diandrus*. In contrast, *B. diandrus* is little affected by competition from *B. hordeaceus*. The reduced abundance of *B. diandrus* in open grassland may result, in part, from its inability to adapt as well as *B. hordeaceus* to lower nutrient availability in soils of the open grassland.

Rosenstock, S.S. 1996. Shrub-grassland small mammal and vegetation responses to rest from grazing. *J. Range Management* 49:199-203.

Between 1989-1991, I studied the effects of livestock grazing on vegetation and small mammals in semiarid shrub-grassland habitats of south-central Utah. Responses were measured at 2 spatial habitat scales; patches and macrohabitats. Patch-scale data were obtained from 4 small (~1 ha) livestock exclosures and nearby grazed areas. Macrohabitat-scale data were collected at 4 actively grazed sites and 4 comparable, excellent condition sites, ungrazed for 30+ years. Ungrazed patch and macrohabitat sites had more surface litter, greater perennial grass cover, and taller perennial grass plants, but treatment response varied among sites. Small mammal responses were apparent only at the macrohabitat scale, where ungrazed sites had 50 % greater species richness and 80% higher abundance. Small mammal reproductive activity and biomass were not affected by rest from grazing at either scale. Small mammal community composition varied greatly among sites and within treatments. This variability has important implications for ecological monitoring efforts involving these species.

Rosiere, R.E. 1987. An evaluation of grazing intensity influences on California annual range. *Journal of Range Management* 40: 160-165.

Influences of grazing intensity on species composition and herbage production of grass-woodland and improved grassland subtypes of annual range were evaluated over a 5-year period in coastal northern California using 3 grazing treatments (100,150, and 200% of moderate stocking). Herbage utilization did not differ significantly between the 2 subtypes but averaged 42,52, and 69% for the respective treatments. Plant species and production responses differed significantly between woodland and grassland subtypes. On woodland, ripgut brome (*Bromus rigidus*) and wild oats (*Avena barbata* and *A. fatua*) were most sensitive to grazing intensity while wild barley (*Hordeum leporinum* and *H. hystrix*) and annual fescue (*Festuca dertonensis* and *F. megalura*) were least sensitive. On improved grassland, subterranean clover (*Trifolium subterraneum*) increased and soft chess (*Bromus mollis*) decreased with increasing grazing intensity. Soft chess remained most plentiful on woodland range under heaviest grazing and it continued to be a major species under heavy grazing of grassland, demonstrating tolerance to grazing intensity. Filaree (*Erodium cicutarium* and *E. botrys*) declined on woodland but increased on grassland as grazing intensified. Peak standing crop was not significantly affected by grazing intensity on woodland range but was greatest at 150% of moderate stocking and lowest at 200% of moderate stocking on grassland range. Decline in grassland herbage yield under heaviest grazing was due to reduction of soft chess which was displaced by subterranean clover. Effects of grazing intensity on range composition and productivity were confounded by innate differences in ranges and yearly weather patterns. Herbage production was impacted more by annual growing conditions than by grazing regimens, but there was no correlation between total annual precipitation and peak standing crop.

Saenz, L. and J.O. Sawyer. 1986. Grasslands as compared to adjacent *Quercus garryana* woodland understories exposed to different grazing regimes. *Madrono* 33(1): 40-46.

The grasslands in northwestern California show striking differences in species composition when compared to understories of adjacent woodlands. In addition, sites that differ in the length of time during which cattle graze are distinct. Native grasses, although present, are not important in any of the areas studied. Greater perennial grass cover occurs only in the grassland grazed for a partial season. Perennial forbs are well represented in the sites grazed for a partial season. A greater cover of introduced annual grasses and reduced species richness are found in sites grazed for a full season. We hypothesize that cropping of leaves over an extended period depletes the storage capacity of the native grasses, and can result in loss of perennials from the vegetation.

Safford, H.D. and S.P. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications* 11(4): 1112-1122.

We compared the native and exotic species composition of ungrazed roadside verges with that of adjacent grazed interiors in the grasslands of California's inner northern coast range (Napa and Lake Counties). We sampled 72 pairs of verge and interior quadrats at five sites representative of the region's grasslands, on both fertile (loam) and infertile (serpentine) soils, avoiding all obvious forms of roadside physical disturbance. We found that, on serpentine soils, ungrazed verges had a higher proportion of exotic species than grazed interiors; on nonserpentine soils, the reverse was true. Within serpentine soils, native species were more prevalent in quadrats with lower biomass; within nonserpentine, natives were more prevalent in quadrats receiving less radiation. Overall, the total species diversity was higher in grazed interiors than on ungrazed verges, regardless of the fertility of the substrate. Our results indicate that the ecological role of roadside verges depends on the interactive effects of community composition and history, environmental gradients, and land use practices that characterize a region.

Savelle, G.D. 1977. Comparative structure and function in a California annual and native bunchgrass community. Dissertation. University of California, Berkeley, CA.

Periodic measurements were obtained for selected structural and functional parameters within an annual grassland and a *Stipa pulchra* bunchgrass community naturally established on the Hopland Field Station under conditions of nearly identical climate, soil, topography and potential organisms. The area is typical of north-central Coast Ranges that now support grassland or woodland understory of predominantly annual grasses and forbs but which have scattered stands of perennial bunchgrasses that are recognized as quasi-remnants of the original California prairie. The study spanned the period of December 1970 to April 1973, a time interval encompassing both a regionally normal rainfall and herbage production year and an extremely droughty growing season. During initial development, energy flow and turnover are much slower in the perennial grassland because detritus tends to accumulate and to act as a large energy sink. When the communities are mature, and with normal climatic conditions prevailing and all other environmental factors being equal, the *Stipa* community is potentially capable of higher net biomass and energy production because of the coexistence of annual and perennial life-forms that permit a more complete occupation of a site both above- and below-ground. Under conditions of environmental stress, the perennial community is less stable and will exhibit large fluctuations in net productivity.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences*, 100:13384–13389.

The dynamics of invasive species may depend on their abilities to compete for resources and exploit disturbances relative to the abilities of native species. We test this hypothesis and explore its implications for the restoration of native ecosystems in one of the most dramatic ecological invasions worldwide, the replacement of native perennial grasses by exotic annual grasses and forbs in 9.2 million hectares of California grasslands. The long-term persistence of these exotic annuals has been thought to imply that the exotics are superior competitors. However, seed-addition experiments in a southern California grassland revealed that native perennial species, which had lower requirements for deep soil water, soil nitrate, and light, were strong competitors, and they markedly depressed the abundance and fecundity of exotic annuals after overcoming recruitment limitations. Native species reinvaded exotic grasslands across experimentally imposed nitrogen, water, and disturbance gradients. Thus, exotic annuals are not superior competitors but rather may dominate because of prior disturbance and the low dispersal abilities and extreme current rarity of native perennials. If our results prove to be general, it may be feasible to restore native California grassland flora to at least parts of its former range.

Shariff, A. R., M. E. Biodini, and C. E. Grygiel. 1994. Grazing intensity effects on litter decomposition and nitrogen mineralization. *Journal of Range Management* 47:444–449.

A 2 year study in south central North Dakota determined the responses of (1) litter and root decomposition and nitrogen (N) release, and (2) soil N mineralization to grazing intensity. The treatments were: long term not grazed, moderate grazing, and heavy grazing. The moderate grazing and the heavy grazing treatments removed 45% and 77% of annual above-ground growth respectively. The moderate grazing treatment resulted in higher decomposition and soil N mineralization rates, and lower N releases via decomposition than the long term not grazed and heavy grazing treatments. No consistent differences were found between the long term not grazed and heavy grazing treatments. Annual litter and root decomposition rates in the moderate grazing treatment averaged 55% for 1989-1990 and 63% for 1990-1991 while the long term not grazed and heavy grazing treatments had rates for the same periods of 13 % and 19 % . The moderate grazing treatment had a net soil N mineralization of 60 pg.g⁻¹ and 269 ug.g⁻¹ during the 1989 and 1990 growing seasons, whereas the long term not grazed and heavy grazing treatments had net soil immobilization for the same periods of -59 pg.g⁻¹ and -115 pg.g⁻¹. Annual N release from litter and root decomposition in the heavy grazing and long term not grazed treatments averaged 70 % and 38 % respectively during the 1989-1990 incubation period, and 51% and 23 % during 1990-1991. The equivalent values for the moderate grazing treatment were 47% and -6% (net N immobilization) for 1989-1990 and 41% and 23% for 1990- 1991. Results from this study seem to indicate that the standard grazing rule of “take half leave half” may have a significant impact in N conservation and the supply of mineral N for plant growth.

Sierra Nevada Ecosystem Project. 1996. Rangelands. Pp 114-122 in: SNEP, Volume I. Assessment summaries and management strategies. University of California, Centers for Water and Wildland Resources. Davis, CA.

Key findings: 1) Historic unregulated grazing, which ended in the early 1900s, created widespread, profound, and in some places, irreversible ecological impacts. Foothill habitats have suffered physical and biological damage of many riparian systems and virtual replacement of the native perennial flora by Eurasian annuals. 2) Current livestock grazing practices continued to exert reduced but significant impacts on the biodiversity and ecological processes of many middle- to high-elevation rangelands, even though properly managed grazing (appropriate timing, intensity, duration of use, control of cowbirds, and exclusion from wetlands) can be compatible with sustainable ecological functions. 3) Increases in native perennial grasses are occurring on some east-side sagebrush steppe rangelands, but the continuing cheatgrass invasion of these habitats indicates that complete restoration of native plant communities is highly unlikely. Any continuation of improper grazing practices will surely exacerbate the spread of invasive weeds. 4) Easily damaged by improper grazing, montane meadows and riparian systems are resilient relative to restoration of plant cover, but restoration of stream channel shape, system function, and biodiversity may take decades. 5) Human settlement patterns represent the largest threat to continued sustainability of ecological functions on hardwood rangelands. 6) Oak woodlands (particularly blue oak) are much more stable than previously thought; concerns about regeneration are not well founded.

Smith, W.P. 1985. Plant associations within the interior valleys of the Umpqua River basin, Oregon. *Journal of Range Management* 38(6): 526-530.

Eleven plant associations were identified and characterized according to the frequency, percent cover, and relative dominance of the herbaceous and woody species among the vegetative strata, including stem density, diameter breast height (dbh), and basal area for tree species: *Cynosurus echinatus*/*Taeniatherum asperum*; *Bromus mollis*/*Cynosurus echinatus*; *Rhus diversiloba*/*Cynosurus echinatus*; *Quercus garryana*/*Rhus diversiloba*/*Taeniatherum asperum*/*Cynosurus echinatus*; *Quercus garryana*/*Rhus diversiloba*/*Dactylis glomerata*; *Pseudotsuga menziesii*/*Quercus garryana*/*Rhus diversiloba*/*Polystichum munitum*; *Quercus garryana*/*Arbutus menziesii*/*Rhus diversiloba*/*Cynosurus echinatus*; *Arbutus menziesii*/*Rhus diversiloba*/*Festuca arundinacea*; *Quercus garryana*/*Fraxinus latifolia*/*Rosa eglanteria*/*Juncus effusus*; *Pseudotsuga menziesii*/*Corylus cornuta*/*Cynosurus echinatus*. The intensity and duration of recent disturbance distinguished early seral stages which were characterized by a paucity of native shrub and herbaceous species and an abundance of annual invaders in the understory. The primary forces that influenced existing plant assemblages were fire and more recently agricultural practices, especially among grasslands and savannas. Grasslands without recent livestock use exhibited greater species diversity, supporting more species and a more homogeneous distribution of relative abundance among species.

Standiford, R.B., J. Klein and B. Garrison. 1996. Sustainability of Sierra Nevada hardwood rangelands. Pp. 637-680 in: Sierra Nevada Ecosystem Project: final report to Congress. Volume III: Assessments, commissioned reports and background information. Centers for Water and Wildland Resources, University of California, Davis, CA.

With the introduction of domestic livestock and exotic annual grasses during the Spanish mission days, hardwood rangeland ecosystems in the Sierra Nevada have changed dramatically. The herbaceous layer has changed from a perennial layer to an annual layer. Fire intervals have increased dramatically and fire intensity has also increased. The overstory layer if not converted to another land use, has generally increased. Soil moisture late in the growing season has decreased, and bulk density has increased due to compaction from higher herbivore densities, primarily domestic livestock. Riparian zones are now less dense and diverse. The effects of these changes on ecosystem processes are discussed in more detail. "Livestock grazing has had a major impact on the oak woodlands of California's Sierra Nevada. Grazing has both positive and negative effects on hardwood rangeland sustainability. Some of the positive effects of livestock grazing include: 1) reduced moisture competition between oaks and herbaceous material, 2) reduced transpiration surface area in seedlings, which may help conserve moisture late in the growing season, 3) reduced habitat for rodents who consume acorns and young oak seedlings. Some of the potential negative effects of grazing are: 1) livestock consume oak seedlings and acorns, 2) grazing may increase soil compaction, making root growth for oak seedlings more difficult, and 3) soil organic matter may be reduced."

Stromberg, M. R. and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers and grazing. *Ecological Applications* 6(4): 1189-1211.

Grasslands at the Hastings Natural History Reservation (HNHR) and in adjacent Santa Lucia coastal range of Monterey County, California were sampled from 1971 to 1991. Grasslands on HNHR showed two distinct and stable associations: stands with and without historical cultivation (\approx 1865-1937). Relict stands dominated by native, perennial grasses (e.g., *Nassella pulchra*, *Poa secunda*) are limited to uncultivated, steeper stands, often where soils have more clay. Abandoned agricultural fields have stable compositions dominated by *Avena fatua*, *Bromus mollis*, *B. diandrus*, *Erodium* spp., *Hypochaeris glabra*, *Vulpia* spp., *Eremocarpus setigerus*, and *Amsinckia* spp. Patterns in species composition were associated with gradients in soil texture, gopher abundance, and slope. Gophers provide a significant and continuous source of soil disturbance and may slow successional processes in old fields. Where gophers are excluded, above-ground biomass accumulates. Germination and establishment of native perennial grasses (compared to introduced, annual grasses) are reduced on gopher tailings in old fields. Species composition patterns reflecting past cultivation on both grazed and ungrazed stands are apparent. Relict (uncultivated) stands of native grasses persist under many historical levels of grazing. Effects of grazing are often only seen on old fields, and not on relict grasslands. Compared to stands where grazing was removed in 1937, stands currently or recently grazed by cattle show higher soil nitrogen, but reductions in cover of gopher tailings, species diversity, soil phosphate, and sulphate.

Stromberg, M. R., P. Kephart and V. Yadon. 2001. Composition, invasibility, and diversity in coastal California grasslands. *Madroño* 48: 236-252.

We present a detailed floristic study of coastal terrace prairies in central California that are poorly described in California's ecological literature. Definitive native grasses include *Danthonia californica*, *Nassella pulchra*, and *Festuca rubra*. Definitive native forbs include *Baccharis pilularis*, *Viola*, *Sidalcea*, *Cammissonia* and *Acaena*. Species richness in the coastal prairies (1 m²) averaged 22.6, nearly twice that of relatively diverse serpentine California grasslands, and other North American grasslands. We sampled 33 coastal prairies and found 340 plant species including 258 forbs. Nearby plant communities (Monterey Pine, Coastal Scrub) had much lower species diversity at all spatial scales studied. Three distinct coastal grasslands, each associated with a land form, can be defined by distinct species composition; coastal terraces, uplifted "bald hills" and inland ridges. We compared 29 coastal terrace prairies (those without tree or shrubs) to 80 inland *Nassella* prairies with regard to 27 floristic variables (cover, number of natives/exotics, perennials/annuals, grasses/forbs) along a gradient from interior-coastal valley and from north to south along the coast. Coastal terrace prairies were invaded by exotics, but far less so than inland *Nassella* prairies. Species diversity (0.1 ha) and total cover were positively correlated. Relative cover of exotic species was negatively correlated with total cover, based on all sites. Number of exotic species was positively correlated with species richness in inland *Nassella* prairies but not coastal terrace prairies. Canonical correspondence analysis indicated that coastal terrace prairies with higher cover of non-native species had reduced total cover and/or reduced diversity of native perennial species of grasses and forbs. Native perennial grasslands, including coastal terrace prairies, are rare and have been eliminated by development along the narrow corridor of land between the sea and the inland ridges of central, coastal California. If protection of biodiversity is a management goal in land use plans, coastal grasslands should be protected as biodiversity "hotspots" with development focused in nearby relatively depauperate communities.

Swiecki, T.J., E.A. Bernhardt and C. Drake. 1997. Factors affecting blue oak (*Quercus douglasii*) sapling recruitment. Pp. 157-167 in: Proceedings of the symposium on oak

woodlands: ecology, management and urban interface issues. USDA Forest Service Pacific Southwest Research Station, Gen. Tech. Report PSW-GTR-160. Berkeley, CA.

Grazing and browsing variables were negatively associated with recruitment in within-location models for all currently grazed locations and in the all-location model. From these results and our field observations of browsing damage, we conclude that browsing by livestock is a major constraint to both blue oak sapling recruitment and the regeneration of other woody species at many locations. Other studies (Bernhardt and Swiecki 1997, Borchert et al. 1989, Hall et al. 1992) have also documented strong adverse effects of cattle on the growth and survival of oak seedlings and saplings in California. Livestock may inhibit blue oak sapling recruitment by both depleting the understory stock of seedling advance regeneration and adversely affecting sapling survival.

Trimble, S. W., and A. C. Mendel. 1995. The cow as a geomorphic agent, a critical review. *Geomorphology* 13: 233-253.

Cows are important agents of geomorphological change. On the uplands, heavy grazing compacts the soil, reduces infiltration, increases runoff, and increases erosion and sediment yield. However, light and moderate grazing have effects that are much less significant. In riparian zones, grazing decreases erosional resistance by reducing vegetation and exposing more vulnerable substrate. Trampling directly erodes banks, thus increasing turbulence and consequent erosion. Future studies should be framed within the hydroclimatological, edaphic and geomorphological dimensions of the areas being studied so that controlling variables may be more readily isolated. We believe that both empirical studies and deterministic modeling can provide insights as to the effects of grazing on geomorphology.

Valone, T.J., M. Meyer, J.H. Brown and R.M. Chew. 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. *Conservation Biology* 16: 995-2002.

Over the past two centuries, perennial grass cover has declined and shrub density has increased in many arid grasslands. These changes in vegetation, characteristic of desertification, are thought to have occurred often following prolonged periods of intense grazing by domestic livestock. At many such sites, however, the subsequent removal of livestock grazing for up to 20 years has not resulted in increased grass cover. The apparent stability of vegetation following the cessation of livestock grazing has led to the hypothesis that desertified arid grasslands exist in alternate stable states of either grassland or shrubland over timescales relevant to management. To better understand the timescale of grass recovery in historic arid grasslands dominated by shrubs, we examined the vegetation at two nearby desertified sites that differed in the length of time since livestock removal. There was little difference between the site ungrazed for 20 years and the shrub-dominated vegetation on the other side of the exclusion fence. At a site ungrazed for 39 years there was significantly higher perennial grass cover inside the exclusion fence than outside, and nearly all the increase had occurred over the past 20 years. These data suggest that there may be time lags of 20 years or more in the response of perennial grasses to removal of livestock in historic grassland ecosystems dominated by shrubs.

Wagner, F.H. 1989. Grazers, past and present. Pp. 151-162 In L.F. Huenneke and H.A. Mooney, (eds.) *Grassland Structure and Function: California Annual Grasslands*. Kluwer Academic Publishers, Boston, MA.

This paper presents a review of the herbivorous fauna that prevailed in, and influenced, the California grassland during its formation, during its existence in prehistory, and during the changes it has undergone since European colonization. The California grasslands sustained heavy grazing pressures from a diverse herbivorous fauna during the late Pleistocene, and possibly up to the start of the recent epoch ca. 10,000 B.P. The first Europeans arriving in 16th century A.D. encountered large numbers of three ungulate species – black-tailed deer, pronghorn antelope and tule elk – none is an obligate grazer. Livestock herds were first developed by the Spaniards along the coast, subsequently in the Central Valley by Indians and large numbers of feral horses and cattle. The ranching industry did not develop until after the gold rush. Beef cattle numbers reached 1.8 million by 1860, declined by over half by 1870 due to drought, then increased to all-time highs (2.9 million on rangelands) in the last half of the century. Sheep numbers peaked around 1880 at 6 million, and have declined since to a contemporary total of less than half a million. Grazing pressures on public rangelands have stabilized for several decades, but might be at an all-time high on private ranges. By the 16th century, California perennial bunchgrass vegetation might have been a relict of a previous, more favorable climate. Its survival might have been abetted by a depauperate ungulate fauna comprised only of browsers which protected it from competition by woody species.

White, K.L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation, California. *Ecology* 48: 949-955.

Species composition, cover, and standing crop were sampled in 13 small patches of the native bunchgrass *Stipa pulchra* on an area protected from grazing for 27 years. The common species present were representatives of lightly grazed annual grassland. Cover of *Stipa*, as basal area intercept, averaged 11%. Standing crop of all species averaged 98 g/m², with *Stipa* comprising 37% of the total. Comparison of the 13 protected stands with four grazed stands showed differences in species composition, but basal area intercept and standing crop of *Stipa* were not significantly different. An ordination of all 17 stands using species frequency in quadrats showed a pattern consistently related to percentage slope.

Young, J.A. and R.A. Evans. 1989. Seed production and germination dynamics in California annual grasslands. Pp. 39-45 In L.F. Huenneke and H.A. Mooney, (eds.) ***Grassland Structure and Function: California Annual Grasslands***. Kluwer Academic Publishers, Boston, MA.

The most striking factor apparent in the dynamics of populations of seeds in annual grassland communities is the relatively few germinable seeds carried from year to year in the litter and surface soil. Coupled with this phenomenon is the very rapid depletion of reproductive reserves during the brief germination period following the first effective rain each fall. The location of the bulk of the seed reserves in the litter and surface soil, along with the moderating effect of litter in terms of temperature and moisture, supports the concepts of Harold Heady regarding the role of litter in controlling plant succession in these communities.

II. LIVESTOCK GRAZING AND EXOTIC PLANT SPECIES

Allen, B.H. and J.A. Bartolome. 1989. Cattle grazing effects on understory cover and tree growth in mixed conifer clearcuts. *Northwest Science* 63(5): 214-220.

A long-term study of cattle grazing effects on shrub and herbaceous cover and tree growth in mixed conifer clearcuts began at Blodgett Forest Research Station on the west slope of the Sierra Nevada (California, USA) in 1977. Until that time, no studies had quantified the relationships between cattle grazing and reduction in non-tree vegetation, and grazing damage to tree regeneration. Yet, with the ban on use of herbicides in Federal forest management, alternative tools for reducing unwanted vegetation were needed. Cattle grazing reduced shrub and herbaceous canopy cover to 8 percent six years after harvesting, and 31 percent eight years after harvesting on two mixed conifer clearcuts. These cover levels were within timber management objectives for tree growth. No significant trampling damage occurred and browsing damage to white and Douglas-fir seedlings was primarily caused by deer. Tree seedlings showed no significant differences in height or basal diameter growth under any treatment. Thus, cattle grazing appears to be a viable tool for meeting brush/grass objectives in forest plantations.

Baker, H.G. 1989. Sources of the naturalized grasses and herbs in California grasslands, Pp 29-38. In L.F. Huenneke and H.A. Mooney, (eds.) ***Grassland Structure and Function: California Annual Grasslands***. Kluwer Academic Publishers, Boston, MA.

A brief presentation of the topographic and climatic history of California relating to the development of grassland is given. Grassland and savannas became increasingly extensive with the progressive reduction in rainfall, particularly in the summer months, that began in the Miocene epoch and persisted till the end of the Tertiary period. With the exception of some relationship to the Palouse prairie of northwestern North America, the grasslands of California developed largely without contributions from the flora of the grasslands to the east of the Sierra. A rich representation of perennial bunchgrasses (with associated annuals) appears to have developed in the absence of bison grazing and persisted until the beginning of the 19th century when the oft-described influence of European man and his livestock began to be felt. Grasslands in the subalpine and alpine zones of the California mountains show little effect of grazing pressure from domestic livestock, but the valley and hill grasslands and north coastal prairies were markedly affected by the heavy grazing that developed in the 19th century and led to the establishment of annual grasses and forbs from other parts of the world with appropriate climatic conditions. Coastal prairies have been less affected than inland grasslands and have a greater prospect of recovering a "natural" community life-form with the cessation of grazing by domestic livestock. Comparisons are made between the introduced taxa that have invaded the grasslands and those that are also introduced, but did not become established in grasslands. The latter have a wider range of geographical origins.

Belsky, A.J. and J.L. Gelbard. 2000. Livestock grazing and weed invasions in the arid West. Unpublished report of the Oregon Natural Desert Association available online at: <http://www.onda.org/library/papers/WeedReport.pdf>.

Non-indigenous plants (also referred to as alien, exotic, or introduced weeds) are invading arid and semi-arid grasslands, shrublands, and woodlands of the American West at an exponential rate. Management efforts intended to control their spread have been largely ineffective. This may be due to a lack of attention to domestic livestock grazing, the dominant land use of the region. The contribution of livestock grazing to weed invasions has generally been downplayed while the effects of drought, historic overgrazing, fire, and seed introductions associated with outdoor recreation, roads, and wildlife have been emphasized. In this paper, we review the scientific literature relating livestock grazing to the invasion of non-indigenous plant species in the arid and semiarid lands west of the Rocky Mountains. At the landscape and regional scales, livestock grazing is one of several factors causing and enhancing the invasion of alien weeds into grassland, shrubland, and woodland communities; but at the community scale, livestock may be the major factor causing these invasions. Most studies find that plant communities grazed by domestic livestock contain a greater density, frequency, or cover of non-indigenous plants than ungrazed communities. A few studies document positive, but only temporary, reductions of weed numbers by sheep and goats, but most weedy species are avoided by cattle. Livestock contribute to alien weed invasions by: (1) transporting weed seeds into uninfested sites on their coats and feet and in their guts, (2) preferentially grazing native plant species over weed species, (3) creating patches of bare, disturbed soils that act as weed seedbeds, (4) destroying microbiotic crusts that stabilize soils and inhibit weed seed germination, (5) creating patches of nitrogen-rich soils, which favor nitrogen-loving weed species, (6) reducing concentrations of soil mycorrhizae required by most western native species, and (7) accelerating soil erosion that buries weed seeds and facilitates their germination. This review suggests that non-indigenous weeds will continue to spread through arid and semi-arid grasslands, shrublands, and woodlands in the western United States unless selective grazing, nutrient redistribution, and soil disturbances by livestock are greatly reduced or eliminated.

Belsky, A.J. and J. L. Gelbard. 2002. [Comrades in harm: Livestock and exotic weeds in the intermountain West](#). Pp. 203-205 in Wuerthner, G. and M. Mattson, eds. *Welfare Ranching: The Subsidized Destruction of the American West*. Island Press. Washington D.C.

Exotic weed invasion is one of the greatest ecological threats to grass and shrub ecosystems in the arid West, and livestock grazing is a leading cause of weed invasion. Livestock carry in weed seeds on their coats and in their digestive systems; they weaken native plants by grazing them; and they disturb the soil surface, thereby creating more favorable conditions for exotic invaders and less favorable conditions for native plants.

Bossard, C.C., J.M. Randall, and M.C. Hoshovsky (eds.). 2000. *Invasive Plants of California's Wildlands*. University of California Press, Berkeley.

This book begins with a brief overview of the impacts of invasive plants and what is known about the characteristics of plant species most likely to invade and the habitats and communities most likely to be invaded. This is followed by a discussion of strategies and methods appropriate for the control of invasive plants in parks, reserves and other wildlands. The remainder of the book consists of species accounts for 78 invasive species listed as Exotic Invasive Plants of Greatest Ecological Concern as of 1996 by the California Exotic Pest Plant Council. Each account helps readers to identify the species and understand important aspects of its biology and lists specific control methods that are regarded as relatively effective, as well as some found to be ineffective.

Bullock, J.M., Clear Hill, B. and Silvertown, J. 1994. Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology* 82:101-111

The complete demographies of 16 populations of *Cirsium vulgare* were followed in a replicated experiment. The experiment was a factorial combination of two intensities of sheep grazing in each of three seasons-winter (grazed or ungrazed), spring (grazed or ungrazed), and summer (light or heavy grazing)-giving eight treatments in two blocks. For 6 years from 1987 to 1992 the population sizes of *C. vulgare* were monitored in each of the 16 paddocks. After 1989 grazing in spring or winter or increased grazing in summer all increased population sizes. Population sizes fluctuated widely between years. The effects of the grazing treatments and plant sizes on the transitions between nine life-history stages were determined. There were no grazing effects on seed numbers per flowerhead, post-dispersal seed survival or between year seed survival in the seed bank. More-intense summer or winter grazing increased seedling emergence by increasing the proportion of microsites with no canopy or with no litter. Emergence was found to respond positively to these factors. Seedling survival was increased by winter or spring grazing and winter grazing increased the year-to-year

survival of small and medium-sized rosettes. These effects probably occurred through selective grazing decreasing competition from the dominant grasses. Larger rosettes had lower mortality rates which were unaffected by the grazing treatments. There was a minimum rosette size threshold for flowering above which flowering probability increased with size. Because winter grazing increased the survival of smaller rosettes it increased the proportion of smaller rosettes in the populations and thus decreased the proportion of rosettes flowering. By the same process winter grazing decreased the average size of flowering rosettes and, because smaller rosettes produced fewer flowerheads, this treatment decreased the flowerhead number of flowering rosettes. The lepidopteran seed predator *Eucosma cana* attacked a larger proportion of heads on plants with more flowerheads. By decreasing the average number of flowerheads per flowering plant winter grazing decreased the proportion of flowerheads on a plant attacked. Matrix analysis of life tables for each paddock showed that winter and spring grazing and increased summer grazing all significantly increased the population growth rate λ . The population sizes of each paddock correlated significantly with the estimated λ values. Elasticity analysis was performed on each matrix and elasticity values within each matrix were summed to give a value for fecundity (e_F), stasis (e_I) and growth (e_G). Triangular ordination of e_F , e_I and e_G showed that λ became more sensitive to small changes in fecundity and less sensitive to small changes in stasis as grazing intensity increased.

Callihan, R.H., and J.O. Evans. 1991. Weed dynamics on rangeland. p. 55-61. *In*: L.F. James, J.O. Evans, M.H. Ralphs, and R.D. Child, eds. *Noxious Range Weeds*. Westview Press. Boulder, Colorado.

Historical evidence indicates that western ranges once had much more perennial grasses as dominant species in their plant communities. The degradation of these ranges can be traced from the 19th century with the wide-scale grazing of domestic livestock. Alien plants intentionally or accidentally introduced to western rangelands exhibit extreme competitive abilities and dominate vast areas weakened by unfavorable management strategies or stresses to native plant populations from environmental events such as wildfires. Much western rangeland has such low residual grass populations at present that revegetation is essential.

Carlsen, T.M., J.W. Menke and B.M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology* 8(1): 18-23.

Populations of the rare annual forb *Amsinckia grandiflora* may be declining because of competitive suppression by exotic annual grasses, and may perform better in a matrix of native perennial bunchgrasses. We conducted a field competition experiment in which *Amsinckia* seedlings were transplanted into forty 0.64-m² experimental plots of exotic annual grassland or restored perennial grassland. The perennial grassland plots were restored using mature 3 cm-diameter plants of the native perennial bunchgrass *Poa secunda* planted in three densities. The exotic annual grassland plots were established in four densities through manual removal of existing plants. Both grass types reduced soil water potential with increasing biomass, but this reduction was not significantly different between grass types. Both grass types significantly reduced the production of *Amsinckia* inflorescences. At low and intermediate densities (dry biomass per unit area of 20–80 g/m²), the exotic annual grasses reduced *Amsinckia* inflorescence number to a greater extent than did *Poa*, although at high densities (>90 g/m²) both grass types reduced the number of *Amsinckia* inflorescences to the same extent. The response of *Amsinckia* inflorescence number to *Poa* biomass was linear, whereas the same response to the annual grass biomass is logarithmic, and appeared to be related to graminoid cover. This may be because of the different growth forms exhibited by the two grass types. Results of this research suggest that restored native perennial grasslands at intermediate densities have a high habitat value for the potential establishment of the native annual *A. grandiflora*.

Clausnitzer, D. W., M. M. Borman, and D. E. Johnson. 1999. Competition between *Elymus elymoides* and *Taeniatherum caput-medusae*. *Weed Science* 47:720–728.

Two field experiments were conducted from 1993–1994 through 1995–1996 growing seasons in Harney County, OR, to determine the relative competitive abilities of *Elymus elymoides* (squirreltail) a native perennial range grass, and *Taeniatherum caput-medusae* (medusahead), an exotic annual grass weed. The 1993–1994 growing season was very dry, 1994–1995 was dry, and 1995–1996 was wetter than average. One experiment tested seedlings vs. seedlings in each of three seasons. The second experiment tested seedlings plus second- and third-year established *E. elymoides* plants vs. *T. caput-medusae* over 2 yr. Biomass, seed production, and soil moisture utilization 15, 30, 45, and 60 cm deep by the two species were measured. A randomized block design with factorial arrangement was used, with 25 2.25-m² plots per block. Initial seeding densities of each species were 0, 10, 74, 550, and 4,074 seeds m⁻² in all combinations of density. In the seedling vs. seedling experiment, intraspecific competition by *T. caput-medusae* on itself was always significant ($P \leq 0.10$) for both biomass and seed production. Interspecific competition by *E.*

elymoides seedlings on *T. caput-medusae* biomass and seed production was not significant ($P \geq 0.10$) in 2 of 3 yr and was always less than intraspecific competition by *T. caput-medusae*. Only 0.4% of *E. elymoides* seed germinated, and no seed was produced in the very dry first year, but 84% of remaining seed was viable for the next year, which had better moisture conditions for germination and establishment. Interspecific competition affected ($P \leq 0.10$) *E. elymoides* seedling biomass and seed production throughout the study. Intraspecific competition affected ($P \leq 0.10$) seedling *E. elymoides* seed production in the dry year but not in the wetter than average year. In the mature *E. elymoides* experiment, intraspecific competition by *T. caput-medusae* on weight and seed production per plant was greater than interspecific competition from *E. elymoides*. Seedling/mature *E. elymoides* reduced *T. caput-medusae* weight per plant in the dry year but the effect was not biologically significant. Larger, mature *E. elymoides* plants produced 600 to 3,000 seeds per plant during the wet year; neither intra- nor interspecific competition was a factor. *Taeniatherum caput-medusae* was better able to access deeper soil moisture and was more aggressive at extracting soil moisture than were *E. elymoides* seedlings in the wet year. Cold soils and low oxygen due to wet soils may have restricted *E. elymoides* seedling root activity. Mature *E. elymoides* plants did not appear restricted by cold soils or low oxygen. Established second- and third-year *E. elymoides* plants were able to compete for soil moisture down to 45 cm. The generally greater interspecific competitive effects of *T. caput-medusae* on *E. elymoides* than vice versa suggested that it will be difficult to establish an *E. elymoides* stand in an existing *T. caput-medusae* community without first suppressing *T. caput-medusae*. Individual *E. elymoides* plants did establish and were productive with and without *T. caput-medusae* competition.

Corbin, J.D. and C.M. D'Antonio. 2004b. Can carbon addition increase competitiveness of native grasses? A case study from California. Restoration Ecology 12:36-43.

There is growing interest in the addition of carbon (C) as sucrose or sawdust to the soil as a tool to reduce plant available nitrogen (N) and alter competitive interactions among species. The hypothesis that C addition changes N availability and thereby changes competitive dynamics between natives and exotics was tested in a California grassland that had experienced N enrichment. Sawdust (1.2 kg/m) was added to plots containing various combinations of three native perennial bunchgrasses, exotic perennial grasses, and exotic annual grasses. Sawdust addition resulted in higher microbial biomass N, lower rates of net N mineralization and net nitrification, and higher concentrations of extractable soil ammonium in the soil. In the first year sawdust addition decreased the degree to which exotic annuals competitively suppressed the seedlings of *Nassella pulchra* and, to a lesser extent, *Festuca rubra*, both native grasses. However there was no evidence of reduced growth of exotic grasses in sawdust amended plots. Sawdust addition did not influence interactions between the natives and exotic perennial grasses. In the second year, however, sawdust addition did not affect the interactions between the natives and either group of exotic grasses. In fact, the native perennial grasses that survived the first year of competition with annual grasses significantly reduced the aboveground productivity of annual grasses even without sawdust addition. These results suggest that the addition of sawdust as a tool in the restoration of native species in our system provided no significant benefit to natives over a 2-year period.

Corbin, J.D. and C.M. D'Antonio. 2004c. Nitrogen cycling, retention and leaching losses in a coastal prairie grassland: importance of vegetation productivity, phenology, and tissue chemistry. In: Proceedings, Ecology and Management of California Grasslands, April 2-3, 2004, Berkeley, CA. Available online at: <http://cbc.berkeley.edu/grass/Abstracts.htm>

Differences in growth rate, phenology, and tissue chemistry between native perennial bunchgrasses, exotic perennial grasses, and exotic annual grasses have the potential to change nitrogen dynamics in California grassland ecosystems as community composition shifts. In 1999 we established field plots to compare N retention and N leaching loss rates between experimental communities dominated by each group of species. We had hypothesized that, because of differences in litter decomposition rates and phenology between exotic annual grasses and either native or exotic perennial grasses, plots associated with exotic annual grasses would have significantly faster rates of N cycling and significantly greater rates of N leaching losses. While N concentrations in leachate were higher in annual-dominated plots, as we had predicted, N cycling rates were actually *lower* in exotic annual-dominated plots as compared to either perennial group. Retention of ^{15}N ammonium was also significantly higher under annual plots than under perennials, despite the fact that the annual species had to germinate from seed at the time the tracer was added. The results indicate that more detailed mechanisms control N cycling and leaching losses in these herbaceous-dominated ecosystems than had been previously considered.

D'Antonio, C. M., T. Dudley, and M. Mack. 1999. Disturbance and biological invasions: direct effects and feedbacks. Pages 413–452 in L. Walker, editor. *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam, The Netherlands.

This paper provides a review of peer-reviewed studies assessing the conditions under which major disturbances – categorized by spatial scale and type (e.g. overtly anthropogenic vs. more or less natural) – either promote or inhibit invasion by non-native plant species into terrestrial ecosystems. The authors also examine how invading species themselves alter the disturbance regime. Finally they assess how altered disturbance regimes caused by introduced species may promote or inhibit further invasions. Primary findings of this review include the following: 1) introduced plant species are common along roads and other disturbance corridors, which may act as foci from which invaders may enter adjacent habitats; 2) a relatively small number of studies correlate recent livestock grazing with an increase in biological invasions, however, the removal of livestock after decades of grazing often does not result in the recovery of native community; 3) invasive species are generally most abundant and pervasive on lands that have been affected by catastrophic disturbance, whether natural (e.g. hurricanes, floods) or anthropogenic (logging, agriculture); 4) the majority of studies investigating fire reported that it generally promotes or enhances invasion by non-native species, particularly where the fire regime has been altered from general historic patterns; 5) introduced plant species can sometimes invade natural habitats without disturbance, especially in desert, island and coastal habitats; and 6) introduced species themselves often cause a change in the disturbance regime, particularly where invaders differed qualitatively from natives in a suite of traits that affected disturbance regimes.

D'Antonio, C.M. and K. Haubensak. 1998. Community and ecosystem impacts of invasive non-native plant species in California. *Fremontia* 13-18.

This article provides an overview of what is known about the impacts of invasive, non-native plants on wildland communities in California. The ecological impacts of these species can be broadly lumped into the following categories: 1) direct competition and displacement of native species, 2) alteration of natural disturbance regimes, 3) alteration of substrate stability and geomorphology, 4) alteration and simplification of food webs, 5) rapid preemption of resources following disturbance, and 6) alteration of soil chemistry or chemical processes. Many of these changes adversely impact regional biodiversity and ecosystem services such as water and topsoil retention, successful pollination, support of wildlife, and aesthetic and recreational enjoyment. Our knowledge about the effects of invaders on communities and ecosystems is far from complete.

D'Antonio, C.M., E. Berlow and K.A. Haubensak. 2004. Exotic invasive plant species in Sierra Nevada ecosystems. Pp. 175-184 in: P. Stine, D. Graber, D. Murphy, eds., *Proceedings from the Sierra Nevada Science Symposium, October 7-10, Kings Beach, CA. USDA Forest Service Pacific Southwest Research Station General Tech. Report PSW-GTR-193. Albany, CA.*

As in many areas of the world, the biodiversity of the Sierra Nevada region is undergoing change due to alterations in human uses and fire regimes, climate change, and invasions by non-native species. This paper provides an overview of invasive non-native plants and potential threats they pose to currently held values for Sierra Nevada ecosystems, and address the following questions: 1) what exotic species are invading the Sierra Nevada region and what habitats are being most invaded? 2) which species have the potential to dramatically reduce local native biodiversity or transform ecosystems? 3) what environmental conditions are likely to promote the spread of these species and consequent impacts? This information can ultimately help identify ecosystems at risk of invasion by potentially undesirable species and prevent further invasions. Invasion by many potentially problematic plant species in the Sierra Nevada are still at a relatively early stage. More knowledge is needed regarding pathways of introduction and dispersal, including the roles of logging, roads, pack animals and livestock. Second, the extensive conifer forests of the Sierra are currently less invaded than adjacent lower elevation habitats. Third, in establishing priorities for control efforts, it is essential to ascertain which species a) are moving from disturbed corridors into wildland habitat and b) pose the greatest ecological threats once they become established. The threat posed to endemic or rare species by invasive exotics needs to be evaluated. Managers will benefit from systematic surveys of distribution and abundance of the main problem invaders, with coordination for monitoring and control efforts at a regional scale.

D'Antonio, C.M., J. Levine and M. Thomsen. 2001. Propagule supply and resistance to invasion: A California botanical perspective. *Journal of Mediterranean Ecology* 2:233-245.

No abstract or summary available.

D'Antonio, C.M., N. Jackson, C. Horvitz and R. Hedberg. 2004. Invasive plants in wildland ecosystems: merging the study of invasion processes with management needs. *Frontiers in Ecology and Environment* 2(10): 513-521.

Increasing numbers of non-native species threaten the values of wildland ecosystems. As a result, interest in and research on invasive plant species in wildland settings has accelerated. Nonetheless, the ecological and economic impacts of non-native species continue to grow, raising the question of how to best apply science to the regulation and management of invasive plants. A major constraint to controlling the flow of potentially undesirable plant species is the lack of a strong regulatory framework concurrent with increases in trade volume. To address this, ecologists have been developing models to predict which species will be harmful to wildland values and are working with the horticultural industry to apply this information to the sale of species. The management of established invasive plants is hampered by conflicting goals, a lack of information on management outcomes, and a lack of funding. Ecologists and weed scientists can provide a scientific basis for prioritizing species for control and for managing species composition through the application of control technology, which can take place simultaneously with the manipulation of the ecological processes that influence community susceptibility to invasion. A stronger scientific basis for land management decisions is needed and can be met through nationally funded partnerships between university and agency scientists and land managers.

D'Antonio, C.M. and L.M. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* 10(4): 703.

Exotic species have become increasingly significant management problems in parks and reserves and frequently complicate restoration projects. At the same time there may be circumstances in which their removal may have unforeseen negative consequences or their use in restoration is desirable. We review the types of effects exotic species may have that are important during restoration and suggest research that could increase our ability to set realistic management goals. Their control and use may be controversial; therefore we advocate consideration of exotic species in the greater context of community structure and succession and emphasize areas where ecological research could bring insight to management dilemmas surrounding exotic species and restoration. For example, an understanding of the potential transience of exotics in a site and the role particular exotics might play in changing processes that influence the course of succession is essential to setting removal priorities and realistic management goals. Likewise, a greater understanding of the ecological role of introduced species might help to reduce controversy surrounding their purposeful use in restoration. Here we link generalizations emerging from the invasion ecology literature with practical restoration concerns, including circumstances when it is practical to use exotic species in restoration.

DiTomaso, J. M., G. B. Kyser, S. B. Orloff, and S. F. Enloe. 2000. Integrated approaches and control option considerations when developing a management strategy for yellow starthistle. *California Agriculture* 54: 30-36.

Ongoing research projects integrate chemical, mechanical, cultural and biological techniques to control yellow starthistle, a prolific weed now infesting between 10 million and 15 million acres in California. With many options available to land managers, developing a long-term, strategic management plan most suitable to a specific area can be complicated. It requires careful consideration of the advantages and disadvantages of each option and how best to incorporate appropriate ones into an effective program. Management strategies include timely mowings, grazing, clover plantings, biological control insects, prescribed burning and selective applications of herbicides. In addition to new developments in the management of yellow starthistle, public awareness of invasive weed issues has translated into major legislative changes that should encourage and assist private and public landowners and managers to initiate long-term programs to prevent and manage invasive weeds, particularly yellow starthistle.

DiTomaso, J.M. 2000. Invasive weeds in rangelands: species, impacts and management. *Weed Science* 48:255-265.

Rangeland and pastures comprise about 42% of the total land area of the United States. About three-quarters of all domestic livestock depend upon grazing lands for survival. Many ranges have had domestic stock grazing for more than 100 years and, as a result, the plant composition has changed greatly from the original ecosystems. Western rangelands previously dominated by perennial bunchgrasses have been converted, primarily through overgrazing, to annual grasslands that are susceptible to invasion by introduced dicots. Today there are more than 300 rangeland weeds in the United States. Some of the most problematic include *Bromus tectorum*, *Euphorbia esula*, *Centaurea solstitialis*, *C. diffusa*, *C. maculosa*, and a number of other *Centaurea* species. In total, weeds in rangeland cause an estimated loss of \$2 billion annually in the United States, which is more than all other pests combined. They impact the livestock

industry by lowering yield and quality of forage, interfering with grazing, poisoning animals, increasing costs of managing and producing livestock, and reducing land value. They also impact wildlife habitat and forage, deplete soil and water resources, and reduce plant and animal diversity. Numerous mechanical and cultural control options have been developed to manage noxious rangeland weeds, including mowing, prescribed burning, timely grazing, and perennial grass reseeding or interseeding. In addition, several herbicides are registered for use on rangelands and most biological control programs focus on noxious rangeland weed control. Successful management of noxious weeds on rangeland will require the development of a long-term strategic plan incorporating prevention programs, education materials and activities, and economical and sustainable multi-year integrated approaches that improve degraded rangeland communities, enhance the utility of the ecosystem, and prevent reinvasion or encroachment by other noxious weed species.

DiVittorio, C.T., J.D. Corbin and C.M. D'Antonio. 2004. Patterns of seed rain and seed banks of native and exotic species. In: Proceedings, Ecology and Management of California Grasslands, April 2-3, 2004, Berkeley, CA. Available online at: <http://cbc.berkeley.edu/grass/Abstracts.htm>

This study quantifies the species composition of the seed rain and seed bank in a coastal California grassland. We sampled the seed rain and seed bank at Tom's Point Preserve (Marin County) in early April and late June, and classified species according to native/exotic, annual/perennial, and monocot/dicot. We also compared seedling recruitment into undisturbed and experimentally disturbed patches. Seed rain and seed banks were dominated largely by the suite of species found in the local ambient community, suggesting short (<10m) dispersal distances. Native species regenerated on disturbed habitat and dominated the seed rain where native species were the dominant ambient vegetation. However, in mixed communities copious exotic annual seed input ($\leq 30\,000$ seeds/m²) overwhelmed native seed input ($\leq 1\,600$ seeds/m²) leading to exotic dominance. This suggests that native species are poor at competing as seedlings when seed input is heavily asymmetrical. Late season seed rain had a greater proportion of perennial species and native species as compared to early seed rain. Late season disturbances demonstrated a similar pattern. Differences in the phenology of perennial versus annual species is believed to drive this pattern. Over 98% of the native species in the surrounding community were perennial, so managing for perennial species will help maintain native communities. Furthermore, restoration efforts should focus on allowing native species to self-regenerate while limiting exotic seed inputs.

Dukes, J.S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecological Applications* 12: 602-617.

In a microcosm experiment, I tested how species composition, species richness, and community age affect the susceptibility of grassland communities to invasion by a noxious weed (*Centaurea solstitialis*). I also examined how these factors influenced *Centaurea*'s impact on the rest of the plant community. When grown in monoculture, eight species found in California's grasslands differed widely in their ability to suppress *Centaurea* growth. The most effective competitor in monoculture was *Hemizonia congesta* ssp. *luzulifolia*, which, like *Centaurea*, is a summer-active annual forb. On average, *Centaurea* growth decreased as the species richness of communities increased. However, no polyculture suppressed *Centaurea* growth more than the monoculture of *Hemizonia*. *Centaurea* generally made up a smaller proportion of community biomass in newly created ("new") microcosms than in older ("established") microcosms, largely because *Centaurea*'s competitors were more productive in the new treatment. Measures of complementarity suggest that *Centaurea* partitioned resources with annual grasses in the new microcosms. This resource partitioning may help to explain *Centaurea*'s great success in western North American grasslands. *Centaurea* strongly suppressed growth of some species but hardly affected others. Annual grasses were the least affected species in the new monocultures, and perennial grasses were among the least affected species in the established monocultures. In the new microcosms, *Centaurea*'s suppression of competing species marginally abated with increasing species richness. This trend was a consequence of the declining success of *Centaurea* in species-rich communities, rather than a change in the vulnerability of these communities to suppression by a given amount of the invader. The impact of the invader was not related to species richness in the established microcosms. The results of this study suggest that, at the neighborhood level, diversity can limit invasibility and may reduce the impact of an invader.

Dudley, T. and M. Embury. 1995. Non-indigenous species in wilderness areas: the status and impacts of livestock and game species in designated wilderness in California. Oakland, CA: Pacific Institute for Studies in Development, Environment and Security. 38 p.

Although this study focuses primarily on the status and impacts of introduced animals (livestock and game species), rather than plants, it highlights several controversies surrounding wilderness management that relate directly to problems with invasive exotic plants. First, livestock grazing may facilitate exotic plant invasions by disturbing and eroding soils, particularly in invasion-prone streamside areas. Second, few wilderness areas have systematic ecological monitoring programs, so the actual distribution, abundance, and impacts of introduced plants in most California wilderness areas remains unknown. Third, many wilderness managers express concerns over the impacts of recreational pack stock because of their potential to disturb soil and transport invasive plant seeds.

Eliason, S.A., and E.B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology* 5:245-255.

No abstract or summary available.

Enloe, S.F., J.M. DiTomaso, S.B. Orloff and D.J. Drake. Soil water dynamics differ among rangeland plant communities dominated by yellow starthistle (*Centaurea solstitialis*), annual grasses, or perennial grasses. *Weed Science* 52 (6): 929–935.

California's interior grasslands have undergone dramatic changes during the last two centuries. Changes in land-use patterns and plant introductions after European contact and settlement resulted in the conversion of perennial-dominated grasslands to exotic annual grasses. More recently, the annual grasslands have been heavily invaded by the deeply rooted late-maturing forb yellow starthistle. This series of invasions and conversions has changed the community structure and phenology of the grasslands. We hypothesized that these changes have resulted in significant differences in soil water–use patterns in the grasslands. We studied soil water depletion and recharge patterns of three grassland community types dominated by perennial grasses, annual grasses, or yellow starthistle with contrasting phenology and rooting depths for 4 yr. Soil moisture measurements were taken every month from March to December in 1998, 1999, and 2000 and every other month in 2001. Measurements were taken with a neutron probe at depths of 30 to 150 cm at 30-cm intervals. The results indicate that the yellow starthistle community maintained a significantly drier soil profile than the annual grass community. The perennial grass community maintained an intermediate soil water content that was not significantly different from either of the other two communities. Significant time by community and depth by community interactions indicated that the yellow starthistle community continued depleting soil moisture later into the season and at deeper depths than the other grass communities. This study demonstrates the effect of plant invasion on soil water recharge and depletion patterns in California grasslands.

Evans, R.A. and J.A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. *Weed Science* 23: 354-357.

Seedling emergence and growth of downy brome (*Bromus tectorum*), medusahead (*Taeniatherum asperum*) and tumble mustard (*Sisymbrium altissimum*) were favored by seed burial, pitting of the soil surface, and soil movement. These conditions maintained temperatures and soil and atmospheric moisture in the range required for establishment.

Evans, R. A. and J. A. Young. 1970. Plant litter establishment of alien annual weed species in rangeland communities. *Weed Science* 18:697–703.

Plant litter that covers the soil surface acts a layer of mulch that moderates temperature and moisture, and creates favorable microsites for germination and establishment of annual weed species in rangeland communities of California. Accumulation of plant litter is an important factor influencing succession, and high levels of mulch tends to culminate in dominance of alien annuals, downy brome (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) in these communities.

Fehmi, J.S., K.J. Rice and E.A. Laca. 2004. Radial dispersion of neighbors and the small-scale competitive impact of two annual grasses on a native perennial grass. *Restoration Ecology* 12(1): 63-69.

In California's Mediterranean type grasslands, native perennial grasses such as *Nassella pulchra* are surrounded by introduced annual species and these annuals are thought to have displaced natives through much of their range. Amongst other invaders, two grasses *Lolium multiflorum* and *Bromus hordeaceus*, commonly dominate portions of the grassland with potential for *N. pulchra* restoration. We hypothesized that competitor species differences and small-scale gaps (150 cm²) could be important determinants of *N. pulchra* survival and performance on these sites. *Lolium multiflorum* and *B. hordeaceus* were planted in 20 cm diameter circular plots at a constant rate of 1 seed per cm²

surrounding newly transplanted *N. pulchra* plants. *Nassella pulchra* showed no significant effect of the species of competitor or from the distribution of the competitors. Both interspersed patches of bare ground and separation of competitors into patches did not increase *N. pulchra* pre-dawn water potential, basal area change, number of seeds produced, or average weight of seeds. The presence of *L. multiflorum* was associated with a decrease in *N. pulchra* survival compared with plots with only *B. hordeaceus*. Plants with increases in basal area of less than 0.75 cm² during the growing season had 74% mortality compared with no mortality in plants with more growth. However, initial *N. pulchra* plant size was not a good predictor of mortality. Limiting competition from annuals may increase survival of *N. pulchra* plantings, but 60% of the plants survived for at least 1 year, despite being transplanted into soil containing substantial annual grass seed.

Fox, M.D. 1990. Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. Pages 179–200 in: F. di Castri, A.J. Hansen, and M. Debussche, editors. *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, Netherlands.

The five regions of the world sharing a climate like that of the Mediterranean Basin have exchanged, and continue to exchange, weedy plant species. This exchange is seen to be of two forms: an earlier primary invasion of the other four regions by aggressive annual weeds from the Mediterranean Basin, and a later secondary invasion by woody species, often between the four regions and from them back to the Mediterranean. Of the woody invaders two interesting groups are the conifers and the succulents. There is also a tertiary invasion within each of the Mediterranean regions of native species that have become more invasive as a result of human disturbance. The five regions are seen to comprise three groups. The pivotal ‘crossroads’ of the Mediterranean Basin itself, the other more recent group of Chile and California, and the older group of South Africa and southern Australia. As well as sharing important evolutionary and biogeographic traits, the two subsidiary groups are seen as sharing important patterns of settlement and subsequent trade. California and Chile, as well as having other strong links with the Mediterranean, were discovered and first settled by people from the Mediterranean Basin and this early contact must have dictated the rate and extent of invasions. The two older, southern regions, Australia and South Africa, on the other hand, were settled by people from northern Europe and only latterly had direct trade links with Mediterranean countries. The prognosis for the future of invasions in the Mediterranean regions is for a reduction in agrestal weeds but an increase in community weeds, particularly woody secondary invasions.

Frost, R.A. and K.L. Launchbaugh. 2003. Prescription grazing for wildland weed management: A new look at an old tool to control weeds on rangelands. *Rangelands* 25:43-47

Over the past decade there has been increased interest in the use of livestock grazing to reduce the biomass of introduced species and increase the diversity and abundance of native species in grassland settings. Grazing may benefit native vegetation by disproportionately targeting exotic biomass, thereby reducing the exotics’ competitive advantages; by reducing exotic seed production; or both.

Gelbard, J.L. and S. Harrison. 2005. Invasibility of roadless grasslands: An experimental study of yellow starthistle *Ecological Applications* 15(5): 1570-1580.

Roadless habitats are commonly found to be less invaded than habitats near roads, but few studies have tested whether this pattern is due to propagule limitation or to greater invasion resistance of roadless sites. We examined reasons for the lower frequency and cover of yellow starthistle (*Centaurea solstitialis*) in grassland sites .1000 m vs. 10 m from roads in an inland California, USA, foothill landscape. During winter 2001 and 2002, we planted 100 *Centaurea* seeds in 64 pairs of 30 x 30 cm plots (uncleared and cleared of aboveground plant material) at sites stratified by distance from roads (10 m and .1000 m), soil type (non-serpentine and serpentine), and aspect (cool, warm, and neutral slopes). In non-serpentine grasslands, *Centaurea* survival was greater in uncleared (but not cleared) near (10 m) plots than in distant (.1000 m) plots. These findings suggest that the effect of distance from roads on survival corresponds with higher above-ground biotic resistance in distant sites than in near sites. *Centaurea* biomass was greater in near than in distant plots (both uncleared and cleared) on non-serpentine soil, suggesting that either abiotic resistance or below-ground biotic resistance could limit its growth in distant sites. These distance effects were no longer significant in models that included two biotic covariates: native grass cover (which was higher in distant sites and negatively correlated with *Centaurea* performance) and bare ground (which was lower in distant sites and positively correlated with *Centaurea* performance). Our results suggest that *Centaurea* seeds can germinate in non-serpentine and serpentine grasslands regardless of distance from roads. Beyond the seedling stage, however, biotic resistance

associated with higher nativegrass cover and lower levels of disturbance may inhibit *Centaurea* invasion of non-serpentine grassland sites that are distant from roads.

Gelbard, J.L. 2003. Understanding the distribution of native versus exotic plant diversity in California's grassland landscapes. Ph.D. Dissertation. University of California, Davis, CA.

The invasion of California's grasslands by exotic plants has been so extensive that the questions of where remnant native-dominated grasslands are located and why have been termed an ecological murder mystery. I examined the effects of distance from roads and its interactions with soil type (non-serpentine and serpentine), aspect (cool, warm, and neutral slopes), and land use (presence and absence of livestock grazing), on native and exotic plant diversity in an inland California grassland landscape. I found that patterns of native persistence and exotic invasion differed depending on plant life form and interactions among predictors. Non-serpentine grasslands > 1000-m from roads (distant) had more native grass species and fewer exotic forb species than grasslands 10-m from roads (near). In serpentine grasslands, there was no effect of distance from roads. Similarly, remote grassland islands (grassland patches \leq 2 ha, isolated within chaparral or woodlands) contained greater native grass cover than grasslands > 10 ha and contiguous with roads and other grasslands. I conducted a field experiment to test whether the effect of distance from roads was due to resistance or propagule limitation at distant sites. I planted 100 *Centaurea* seeds in 64 pairs of plots uncleared and cleared of above-ground plant material at all near and distant sites from the first study. On non-serpentine soils, *Centaurea*'s seedling survival was greater in uncleared (but not cleared) 10-m than > 1000-m plots. These results suggest that beyond the seedling stage, biotic resistance inhibits *Centaurea* invasion of non-serpentine grasslands at sites distant from roads more than at sites near roads. Finally, I used classification-tree analysis to ask whether distance from roads, soil, aspect, and land use can predict locations of hot spots of native plant diversity, as well as the presence of 3 exotic species. Classification-tree models correctly predicted characteristics of sites containing high native perennial grass and native annual richness in 83% and 63% of sites that contained those characteristics. In addition, they correctly predicted characteristics of sites containing *Centaurea solstitialis*, *Aegilops triuncialis*, and *Taeniatherum caput-medusae* in 79%, 62%, and 83% of cases, respectively. By illustrating how combinations of natural and anthropogenic factors may interactively influence vegetation patterns, I propose that my approach can be used as a conceptual framework for understanding how to (1) locate and protect remnant native plant communities in invaded landscapes and (2) explain confounding exceptions to generalizations.

Gelbard, J.L. and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semi-arid landscape. *Conservation Biology* 17(2): 420–432.

Roads are believed to be a major contributing factor to the ongoing spread of exotic plants. We examined the effect of road improvement and environmental variables on exotic and native plant diversity in roadside verges and adjacent semiarid grassland, shrubland, and woodland communities of southern Utah (U.S.A.). We measured the cover of exotic and native species in roadside verges and both the richness and cover of exotic and native species in adjacent interior communities (50 m beyond the edge of the road cut) along 42 roads stratified by level of road improvement (paved, improved surface, graded, and four-wheel drive track). In roadside verges along paved roads, the cover of *Bromus tectorum* was three times as great (27%) as in verges along four-wheel-drive tracks (9%). The cover of five common exotic forb species tended to be lower in verges along four-wheel-drive tracks than in verges along more improved roads. The richness and cover of exotic species were both more than 50% greater, and the richness of native species was 30% lower, at interior sites adjacent to paved roads than at those adjacent to four-wheel-drive tracks. In addition, environmental variables relating to dominant vegetation, disturbance, and topography were significantly correlated with exotic and native species richness and cover. Improved roads can act as conduits for the invasion of adjacent ecosystems by converting natural habitats to those highly vulnerable to invasion. However, variation in dominant vegetation, soil moisture, nutrient levels, soil depth, disturbance, and topography may render interior communities differentially susceptible to invasions originating from roadside verges. Plant communities that are both physically invulnerable (e.g., characterized by deep or fertile soils) and disturbed appear most vulnerable. Decision-makers considering whether to build, improve, and maintain roads should take into account the potential spread of exotic plants.

Germano, D.J. et al. 2001. Managing exotic species and conserving declining species in California. *Wildlife Society Bulletin* 29(2): 551-559.

Exotic annual grasses have become the dominant vegetation in many habitats in California's San Joaquin Valley. The authors maintain that plants and animals native to the area are adapted to relatively open desert habitats, and the dense exotic grass cover is having a negative effect on their survival. They conclude that the best method to control exotic grasses is through the use of livestock. Although livestock overgrazing is often responsible for the initial invasion of

exotic plants, they say that discontinuing grazing rarely allows native vegetation to reestablish itself. If properly used, grazing can be used to reduce nonnative vegetation density, thereby allowing natives to gain a foothold. While the authors feel that grazing is the most important tool available to combat exotic grasses, they also list the potential problems with this approach and make it clear that this use of livestock must be closely managed, allowing for flexibility in the extent and intensity of grazing to respond to plant growth and climatic conditions.

Gordon, D.R., and K.J. Rice. 1992. Partitioning of space and water between two California annual grassland species. *American Journal of Botany* 79:967-976.

No abstract or summary available.

Harrod, R.J. 2001. The effect of invasive and noxious plants on land management in eastern Oregon and Washington. *Northwest Science* 75, special issue: 85-91.

A key issue for forest and rangeland health and productivity in eastern Oregon and Washington is invasive species. Although some exotic plant introductions were accidental, many were intentional for wildlife habitat improvement, ornamental purposes, wood or fiber production, soil conservation, livestock forage production, or other crop uses. Exotic species, or weeds, can be a significant component of environmental change because of their potential to alter primary productivity, decomposition, hydrology, nutrient cycling and natural disturbance regimes. At smaller scales, they alter the structure, composition and successional pathways of ecosystems. They lower diversity by out-competing native plants. Disturbance caused by forest restoration activities (e.g. thinning and prescribed fire) can promote weed spread, but ultimately will improve native plant diversity and productivity, improving ecosystem resistance to weed invasion. Restoration strategies need to include consideration of weed prevention and control and restoration of natives. Prevention includes restoring ecosystem processes; control includes biological, manual, mechanical, herbicidal, and prescribed burning methods; restoration involves returning native plants to a site. Monitoring is important to provide managers with information that will allow them to evaluate restoration activities and modify ineffective restoration approaches.

Hilken, T.O. and R.R. Miller. 1980. Medusahead (*Taeniatherum asperum*, Nevski): A review and annotated bibliography. Agriculture Experiment Station Bulletin 644, Oregon State University, Corvallis, OR.

Medusahead (*Taeniatherum asperum*, Nevski), a winter annual native in the Mediterranean region of Eurasia, has infested several million acres of rangeland in the northwestern United States. It has been estimated that carrying capacity for domestic livestock on infested ranges has been reduced 75 percent. The review is a condensed summarization of the literature pertaining to medusahead. Four tables contain the types and effectiveness of various controls applied to medusahead. The bibliography is a result of an extensive literature review on this species.

Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions. Pages 389-405 in: Drake, J.A., H.A. Mooney, F. Di Castri, R.H. Groves, F.J.. Kruger, M. Rejmanek, editors. *Biological Invasions: A Global Perspective*. John Wiley and Sons, Chinchester, UK.

The author outlines a simple experimental approach to the question of what determines the invasibility of natural plant communities. Using the example of a number of different communities in southwest Australia, the effect of soil disturbance and nutrient addition on invasion by introduced annual species is investigated. Soil disturbance enhanced establishment of introduced species, but their subsequent growth was greatly increased when soil disturbance was combined with nutrient addition. Other studies have found similar effects of nutrient addition alone. It appears that the attributes of the system in question determine the influence of disturbances on invasibility. What resources are limiting and the natural disturbance regime will determine which disturbances are likely to have the largest effect. A general truism might be that disturbance will enhance invasibility to the extent that it increases the availability of a limiting resource.

Hobbs, R.J. and S.E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9(4): 761-770.

Plant invasions are a serious threat to natural and managed ecosystems worldwide. The number of species involved and the extent of existing invasions renders the problem virtually intractable, and it is likely to worsen as more species are

introduced to new habitats and more existing invaders move into a phase of rapid spread. We contend that current research and management approaches are inadequate to tackle the problem. The current focus is mostly on the characteristics and control of individual invading species. Much can be gained, however, by considering other important components of the invasion problem. Patterns of weed spread indicate that many species have a long lag phase following introduction before they spread explosively. Early detection and treatment of invasions before explosive spread occurs will prevent many future problems. Similarly, a focus on the invaded ecosystem and its management, rather than on the invader, is likely to be more effective. Identification of the causal factors enhancing ecosystem invasibility should lead to more-effective integrated control programs. An assessment of the value of particular sites and their degree of disturbance would allow the setting of management priorities for protection and control. Socioeconomic factors frequently play a larger part than ecological factors in plant invasions. Changes in human activities in terms of plant introduction and use, land use, and timing of control measures are all required before the plant invasion problem can be tackled adequately. Dealing with plant invasions is an urgent task that will require difficult decisions about land use and management priorities. These decisions have to be made if we want to conserve biodiversity worldwide.

Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity and invasion: Implications for conservation. *Conservation Biology* 6(2): 324-337.

Disturbance, a critical element of natural ecosystems that helps maintain biotic diversity, may also promote invasions of nonnative plants by increasing the invasibility of communities. The authors discuss and provide examples of the types of disturbance important in maintaining plant species diversity and those that promote invasions. Focusing primarily on grasslands, they address fire, grazing, soil disturbances, nutrient inputs, trampling, fragmentation, and interactions among these types of disturbances. They conclude that it is often alterations to existing regimes and interactions between different disturbances that most often promote invasions. Natural disturbance regimes have now been disrupted in most areas of conservation concern, and fragmentation and anthropogenic changes have modified physical and biotic conditions. The authors therefore encourage managers to take an active role in implementing disturbance regimes that fit the landscape, the biotic community, and specific conservation goals.

Huenneke, L.F. 1996. Ecological impacts of invasive plants in natural resource areas. *Proceedings: Western Society of Weed Science*; 1996 March 11–14; Albuquerque, NM. Newark, CA: 49: 119–121.

This paper describes a number of ecological effects brought on by nonnative plant invasions, including the direct displacement of native plants, negative effects on wildlife, increased soil erosion, changes in soil chemistry and nutrient cycles, changes in hydrology and stream flow, and changes in disturbance regimes. The author emphasizes that the absence of disturbance is no guarantee against invasion, and that the early detection and control of invasive species is an important part of an invasive plant management strategy.

Jackson, L.E. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* 12:349-361.

Annual grasses from the Mediterranean Basin have become the dominant species in the extensive California grasslands, replacing native perennial and annual grasses. This study compared the ecology of Mediterranean annual grasses between California and their homeland to determine their preadaptation to conditions in California. In six regions of the Mediterranean Basin (southern France, western Spain, southeastern Spain, southern Tunisia, Crete and Israel), annual grasses now common in California are mainly ruderal species in early successional grasslands or in open degraded maquis. In none of these regions do they form stable annual grassland communities as in California. In the Mediterranean Basin, climatic factors associated with highest abundances of annual grasses are high rainfall in winter or long, dry summers, which are both found in California. Ruderal life history characteristics, combined with suitable climatic conditions, allowed the rapid spread of Mediterranean annual grasses during periods of overgrazing and drought in the last century, at the time of European settlement. Both alien and native perennial grasses have slower winter growth rates and lower reproductive outputs during their first year than annuals, and presumably they would have been reduced by the high densities of the introduced annuals.

Keeley, J.E. 2002. Plant diversity and invasives in blue oak (*Quercus douglasii*) savannas of the southern Sierra Nevada. Pp. 693-704 in: *Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape*. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-184. Berkeley, CA.

Blue oak savannas were found to be substantially more diverse at all scales from localized point diversity to the community scale, than higher elevation shrubland and coniferous forests in the southern Sierra Nevada. Also, alien plants were more diverse and represented a substantial fraction of the understory flora in these blue oak savannas, comprising three-fourths of the species at the smallest scale (1-m²) and about half at the largest scale (1,000-m²). Either alien invasion has greatly increases species diversity in these savannas or it has displaced native annuals as opposed to native bunchgrasses as is commonly proposed. Livestock grazing is thought to have played a decisive role in the initial invasion of the blue oak savanna understory. Today there are differences evident between livestock grazed and ungrazed sites and between horse and cattle grazed sites. Grazed sites have slightly higher species richness and higher alien species richness and cover than ungrazed sites. The differences, however, are rather subtle and despite over a century of protection from livestock grazing, ungrazed sites are remarkably similar to sites with a continuing history of grazing. Hypotheses that may explain the persistence of the alien flora in these long ungrazed blue oak savannas are: 1) the native flora that formerly made up the understory has been so severely decimated in the region that dispersal is a major limitation to reestablishment, 2) these savannas are an anthropogenic artifact due to accelerated fire history that has converted a closed canopy woodland/shrubland into a savanna, and thus elimination of the alien flora requires return to the closed canopy condition, and 3) due to Holocene climatic changes, the more arid adapted alien annual grasses, through preadaptation, are better adapted to these sites and consistently outcompete the native flora. These are testable hypotheses that await further experimentation.

Kimball, K. and P. M. Schiffman. 2003. Differing effects of cattle grazing in native and alien plants. *Conservation Biology* 17(6): 1681-1693.

Habitat managers use cattle grazing to reduce alien plant cover and promote native species in California grasslands and elsewhere in the western United States. We tested the effectiveness of grazing as a restoration method by examining the effects of herbivory on native and alien plants. At Carrizo Plain National Monument, California, we surveyed native and alien species cover in adjacent grazed and ungrazed areas. We also established experimental plots in which plants were clipped or mulch (dead biomass) was removed. In addition, we clipped plants grown in pots and plants in the field that grew with and without competitors. Native species were negatively affected by clipping in 1999, 2000, and 2001, whereas alien species were unaffected. In the experimental field plots, the European annual forb *Erodium cicutarium* compensated in growth and reproduction following simulated herbivory. In contrast, growth and reproduction of the native perennial bunchgrass *Poa secunda* were reduced 1 year after clipping. In pots, *E. cicutarium* overcompensated and grasses undercompensated. In the field, European grasses were unaffected by the removal of competitors. It is unclear by what mechanism *E. cicutarium* was able to compensate, but the ability may be related to its basal rosette growth form and indeterminately growing inflorescences. The native California grassland community assembled in the absence of grazing herds, whereas invasive European species have been exposed to grazing for centuries. It may be that these invaders have adaptations that better enable them to recover from grazing. In the grassland we studied, the strategy of livestock grazing for restoration is counterproductive. It harms native species and promotes alien plant growth.

Knops, J.M.H., J.R. Griffin and A.C. Royalty. 1995. Introduced and native plants of the Hastings Reservation, central coastal California: a comparison. *Biological Conservation* 71(2): 115-123.

Introduced plant species at the Hastings Reservation comprise 17% of the total flora, and are predominantly annual herbs and grasses. No introduced species are present in chaparral, coastal sage or rock outcrops and very few (4% of the total species number) in the mixed evergreen woodland. The highest percentage of introduced species is found in disturbed areas (40%), such as roadsides and around buildings. Introduced species have successfully invaded native grasslands (22%), oak foothill woodland (15%) and riparian areas (15%). In these vegetation types, introduced plants form an integral part, and in grasslands and the understory of oak foothill woodland, annual introduced grasses are the dominant species. The only difference found between established and recorded, but not-established, is that the latter is more recorded in disturbed areas. This reinforces anecdotal evidence that humans are the main cause of, intentional or accidental, dispersal into this reservation and that the most likely habitats of first establishment are the disturbed areas around houses and roads. Not all introduced species are capable of establishing a foothold in these disturbed areas and an even smaller portion is capable of intruding into grassland and oak foothill woodland. Both these vegetation types are characterized by high natural disturbance, mainly caused by pocket gophers. Vegetation types with less frequent disturbance, such as chaparral, coastal sage and mixed evergreen oak woodlands are not, or much less, invulnerable. Finally, most of the introduced species trace their origin to a similar Mediterranean climate in Europe.

Kolb, A., Alpert, P., Enters, D. & Holzapfel, C. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* 90(5): 871-881.

Relatively few studies have looked for patterns of invasion by non-native species within communities. We tested the hypotheses that: (i) some types of microhabitats within a community are more invasible than others; (ii) microhabitat types that differ in invasion also differ in resource availability; and (iii) invasibility is mediated by effects of these resources on competition between native and non-native species. To test the first two hypotheses, we measured plant cover and soils in a coastal grassland in northern California. Consistent with these hypotheses, cover of non-native plants was consistently high where nitrogen-fixing shrubs had recently grown, in the bottoms and sides of gullies and on deep soils, and these microhabitats tended to have relatively high nitrogen or water availability. Cover and number of native species tended to be lower where cover of non-native species was higher, indicating that non-native species as a group negatively affected native species. However, the number of non-native species also tended to be lower where the total cover of non-natives was higher. This suggests that a few non-native species excluded natives and other non-natives alike. To test the third hypothesis, we grew a common non-native, the annual grass *Lolium multiflorum*, and a common native, the perennial grass *Hordeum brachyantherum*, at different levels of water and nitrogen. The relative competitive ability of the native was higher at lower nitrogen availability but not at lower water availability. When 10-week-old native plants were grown with non-native seedlings and nitrogen was relatively low, the native out-competed the non-native. However, the non-native out-competed the native at all resource levels when species were both grown as seedlings. Competition between native and non-native grasses in this system may thus help prevent invasion by non-natives in microhabitats where nitrogen availability is low, but invasion may be relatively irreversible.

Kotanen, P.M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. *Journal of Applied Ecology* 34: 631-644.

Disturbance is widely believed to facilitate invasions by exotic plants, but is also important for the persistence of many native species. Here, I report the results of a series of field experiments designed to investigate the effects of soil disturbance on natives and aliens in California grassland vegetation. I also compare the effects of different types of soil disturbance to establish whether some favor aliens to a greater degree than others. In two experiments, conducted at different locations, three types of soil disturbance (excavation, burial and simulated gopher mounds) were created, and their revegetation was compared with changes in undisturbed control plots over the next three years. A third experiment was used to provide data on the effects of soil disturbance on soil temperature, moisture and KCl-extractable nitrogen. Disturbance affected both soil temperature and chemistry. Buried plots contained the most KCl-extractable nitrogen, and were also the warmest. Effects on soil moisture were relatively small. Initially, most disturbances greatly reduced the numerical abundance both of groups dominated by natives (perennial graminoids and bulbs) and of groups dominated by aliens (annual graminoids). Disturbance also reduced maximal (summer) species richness, but in some cases increased the fraction of richness contributed by natives. In subsequent years, richness rebounded as natives and exotics re-invaded. Native bulbs and perennial graminoids were slow to recover; instead, most disturbances increasingly became dominated by exotic annual grasses, accentuating the effects of a multi-year drought. The differing effects of experimental disturbances on aliens and natives can best be explained by considering relationships between sources of propagules, life histories and geographical origins. Some types of disturbance were less damaging to native-dominated groups than others, but most ultimately favored exotics. Consequently, it may be difficult to develop management strategies that preserve the diversity of disturbance-dependent natives while still excluding weedy aliens.

Kyser, G. B., and J. M. DiTomaso. 2002. Instability in a grassland community after the control of yellow starthistle (*Centaurea solstitialis*) with prescribed burning. *Weed Science* 50:648-657

An open grassland at Sugarloaf Ridge State Park, Sonoma County, CA, was burned during three consecutive summers (1993–1995) to control yellow starthistle. By 1996, the yellow starthistle seedbank, seedling density, and mature vegetative cover were reduced by 99, 99, and 91%, respectively, and the plant community had greater diversity and species richness, particularly of native forbs. After the cessation of the prescribed burning after 1995, the community was monitored for 4 yr to determine if the reduced yellow starthistle population represented a stable state or if the population would quickly recover. The yellow starthistle seedbank rose dramatically over 4 yr. Seedling counts and summer vegetative cover also rose, though less rapidly. Total forb cover, particularly native species, total plant cover, and plant diversity decreased significantly after cessation of the burning. Grass cover did not show any strong trends, and year-to-year variation in the grass cover appeared to be more important than the treatment effects. In the absence of some overall changes in management, e.g., periodic prescribed burning, herbicide treatments, or revegetation, it may not be possible to establish and maintain a stable state with a low population of yellow starthistle in annual grasslands in California.

Lacey, J.R. 1987. The influence of livestock grazing on weed establishment and spread. *Proceedings of the Montana Academy of Science* 47: 131-146.

Weeds are a serious problem on western rangelands. In Montana, nine introduced weeds infest nearly one-eighth of the state's range and grazeable woodland, and limit their usefulness. Range management strategies regarding weeds have evolved from the old and outdated adage that weeds are not a problem when range is in good or excellent ecological condition as described in the quantitative climax approach. It is now recognized that many exotic species are able to out-compete some native species in certain situations. More importantly, they have become a permanent part of the flora and are a factor that must be addressed in developing resource management plans. Livestock influence range vegetation through selective defoliation of preferred forage species and physical impact. They are also an important dispersal agent of weed disseminules. The significance of livestock trampling as a mechanism that "opens" a plant community to invasion should not be overlooked. Weeds tend to invade areas where forage is heavily utilized and in areas of livestock concentration. Livestock have been used as a management tool for the control of sagebrush, snowberry, plains prickly pear, Northwest cinquefoil, sticky geranium Russian thistle, dandelion, tall larkspur and leafy spurge. The potential of using livestock as a weed control technique is limited but merits additional research.

Lavorel, S.A. 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. *Diversity and Distributions* 5: 3-13.

In the Mediterranean region, plant communities are highly diverse with high total and local species richness, and a high spatial heterogeneity. They are also highly resilient to disturbance, which has been related to their evolutionary history of disturbance, and conceptually, although without formal proof, to their high ecological diversity. These ideas take on a new importance in the context of global change. In order to predict potential effects of future land use change, mechanisms underlying the resilience of ecosystems need to be understood. However, a review of the recent literature shows that confusion abounds as to the nature and measurement of resilience. In this paper we present a brief conceptual and methodological clarification and propose avenues for the analysis of mechanisms underlying the relationships between diversity and resilience, using Mediterranean ecosystems as an example. In Mediterranean ecosystems, rapid recovery from fire, soil disturbance and grazing has been attributed to two complementary causes. Firstly, disturbances often modify species relative abundances rather than composition, and recovery only involves the return to initial abundances. Secondly, life histories of dominant life forms in Mediterranean communities include efficient regeneration strategies that allow for recovery from dormant seeds or buds. In this paper, I use experimental results obtained in abandoned agricultural fields of southern France to investigate the mechanisms underlying the resilience of Mediterranean herbaceous communities to soil disturbance. These suggest that ecological diversity contributes to resilience in at least three ways. 1. Post-disturbance dynamics involve shifts in abundances of response groups to disturbance. 2. Within response groups, processes of lottery competition account for the dynamic maintenance of numerous species. 3. At the landscape scale, the fine grained distribution of communities at different successional stages allows for patch dynamics to operate with dispersal of species between patches. Further progress in the understanding of the relationships between ecological diversity and resilience of Mediterranean ecosystems can be achieved along two main avenues. Firstly, resilience of experimentally manipulated communities with differing levels of diversity needs to be assessed. Secondly, comparisons of those experiments across mediterranean-climate regions with different evolutionary disturbance histories need to be coordinated.

Lejune, K. D., and T. R. Seastedt. 2001. *Centaurea* species: the forb that won the West. *Conservation Biology* 15: 1568-1574.

Grasslands of the western United States and Canada are being converted to ecosystems that resemble "old fields," dominated in terms of percent cover or biomass by forb species. In particular, five species of the genus *Centaurea* (star thistle, diffuse, spotted, squarrose, and Russian knapweed) have invaded millions of hectares of western United States and Canadian grasslands. *Centaurea* species are fundamentally different from the preexisting dominant species and may exploit changes in resource availability to become established. We suspect that they then maintain dominance by preventing resources from returning to levels that favor the native species. Increased atmospheric nitrogen deposition, reduced fire frequency, and, possibly, direct and indirect fertilization resulting from cattle grazing appear to have reduced the historically strong nitrogen limitation to which native species of western grasslands are adapted. We suggest that the success of *Centaurea* species in dominating grasslands is explained by their ability to compete successfully for the new limiting resource or resources. Our preliminary evidence suggests that phosphorus limitation or a colimitation of phosphorus and water best explains the current dominance patterns.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London* 270:775-781.

Although the impacts of exotic plant invasions on community structure and ecosystem processes are well appreciated, the pathways or mechanisms that underlie these impacts are poorly understood. Better exploration of these processes is

essential to understanding why exotic plants impact only certain systems, and why only some invaders have large impacts. Here, we review over 150 studies to evaluate the mechanisms underlying the impacts of exotic plant invasions on plant and animal community structure, nutrient cycling, hydrology and fire regimes. We find that, while numerous studies have examined the impacts of invasions on plant diversity and composition, less than 5% test whether these effects arise through competition, allelopathy, alteration of ecosystem variables or other processes. Nonetheless, competition was often hypothesized, and nearly all studies competing native and alien plants against each other found strong competitive effects of exotic species. In contrast to studies of the impacts on plant community structure and higher trophic levels, research examining impacts on nitrogen cycling, hydrology and fire regimes is generally highly mechanistic, often motivated by specific invader traits. We encourage future studies that link impacts on community structure to ecosystem processes, and relate the controls over invasibility to the controls over impact.

Macdonald, I.A.W., Graber, D. M., DeBenedetti, S., Groves, R.H. and Fuentes, E.R. 1988. Introduced species in nature reserves in Mediterranean-type climate regions of the world. *Biological Conservation*. 44: 37–66.

Nature reserves in the Mediterranean-type climatic regions of the world are experiencing invasion by nonnative species. Overall, invasibility is greater in small reserves than large ones. Small reserves in urban areas are especially at risk of invasion by nonnative plants. The major invasions into Mediterranean-type reserves have been primarily by annual grasses from Europe and the Mediterranean basin. However, these reserves also appear to be especially susceptible to invasions by nonnative species from elsewhere on their own continents. Invasions in Mediterranean-type reserves altered fire regimes and reduced densities of the native biota. Because these types of reserves appear to be highly susceptible to invasions, the authors recommend that managers minimize the number of accidental introductions, avoid practices that alter fire regimes and herbivory under which the native biota have evolved, and prevent intentional introductions, even from areas on the same continent.

Mack, M., and C. M. D'Antonio. 1998. Impacts of biological invasion on disturbance regimes. *Trends in Ecology and Evolution* 13:195-198

The evidence clearly indicates that individual invasive species have altered ecosystems by changing disturbance regimes. Indeed, invasive species have changed disturbance regimes in both disrupted and intact systems. The authors focus on three common mechanisms by which this happens. Many invaders change the amount of physical disturbance, by enhancing or suppressing fire, or by increasing or decreasing soil disturbance. Other invaders (primarily animals) have themselves become disturbance agents. Finally, certain invading species act either to intensify or ameliorate the effects of disturbance on the system. Most of the studies reviewed demonstrated that altering disturbance regimes promotes invasive species and contributes to the demise of at least a portion of the native biota. In their conclusion, the authors caution that the continued movement of species around the globe by humans will only compound the negative effects of disturbance and invasions on ecosystems.

Mack, R.N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Pp. 155-179 in: Drake, J.A. et al., eds. *Biological Invasions: A Global Perspective*. John Wiley and Sons, Chichester, England.

The impact of invasive species has been especially severe in temperate grasslands. This article provides an excellent overview of factors promoting invasion in temperate grasslands worldwide, the history of such invasions, and current threats to these ecosystems. The author argues that those temperate grasslands most susceptible to invasion have tussock grasses that evolved in the absence of persistent grazing. These areas include the pampas of Argentina, the interior grasslands of Australia, California's Central Valley, and the U.S. Intermountain West. He then presents a historical perspective on plant invasions for each region. The accidental introduction of invasive plants via agriculture and ornamental horticulture as well as deliberate planting and seeding of potential invasive plants (for example, *Kochia* spp.) for aesthetic reasons or erosion control continue to threaten temperate grasslands. The deliberate release of genetically engineered hybrids (for example, *Agropyron* spp.) could also have unanticipated adverse effects and should be reconsidered.

Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710.

Biotic invaders are species that establish a new range in which they proliferate, spread, and persist to the detriment of the environment. They are the most important ecological outcomes from the unprecedented alterations in the

distribution of the earth's biota brought about largely through human transport and commerce. In a world without borders, few if any areas remain sheltered from these immigrations. The fate of immigrants is decidedly mixed. Few survive the hazards of chronic and stochastic forces, and only a small fraction become naturalized. In turn, some naturalized species do become invasive. There are several potential reasons why some immigrant species prosper: some escape from the constraints of their native predators or parasites; others are aided by human-caused disturbance that disrupts native communities. Ironically, many biotic invasions are apparently facilitated by cultivation and husbandry, unintentional actions that foster immigrant populations until they are self-perpetuating and uncontrollable. Whatever the cause, biotic invaders can in many cases inflict enormous environmental damage: (1) Animal invaders can cause extinctions of vulnerable native species through predation, grazing, competition, and habitat alteration. (2) Plant invaders can completely alter the fire regime, nutrient cycling, hydrology, and energy budgets in a native ecosystem and can greatly diminish the abundance or survival of native species. (3) In agriculture, the principal pests of temperate crops are non-indigenous, and the combined expenses of pest control and crop losses constitute an onerous "tax" on food, fiber, and forage production. (4) The global cost of virulent plant and animal diseases caused by parasites transported to new ranges and presented with susceptible new hosts is currently incalculable. Identifying future invaders and taking effective steps to prevent their dispersal and establishment constitutes an enormous challenge to both conservation and international commerce. Detection and management when exclusion fails have proved daunting for varied reasons: (1) Efforts to identify general attributes of future invaders have often been inconclusive. (2) Predicting susceptible locales for future invasions seems even more problematic, given the enormous differences in the rates of arrival among potential invaders. (3) Eradication of an established invader is rare, and control efforts vary enormously in their efficacy. Successful control, however, depends more on commitment and continuing diligence than on the efficacy of specific tools themselves. (4) Control of biotic invasions is most effective when it employs a long-term, ecosystem-wide strategy rather than a tactical approach focused on battling individual invaders. (5) Prevention of invasions is much less costly than post-entry control. Revamping national and international quarantine laws by adopting a "guilty until proven innocent" approach would be a productive first step. Failure to address the issue of biotic invasions could effectively result in severe global consequences, including wholesale loss of agricultural, forestry, and fishery resources in some regions, disruption of the ecological processes that supply natural services on which human enterprise depends, and the creation of homogeneous, impoverished ecosystems composed of cosmopolitan species. Given their current scale, biotic invasions have taken their place alongside human-driven atmospheric and oceanic alterations as major agents of global change. Left unchecked, they will influence these other forces in profound but still unpredictable ways.

Masters, R.A., and R.L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. *Journal of Range Management* 54:502-517.

Invasive plants reduce the capacity of ecosystems to provide goods and services required by society, alter ecological processes, and can displace desirable species. They can reduce wildlife habitat quality, riparian area integrity, rangeland economic value, and enterprise net returns. The invasion process is regulated by characteristics of the invading plant and the community being invaded. The presence and spread of invasive plants is often symptomatic of underlying management problems that must be corrected before acceptable, long-term rangeland improvement can be achieved. Disturbance appears to be important early in the invasion process because it creates vacant niches that alien plants can occupy. Control of invasive plants may only open niches for establishment of other undesirable plants unless desirable plants are present to fill the vacated niches. In many instances, rangelands have deteriorated to the point that desirable species are either not present, or in such low abundance that plant community recovery is slow or will not occur without revegetation after invasive plants are controlled. Integrated weed management employs the planned, sequential use of multiple tactics (e.g. chemical, biological, cultural, and mechanical control measures) to improve ecosystem function (energy flow and nutrient cycling) and maintain invasive plant damage below economic levels, and emphasizes managing rangeland ecosystem functions to meet objectives rather than emphasizing a particular weed or control method. Sustainable, integrated invasive plant management strategies require assessing plant impacts, understanding and managing the processes influencing invasion, knowledge of invasive plant biology and ecology, and are based on ecological principles. Invasive plant management programs must be compatible with and integrated into overall rangeland resource management objectives and plans. Because of the complexity of managing invasive plants, it is imperative that relevant ecological and economic information be synthesized into user-friendly decision support systems.

Mooney, H.A., S.P. Hamburg, and J.A. Drake. 1986. The invasions of plants and animals into California. Pages 250–272 in H.A. Mooney and J.A. Drake (eds.). *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York, NY.

The flora and fauna of California have undergone substantial changes resulting from the establishment and spread of non-native species. Many non-natives have become firmly established, often at the expense of native species. Some habitats such as grasslands and coastal strand and dune communities have been particularly susceptible to invasion and

subsequent modification of community structure. Other habitats, such as chaparral and some forest ecosystems, have been invaded but with minimal impact on community structure. Such differences in susceptibility appear to be linked to the extent of anthropogenic disturbance. In California, human activity has greatly increased invasion success by creating ecologically “open” habitats. Unfortunately the type and extent of disturbance that increases the vulnerability of an ecosystem to invasion is still unknown. The effects of various types of invaders on the ecosystems they invade is highly variable. Plants in particular have been successful in displacing native species.

Olson, B.E. 1999. Grazing and weeds. Pp. 85-96 in: Sheley, R.L. and J.K. Petroff, eds. 1999. *Biology and Management of Noxious Rangeland Weeds*. Oregon State University Press, Corvallis, OR.

The author relates the spread of many weeds in North America to two major factors: inherent preferences of grazing and browsing ungulates, and plant community succession. In Western North America, native plant species are at a disadvantage in competing for water and nutrients because cattle, the dominant grazer in this system, selectively graze native grasses and have low impact on non-indigenous grasses and weeds. By persistently grazing on native grasses, while avoiding shrubs and forbs, cattle have caused many rangeland ecosystems to retrogress from a climax state of plant community succession. The author recommends restoring a balance to these disturbed systems through the introduction or reintroduction of small ruminants, such as sheep, that prefer non-indigenous forbs. Sheep grazing applies pressure to the forbs within a plant community resulting in succession toward a climax stage. The author states that within the framework of livestock grazing and weeds, different levels of weed infestation necessitate three management strategies: prevention, minimizing the spread of weeds, and controlling weed infestations. In this chapter the author suggests that management strategies address the causes, rather than the symptoms, of weed infestations. Proper grazing management can be used to minimize the spread of certain weeds and to control large weed infestations rather than using herbicides, which are not always cost-effective and which tend to address only the symptoms. Weed control techniques that incorporate the reintroduction of small ruminants to many Western systems, while properly managing large ungulates, will help restore balance to the ecosystem and will also begin to address the cause of the problem.

Osborn, S., V. Wright, B. Walker, A. Cilimburg and A. Perkins. 2002. Linking wilderness research and management – volume 4. Understanding and managing invasive plants in wilderness and other natural areas: an annotated reading list. USDA Forest Service Rocky Mountain Research Station Gen. Tech. Report RMRS-GTR-79 vol. 4. Fort Collins, CO.

Non-native invasive plants are altering ecosystems around the world with alarming speed. They outcompete native plants and ultimately change the composition and function of the ecosystems they invade. This poses a particular problem in wilderness and other natural areas that are set aside to maintain natural conditions. Wilderness managers are not only faced with the challenges of preventing and identifying new invasions, but they also must decide between allowing the unfettered existence and spread of invasive plants and using control strategies that can have unintended consequences. This reading list summarizes approximately 250 books and articles and 25 online resources that provide context for making these management decisions. The first major section examines issues specifically related to invasive plants in wilderness and other natural areas. The second section provides background information about invasive plant ecology, ranging from the factors that contribute to plant invasions to understanding the many effects invasive plants can have on species, communities, and ecosystems. The final section focuses on managing these species, including management planning, ways of preventing, predicting, and finding new invasions, and developing and prioritizing control and eradication strategies. While literature related to understanding and managing specific invasive plant species has been aggregated elsewhere, this document presents an organized framework of literature that addresses concepts pertinent to management.

Popay, I. and R. Field. 1996. Grazing animals as weed control agents. *Weed Technology* 10: 217-231.

Literature on the effectiveness of grazing animals (especially cattle, goats, and sheep) in controlling weeds is reviewed. Availability of animals and the ability to fence them onto or off weed infestations are essential. Weeds of pastures are the most suitable subjects for control, although weeds of arable crops, forestry, and waste places are sometimes amenable to control by grazing animals. Although grazing animals themselves often cause weed problems in pasture, adjusting grazing timing or intensity or both can sometimes redress the balance. Increasing sheep or cattle stocking rates prevents animals from grazing selectively and can help control some weeds. Adjusting grazing pressure can also improve the growth of desirable pasture species so that these are more competitive and able to resist invasion of annual

or biennial weeds. Introducing a different class of stock, like sheep into a cattle system or goats into a sheep system can control many weeds. Goats are capable of browsing on and controlling spiny or poisonous brush weeds, including gorse and poison ivy, without suffering adverse effects. Examples are given of the use of grazing animals for weed control in crops and forestry.

Randall, John M. 2000. Improving management of non-native invasive plants in wilderness and other natural areas. Pp. 64-73 in: D. Cole et al., eds. Wilderness science in a time of change conference—Volume 5: Wilderness ecosystems, threats, and management; 1999 May 23–27; Missoula, MT. USDA Forest Service, Rocky Mountain Research Station RMRS-P-15-VOL-5. Ogden, UT.

This article provides an excellent overview of recent research findings and future research directions in invasive plant ecology. The author first emphasizes that invasive weeds are the second most important threat to biological diversity in the world. He then reviews the causes, consequences, mechanisms, and ecological impacts of such invasions and examines the status of control and restoration efforts. Studies that quantify the positive and negative ecological impacts of control efforts are needed. In addition, managers need to make informed decisions about which invasives to prioritize for control and to use adaptive management strategies. Randall emphasizes the need for improved methods for preventing invasions, mapping, monitoring, and controlling invasive plants, and additional research on the ecological role of introduced plants in native ecosystems.

Randall, John M. 1996. Weed control for the preservation of biological diversity. *Weed Technology* 10(2): 370–383.

Invasive nonnative species pose a magnanimous threat to the world's ecosystems and communities, but terms associated with this phenomenon are often confusing. Randall defines these terms, describes the ways in which exotic plants can displace native species and degrade biological communities (ecosystem effects, habitat dominance, hybridization with native species, promotion of nonnative animals), and discusses the extent of wildland weed problems in the United States. He also outlines a strategy that wildland managers can use to approach the control of exotic plants. In the end, Randall discusses a few of the unique problems associated with wildland weed control and poses a variety of related questions in the hopes of stimulating further research into wildland weeds.

Randall, J.M., and M. Rejmanek. 1993. Interference of bull thistle (*Cirsium vulgare*) with growth of ponderosa pine (*Pinus ponderosa*) seedlings in a forest plantation. *Canadian Journal of Forest Research* 23:1507–1513.

The biennial thistle *Cirsium vulgare* significantly reduced ponderosa pine (*Pinus ponderosa*) seedling growth during the second year of infestation but had insignificant effects in the first year when all thistles were in the rosette stage. Pine stem diameter relative growth rate was significantly negatively correlated with four different indices of thistle interference and with visual estimates of thistle cover. Total thistle density (adults + rosettes) within 2.0 m of target seedlings best explained differences in stem relative growth rate, but density of adults alone and visual estimates of thistle cover were nearly as good. Simple regressions indicated that soil moisture and pine predawn leaf water potential were significantly negatively correlated with thistle density and significantly positively correlated with stem relative growth rate, but multiple regressions and path analyses indicated that their effects on seedling growth were negligible relative to the other (unexplained) effects of thistle density. Foliar nitrogen, phosphorus, and potassium concentrations were not significantly correlated with thistle density and failed to explain differences in seedling growth. Although it remains unclear how thistles suppressed pine seedling growth, if these results hold true at other sites, plantation managers will have at their disposal relatively easy methods for assessing thistle interference.

Reynolds, S. A., J. D. Corbin, and C. M. D'Antonio. 2001. The effects of litter and temperature on the germination of native and exotic grasses in a coastal California grassland. *Madrono* 48:230–235.

Through their effects on seed germination, accumulation of plant litter and temperature may play a role in the invasion of coastal California grasslands by exotic annual and perennial grasses. Germination of native and exotic grasses was examined as a function of both litter cover and temperature. When species were grouped by life form (native perennial grass vs. exotic perennial grass), exotic species germinated at consistently higher rates than native species. Individual species, however, varied in their response to litter addition. While one exotic perennial species, *Festuca arundinacea*, maintained germination rates significantly higher than native species' across three levels of litter cover, the other exotic

perennial species, *Holcus lanatus*, showed no advantage over native species in the presence of a heavy litter layer. Exotic annual grasses had significantly higher germination rates than native perennial or exotic perennial grasses in laboratory growth chambers. Decreasing the average fall temperature in laboratory growth chambers by 5 degrees C significantly reduced the germination percentages of *Bromus diandrus* and *F. arundinacea* relative to other species. The remaining two exotic annual grasses, *Avena barbata* and *Vulpia myuros*, were consistently the first seeds to germinate. Grouping species according to life form masked germination responses of individual species that otherwise provide insight into the potential role of germination conditions in community composition of coastal grasslands in California.

Roche, B.F., C.T. Roche and R.C. Chapman. 1994. Impacts of grassland habitat on yellow star thistle (*Centaurea solstitialis*) invasion. *Northwest Science* 68: 86-96.

Yellow starthistle, a Mediterranean winter annual introduced in southeastern Washington around the turn of the century, expanded rapidly in foothills rangeland of the Blue Mountains in the early 1960s, invading and dominating bluebunch wheatgrass communities on deeper soils of south-facing slopes. Examination of site differences (soil depth and aspect) revealed a high correlation of yellow starthistle with stored soil moisture on south-facing slopes. Yellow starthistle roots grew rapidly and continuously during the winter giving it access to moisture stored deep in the soil profile not depleted by the native plant association. Yellow starthistle seedlings grown under reduced light produced shorter roots, larger leaves, more erect rosettes, and fewer flowers than plants grown in full sunlight. Interaction of shade and moisture stress appeared to reduce yellow starthistle invasion of four species of perennial grass treated with four seasonal clipping regimes: May, July, October and no clipping. The two sod-forming cultivars, "Oahe" intermediate wheatgrass and "Luna" pubescent wheatgrass were generally less susceptible to starthistle invasion under all clipping regimes than the two bunchgrasses, "Nordan" crested wheatgrass and "Whitmar" bluebunch wheatgrass. Yellow starthistle invaded Whitmar bluebunch wheatgrass clipped any time of year. All four grass species resisted starthistle invasion if left unclipped. Two critical factors limiting starthistle invasion appeared to be light intensity at the soil surface during the winter and residual soil moisture during the summer.

Rosentreter, R. 1994. Displacement of rare plants by exotic grasses. Pp. 170-175 In Mosen, S.B. and S.G. Kitchen, eds. *Proceedings – ecology and management of annual rangelands*. USDA Forest Service Intermountain Research Station, Gen. Tech. Report INT-GTR-313.

No abstract or summary available.

Schiffman, P.M. 2000. Mammal burrowing, erratic rainfall and the annual lifestyle in the California prairie: is it time for a paradigm shift? Pages 153-160 in J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham, editors. *2nd Interface Between Ecology and Land Development in California*. U.S. Geological Survey, Open-File Report 00-62.

Schiffman, P.M. 1997. Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization. Pp. 87-94 in: J.O. Luken and J.W. Thieret, eds. *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, NY.

This paper focuses on the importance of animal-mediated dispersal and disturbance in non-native plant invasions. The author discusses ways in which animals contribute to both reproduction and dispersal in exotic plants. Although changes in natural disturbance regimes are almost invariably related to human activities, animals may also change the level or intensity of disturbance and thereby facilitate invasions. The author first provides examples of how indigenous and non-indigenous animals have altered disturbance regimes and facilitated plant invasions. Schiffman then discusses the complex interactions that can develop between native animals and non-native plants. According to the author, managers of natural areas should identify and evaluate all possible exotic plant seed dispersers and attempt to minimize human impacts that lead to greater dispersal by animals. Descriptive, comparative, and experimental studies of relationships between animals and exotic plants will be valuable for enabling managers to control established exotics.

Schwartz, M.W., D.J. Porter, J.M. Randall, and K.E. Lyons. 1996. Impact of non-indigenous plants. Pages 1203–1218 in *Sierra Nevada Ecosystem Project: final report to*

Congress. Volume II: assessments and scientific basis for management options. Centers for Water and Wildland Resources, University of California, Davis.

Non-indigenous species play a dominant role in the vegetation of many ecosystems that adjoin or overlap the Sierra Nevada. Many of these habitats, such as the valley and foothill grasslands, appear to be saturated with these species. In contrast, the high elevations of the Sierra are not as heavily impacted by non-indigenous species. In between these extremes is a gradient of impact that is heavily influenced by the amount and extent of human disturbance of natural ecosystems. The most heavily affected regions within the Sierra Nevada are the foothill grassland and oak savanna habitats, infested with a diversity of Mediterranean annual grasses as well as herbaceous dicots; the riparian zones, infested with woody plants; and the eastern slope, which is strongly dominated by cheat grass. Infestation at middle elevations is most closely linked to disturbances such as clearcuts and roadsides. Non-native species such as cheat grass, yellow star thistle and Scotch broom affect ecosystem attributes such as grazing potential, forest regeneration, and water availability along stream courses. At the present time there are few restrictions on the importation of species that may, in the future, pose additional threats to the integrity and utility of the Sierra Nevada.

Sheley, R.L., M. Manoukian and G. Marks. 1999. Preventing noxious weed invasion. Pp. 69-72 in: Sheley, R.L. and J.K. Petroff, eds. 1999. ***Biology and Management of Noxious Rangeland Weeds***. Oregon State University Press, Corvallis, OR.

This chapter outlines and discusses strategies for preventing the spread of noxious weeds. An effective prevention program typically depends on a combination of methods that limit weed spread. The authors discuss prevention measures such as limiting weed seed dispersal, containing neighboring weed infestations, minimizing soil disturbances, detecting and eradicating weed introductions early, establishing competitive grasses, and properly managing competitive grasses.

Sheley, R.L. and J.K. Petroff, eds. 1999. ***Biology and Management of Noxious Rangeland Weeds***. Oregon State University Press, Corvallis, OR.

Although the focus of this book is on Western rangelands, it contains a great deal of information useful and relevant to natural area managers. The book is divided into two sections. The first 11 chapters deal with the theory, concepts, and principles of rangeland weed management and are organized in the same way that one might develop a weed management plan. These chapters include information on the impacts of weeds, surveying, mapping, and monitoring weeds, coordinating weed management planning, evaluating costs and benefits, integrated management techniques, preventing invasions, and detecting and controlling small infestations. In addition, section I includes chapters on three management techniques — grazing, biological control, and chemical control — and one chapter on revegetation. The second section consists of 25 chapters describing 29 of the most serious noxious weed species in Western United States rangelands. Each of these chapters includes sections with information on invasive plant identification, origin and distribution, invasive potential, ecological and economic impacts, biology and ecology, and management options.

Sheley, R.L., B.E. Olson and L.L. Larson. 1997. Effect of weed seed rate and grass defoliation level on diffuse knapweed. *Journal of Range Management* 50(1): 39-43.

Diffuse knapweed (*Centaurea diffusa* Lam.), an invasive weed, has reduced forage production and biodiversity, and increased soil erosion on over a million hectares of rangeland in the western United States. This study evaluated the effects of a single grass defoliation on establishment of diffuse knapweed seeded at 2 rates into a bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith)/needle-and-thread (*Stipa comata* Trin. & Rupr.) community and a crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) community. Six defoliation levels (0, 20, 40, 60, 80, 100%) and 2 seeding rates (3,000, 6,000 diffuse knapweed seeds) were applied to 1 m² plots in a randomized-complete-block design (n=4). Diffuse knapweed was seeded in the fall of 1992, and grasses were defoliated on 28 April 1993. The number of flowering culms and weed seedlings were counted in September 1993. Densities of diffuse knapweed seedlings, juveniles, and adults, as well as plant standing crop, were determined in May 1994. Seed rate had minimal effect on diffuse knapweed density. By May 1994, densities of diffuse knapweed were about 20 and 30 plants m⁻² on undefoliated bluebunch wheatgrass and crested wheatgrass plots, respectively, indicating that defoliation is not required for this noxious weed to become established. Higher levels of grass defoliation (>60%), especially of bluebunch wheatgrass, enhanced diffuse knapweed establishment, indicating that moderate (<60%) defoliation would not necessarily accelerate invasion by diffuse knapweed.

Simberloff, Daniel; Von Holle, Betsy. 1999. Positive interactions of non-indigenous species: invasional meltdown? *Biological Invasions*. 1: 21–32.

The authors discuss the state-of-knowledge regarding interactions among non-indigenous species. They first review the concept of “environmental resistance,” the process in which competitive or predatory forces oppose a newly introduced non-indigenous species. This concept of resistance has dominated studies that seek to understand why some introduced species survive and spread while others do not. The authors then describe a different model of invasion, which they term “invasional meltdown.” This is a “...process by which a group of non-indigenous species facilitate one another’s invasion in various ways, increasing the likelihood of survival and/or of ecological impact and possibly the magnitude of impact.” The authors reviewed current literature to determine the frequency of the invasion meltdown process and to document examples. They present preliminary evidence that such a process is not uncommon, but they were unable to determine its frequency. A prevalent type of facilitative interaction appears to be that of plants modifying the habitat in such a way that other introduced species are favored over native species. The authors identified the quantification of population-level impacts of non-indigenous species on one another and on native species as an urgent research need.

Stohlgren, T.J. et al. 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. *Biological Invasions* 3: 37-50.

Land managers require landscape-scale information on where exotic plant species have successfully established, to better guide research, control, and restoration efforts. We evaluated the vulnerability of various habitats to invasion by exotic plant species in a 100,000 ha area in the southeast corner of Grand Staircase-Escalante National Monument, Utah. For the 97 0.1-ha plots in 11 vegetation types, exotic species richness (\log_{10}) was strongly negatively correlated to the cover of cryptobiotic soil crusts ($r = -0.47, P < 0.001$), and positively correlated to native species richness ($r = 0.22, P < 0.03$), native species cover ($r = 0.23, P < 0.05$), and total nitrogen in the soil ($r = 0.40, P < 0.001$). Exotic species cover was strongly positively correlated to exotic species richness ($r = 0.68, P < 0.001$). Only 6 of 97 plots did not contain at least one exotic species. Exotic species richness was particularly high in locally rare, mesic vegetation types and nitrogen rich soils. Dry, upland plots ($n = 51$) had less than half of the exotic species richness and cover compared to plots ($n = 45$) in washes and lowland depressions that collect water intermittently. Plots dominated by trees had significantly greater native and exotic species richness compared to plots dominated by shrubs. For the 97 plots combined, 33% of the variance in exotic species richness could be explained by a positive relationship with total plant cover, and negative relationships with the cover of cryptobiotic crusts and bare ground. There are several reasons for concern: (1) Exotic plant species are invading hot spots of native plant diversity and rare/unique habitats. (2) The foliar cover of exotic species was greatest in habitats that had been invaded by several exotic species. (3) Continued disturbance of fragile cryptobiotic crusts by livestock, people, and vehicles may facilitate the further invasion of exotic plant species.

Stohlgren, T.J. et al. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9(1): 45-64.

Several aspects of plant communities play a role in determining patterns of species richness. Consequently, the authors compared the effects of grazing, soil characteristics, and climate at multiple spatial scales in grazed and ungrazed sites. At the landscape scale (1,000-m² plots), there were not significant differences in native species richness or the numbers of native and exotic species between grazed and ungrazed sites. The authors develop five broad generalizations concerning current levels of grazing in Rocky Mountain grasslands: (1) grazing appears to have little effect on native species richness at the landscape scale (greater than 1,000 m); (2) grazing probably does not contribute to the accelerated spread of most nonnative plants at landscape scales; (3) grazing does affect local plant species, life-form composition and cover, but considerable spatial variation exists; (4) soil characteristics, climate, and disturbances appear to have a greater effect on plant species diversity than do current grazing levels; and (5) few plant species show consistent, directional responses to either grazing or the termination of grazing. Although grazing did not appear to facilitate the spread of exotics on a landscape scale in this study, the authors caution that grazing may nonetheless lead to the replacement of native species by exotic species at the local scale. Biomes that evolved under different grazing pressures also may respond differently to grazing than do Rocky Mountain grasslands.

Thomsen C.D., Williams W.A., Vayssieres M., Bell F.L. and George M.R.. 1993. Controlled grazing on annual grassland decreases yellow starthistle. *California Agriculture* 47:36-40

This study examined the effect of cattle, sheep, and goat grazing on yellow starthistle (*Centaurea solstitialis*). Grazing in the bolting stage in late spring and early summer reduced the starthistle canopy, seed production, and thatch accumulation, and enhanced native plant diversity. Most starthistle plants were able to regrow and flower after an initial grazing, so close monitoring and regrazing before spines appeared on the plants were essential. Cattle, sheep, and

goats differed in their acceptance of starthistle. Repeated grazing during starthistle's most vulnerable growth period can effectively manage infestations, but additional control measures are needed to further reduce starthistle populations.

Tu, M., C. Hurd and J.M. Randall. 2001. *Weed Control Methods Handbook: Tools and Techniques for Use in Natural Areas*. Wildland Invasive Species Program, The Nature Conservancy. Available online at <http://tncweeds.ucdavis.edu/handbook.html>.

The handbook begins with a discussion of adaptive management and recommends a strategy for formulating weed control programs. The subsequent chapters describe specific control methods: manual and mechanical removal, grazing, prescribed fire, biological control, with detailed information on 10 herbicides that have been used in natural areas. The advantages and disadvantages of each method are discussed, sometimes in regard to specific species, and examples of successful and unsuccessful use of each method are included. Tools and techniques are also described and recommended. They also discuss the use of different methods in conjunction with each other. The handbook includes abundant information on herbicides, but the authors stress that all available control options should be considered when formulating a weed control program.

Tyler, C.M. and M. Borchert. 2003. Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae), in relation to fire. *Plant Ecology* 165(11):11-20.

Zigadenus fremontii is often a striking component of the flora following fire in the chaparral. Like other geophytes, it produces large numbers of flowers in the first spring after a burn. Although these plants are most conspicuous in the early postfire environment, the question that remains is, how do they persist in the interval between fires? To address this we investigated differences in the growth and reproduction of *Z. fremontii* in burned and unburned chaparral. We monitored marked individuals for nine years at three sites: two that were burned in 1990 and one in the same area that was in unburned mature chaparral. We measured leaf area, and production of flowers and fruits. We also conducted seed experiments in the field to determine the rates and timing of germination. We found that reproduction occurs only in the immediate postfire period: flowering and production of fruits and seeds in the first year following fire, and seedling establishment by year 3. There was a cost of reproduction; plants that flowered (in the burn area) had negative growth rates the following year. In contrast, plants in unburned chaparral, which did not flower, had positive growth rates over the same period. Moreover, plants that produced the most flowers had the lowest growth rates. In the unburned chaparral site, plants were not dormant as predicted from previous literature; instead they produced leaves nearly every year. In most years the average leaf area per plant was greater than that in the burned sites. Our results indicate that postfire reproduction depends on growth and carbohydrate storage in the inter-fire period. We also suggest that this species is relatively long-lived for a herbaceous perennial.

Vitousek, Peter M. 1986. Biological invasions and ecosystem properties: can species make a difference? In: Mooney, Harold A.; Drake, James A., eds. *Ecology of Biological Invasions of North America and Hawaii*. New York, NY: Springer-Verlag: 163–176.

A single introduced species could have dramatic effects on ecosystem structure and function, but what kinds of species are these and why are their effects so large? The significant effects of introduced species that add a new structural life form, such as floating aquatic weeds or *Tamarix* (in other words, salt-cedar, tamarisk) in the desert Southwest, are well documented. Other introduced species that have the potential to alter large-scale structure and processes are those that change soil properties (for example, nitrogen-fixing shrubs), disturbance regimes (for example, fire-prone annual grasses), primary productivity, or the intensity of herbivory, and those that have periods of growth different from natives, either seasonally or during the process of succession. Effects on ecosystems are most pronounced when invaders cause changes that reinforce the original divergence from pre-invasion conditions.

Vitousek, P.M. 1992. Effects of alien plants on ecosystems. Pp. 29-41 in: C.P. Stone et al., eds. *Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research*. Cooperative National Park Service Studies Unit, University of Hawaii Press, Honolulu, HI.

This overview paper describes how invasive plants can change ecosystem-level properties such as the large-scale functioning of ecosystems, community structure, and population dynamics. Through a number of examples, Vitousek offers evidence that the characteristics of individual invading species are important at the ecosystem level. He concentrates on cases where plants invade undisturbed native ecosystems or where they alter the successional course when invading disturbed areas. He specifically describes how different life forms can change ecosystems processes,

how plants can alter resource acquisition and use (for example, nitrogen fixation), and how invasive plants can interact with disturbance vectors (fire and animals).

Walker, L.R. and S.D. Smith. 1997. Impacts of invasive plants on community and ecosystem properties. Pp. 69-86 in: J.O. Luken and J.W. Thieret, editors. *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, NY.

The authors outline a community-level approach for assessing and managing impacts of nonnative plant invasions. Because invasive plants alter both community-level properties (in other words, primary productivity, species diversity, vegetation structure) and processes (in other words, disturbance regimes, succession patterns, nutrient cycles, hydrology), they argue that restoring native ecosystems involves understanding how such properties and processes have been altered by invasion. Five main topics are discussed: primary productivity, soil nutrients, ground water and salinity, disturbance regimes, and community dynamics. For each, the authors provide a conceptual background, recommend ways to measure change in the attribute due to invasion, and discuss management concerns. Case studies of the fayatree in Hawai'i and tamarisk in the Southwestern United States are used to illustrate changes in, and ways of restoring, the attributes that comprised biological communities prior to invasion.

Woods, K.D. 1997. Community response to plant invasion. Pp. 56-68 in: J.O. Luken and J.W. Thieret, eds. *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, NY.

The author reviews the effects of invasive species on relatively undisturbed communities in order to identify (1) characteristics of invasive species that lead to predictable levels and types of community change, (2) characteristics of communities that make them susceptible to invasion, and (3) differences in the community-level impacts of invasions with and without human-induced disturbance. After critically reviewing potential mechanisms and case studies, including those found in the paleoecological record, the author concludes that the effects of disturbance and invasion often cannot be separated. The kinds of invasive species most likely to dramatically change community structure or function are those that outcompete native species for light during critical life history stages, those with alternative morphologies and life history strategies, and those that utilize resources in a novel way. However, such invaders remain difficult, if not impossible, to identify before an invasion has occurred. Similarly, this research failed to identify any previously unreported characteristics of communities that distinguish them as being more prone to invasion than others. For now, carefully documenting the impacts of current invasions is probably the most effective way to successfully predict community-level effects of future invasions.

Young, S.L., J.M. DiTomaso and G.B. Kyser. 2004. The ability of native plants to prevent weed establishment. In: Proceedings, Ecology and Management of California Grasslands, April 2-3, 2004, Berkeley, CA. Available online at: <http://cbc.berkeley.edu/grass/Abstracts.htm>.

Native species have declined on non-agricultural land due to aggressive non-native species, especially annual grasses. A combination of overgrazing, periods of drought, fire suppression and introduction of non-native seed have led to the large-scale replacement of natives by exotics. Deep-rooted weeds, like yellow starthistle, have the potential to invade annual grasslands where deep soil moisture is underutilized by exotic annual grasses. A study has been initiated to 1) assess whether a restored native perennial community can suppress yellow starthistle invasion to a greater extent than a non-native annual grass ecosystem and 2) determine whether adding annual native forbs in the first year to increase functional diversity of a community can suppress subsequent invasion by yellow starthistle. Native species were chosen that had good potential for establishment in Yolo County soil conditions and climate and could take up water primarily either early or late in the growing season. Seeds of the different species were mixed together and broadcast by hand in December 2000. Yellow starthistle was added to the plots by broadcast application in early fall 2001. Cover, density and number of flowering culms (grasses) or stems (broadleaves) of each species was measured at the end of spring and summer. Soil moisture measurements were taken with a neutron probe at 30, 60, 90, 120, 150 and 180 cm approximately every three weeks from April through October. After two years of research, some midpoint observations can be made about plant community resistance to yellow starthistle or annual grasses. For soil moisture: use was less in the early season plant community after two years and an early/late season community had a similar water use pattern to yellow starthistle. Soil moisture depletion was greatest for the late season plant community and the addition of yellow starthistle to an early season plant community caused an increase in water use, indicating that such communities are vulnerable to yellow starthistle invasion. For competition: late season plant communities were most effective in suppressing yellow starthistle. More diverse perennial communities appear to not only compete with yellow starthistle for soil moisture, but also for available light during the growing season.

Yurkonis, K.A., Meiners, S.J. and Wachholder, B.E. 2005. Invasion impacts diversity through altered community dynamics. *Journal of Ecology* 0 (0):

Invading plant species often alter community structure, composition and, in some instances, reduce local diversity. However, the community dynamics underlying these impacts are relatively unknown. Declines in species richness with invasion may occur via displacement of resident species and/or reduction of seedling establishment by the invader. These two mechanisms differ in the demographic stage of the interaction. We document turnover dynamics using long-term permanent plot data to assess the mechanism(s) of invasion impacts of four exotic species on a mixed community of native and exotic species. These mechanisms were evaluated at both the neighborhood (1-m² plot) and population (individual species) scales. During invasion, species richness declined with increasing invader cover for three of the four invaders. All invaders reduced colonization rates, but had no effect on extinction rates at the neighborhood scale. Populations differed in their susceptibility to invasion impacts, with significant reductions in colonization for 10 of 25 (40%) species and increases in extinction for only 4 of 29 (14%) species. At neighborhood and population scales, influences of invasion on community dynamics were essentially the same for all invaders regardless of life-form. While individual resident species had some increase in extinction probability, community richness impacts were largely driven by colonization limitation. The consistency of invasion impacts across life-forms suggests establishment limitation as a general mechanism of invasion impact. This common causal mechanism should be explored in other systems to determine the extent of its generality.

III. EFFECTS OF LIVESTOCK GRAZING ON SOILS

Abdel-Magid, A. H., G. F. Schuman, and R. H. Hart. 1987. Soil bulk density and water infiltration as affected by three grazing systems. *Journal of Range Management* 40(4): 307-309.

The influences of continuous, rotationally deferred, and short duration rotation grazing systems on soil compaction and water infiltration were assessed. Bulk density and water infiltration were measured to evaluate the effects of the 3 grazing systems at moderate and heavy stocking rates. Measurements were made in the spring before grazing and at the end of the grazing season in 1983 and 1984. Bulk density was not affected by grazing systems or stocking rate; bulk density was greater in the fall than in spring of 1984, but not in 1983. Infiltration was significantly lower under the heavy stocking rate than under the moderate stocking rate at the end of the grazing season. The average water infiltration was significantly less in the fall than in the spring for the heavy stocking rate but showed no seasonal effect for the moderate stocking rate. Infiltration was significantly greater under continuous grazing than under rotational deferment but no different from that under short-duration grazing in 1983. However, in 1984 the relationship was reversed. The grazing systems evaluated did not affect soil bulk density and water infiltration in a consistent manner; however, the stocking rate resulted in reduced infiltration during the grazing season.

Abdel-Magid, A.H., M.J. Trlica, and R.H. Hart. 1987b. Soil and vegetation responses to simulated trampling. *J. Range Management* 40 (4): 303-6.

An artificial hoof was used to simulate trampling effects on native shortgrass sods in a greenhouse experiment. Severe to moderate trampling was applied to sods maintained under 3 soil water regimes. Trampling was done either throughout a 32-day period to represent a continuous grazing system, or only during the last 4 of the 32 days to simulate a short-duration grazing system. Soil bulk density increased 3% and infiltration rate declined 57% under severe trampling. Trampling throughout the 32 day period resulted in 4% higher bulk density than did a similar level of trampling that was applied only during the last 4 days of the trial. Dead vegetation was more easily removed by hoof action than was living vegetation, and severe water stress made plant material more brittle. Aboveground biomass production was 7% greater under trampling that simulated short-duration grazing, and 17% more forage remained in the standing crop under this treatment. About 38% more vegetation was detached by hoof action under simulated continuous grazing as compared with the short-duration grazing treatment.

Afzal, M. and W.A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. *Soil Sci. Soc. Am. J.* 56: 1160-66.

Allen, B. 1989. Ten years of change in Sierran stringer meadows: an evaluation of range condition models. Gen. Tech. Rep. PSW-110. USDA Forest Service Pacific Southwest Research Station, Albany, CA.

Allen-Diaz, B. 1991. Water table and plant species relationships in Sierra Nevada Meadows. Amer. Midl. Naturalist 126(1): 30-42.

Archer, S. and D.E. Smeins. 1991. Ecosystem level processes. Pp. 109-139 In Heitschmidt, R.K. and J.W. Stuth, eds. *Grazing Management: An Ecological Perspective*. Timber Press, Portland, OR

The impact of livestock grazing on ecosystems varies in relation to the evolutionary history of the site and the level of grazing pressure. Intermountain grasslands of North America evolved with light grazing and have changed markedly since the introduction of livestock. In contrast, the tall- mixed- and short-grass prairies of North America, which evolved with bison, pronghorn and prairie dogs, have been relatively resistant to stresses associated with livestock grazing. Although plant species in ecosystems that evolved with grazing are well-adapted to defoliation, domestic livestock can substantially impact their growth and persistence in numerous ways: 1) in contrast to wild herbivores, concentrations of livestock can be artificially maintained at consistently high levels; 2) fences prevent the emigration of livestock to new areas when the abundance of desired forage decreases, resulting in higher frequencies and intensities of defoliation than would occur otherwise; 3) supplemental feeding is used to maintain grazing pressure over a greater portion of the year and over a higher frequency of years than would have occurred with native herbivores, both present and prehistoric; 4) in grassland systems that occur in areas capable of supporting trees and shrubs, prolonged grazing may decrease the capacity of grasses to competitively exclude woody plants, while at the same time reducing fire frequency and intensity by preventing the accumulation of fine fuels. Thus, while grazing has been an important selection pressure in many ecosystems, humans have substantially changed its frequency, intensity, extent, and magnitude with the introduction of livestock. The result has been rapid and widespread changes in species composition and productivity of plant communities.

Bartolome, J. 1989. A review of "Holistic Resource Management" by Allan Savory, 1988. Journal of Soil and Water Conservation 44:591-592.

No abstract or summary available.

Bauer, A., C.V. Cole, and A.L. Black. 1987. Soil property comparisons in virgin grasslands between grazed and nongrazed management systems. Soil Sci. Soc. Am. J. 51(1): 176-82.

Belnap, J. 1995. Surface disturbances: their role in accelerating desertification. Environmental Monitoring and Assessment 37:39-57.

Maintaining soil stability and normal water and nutrient cycles in desert systems is critical to avoiding desertification. These particular ecosystem processes are threatened by trampling of livestock and people, and by off-road vehicle use. Soil compaction and disruption of cryptobiotic soil surfaces (composed of cyanobacteria, lichens and mosses) can result in decreased water availability to vascular plants through decreased water infiltration and increased albedo with possible decreased precipitation. Surface disturbance may also cause accelerated soil loss through wind and water erosion and decreased diversity and abundance of soil biota. In addition, nutrient cycles can be altered through lowered nitrogen and carbon inputs and slowed decomposition of soil organic matter, resulting in lower nutrient levels in associated vascular plants. Some cold desert systems may be especially susceptible to these disruptions due to the paucity of surface-rooting vascular plants for soil stabilization, fewer nitrogen-fixing higher plants, and lower soil temperatures, which slow nutrient cycles. Desert soils may recover slowly from surface disturbances, resulting in increased vulnerability to desertification. Recovery from compaction and decreased soil stability is estimated to take several hundred years. Re-establishment rates for soil bacterial and fungal populations are not known. The nitrogen fixation capability of soil requires at least 50 years to recover. Recovery of crusts can be hampered by large amounts of moving sediment, and re-establishment can be extremely difficult in some areas. Given the sensitivity of these resources and slow recovery times, desertification threatens millions of hectares of semi-arid lands in the United States.

Bethlenfalvay, G. J. and S. Sakessian. 1984. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada. *Journal of Range Management* 37:312-316.

The effect of grazing on the colonization of range plants by vesicular-arbuscular mycorrhizal (VAM) fungi was investigated within an enclosure and on degraded Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) rangelands at Medell Flat, near Reno, Nev. Implications of the interaction between mycorrhizae and grazing, relevant to the ecology and management of rangelands, are discussed. Density of forage grasses and their colonization by VAM fungi was significantly reduced as a result of grazing, in some cases by more than 50%. No differences in colonization were found in forage or nonforage broadleaf plants. A significant shift in the floristic composition and density of range plants occurred as a result of the presence or absence of grazing pressure. The decrease in VAM-fungal colonization of grasses under grazing is ascribed to a decrease in leaf areas and an increase in root to shoot ratios—conditions which result in decreased source capacity and increased sink demand.

Blackburn, W.H. 1983. Livestock grazing impacts on watersheds. *Rangelands* 5(3): 1-3.

Livestock grazing affects watershed properties by altering plant cover and physical action of hooves. Reductions in veg cover may: (1) increase impact of raindrops; (2) decrease soil organic matter and soil aggregates; (3) increase surface soil crusts (not defined as microbiotic); and (4) decrease water infiltration rates. These effects may cause increased runoff, reduced soil water content, and increased erosion. Effects greatest for heavy continuous grazing and are less for light or moderate grazing. Average surface runoff and soil loss highest in bunchgrass compared to sodgrass dominated areas.

Burke, M.J.W. and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77(3): 776-90.

A long—term field experiment in limestone grassland near Buxton (North Derbyshire, United Kingdom) was designed to identify plant attributes and vegetation characteristics conducive to successful invasion. Plots containing crossed, continuous gradients of fertilizer addition and disturbance intensity were subjected to a single—seed inoculum comprising a wide range of plant functional types and 54 species not originally present at the site. Several disturbance treatments were applied; these included the creation of gaps of contrasting size and the mowing of the vegetation to different heights and at different times of the year. This paper analyzes the factors controlling the initial phase of the resulting invasions within the plots subject to gap creation. The susceptibility of the indigenous community to invasion was strongly related to the availability of bare ground created, but greatest success occurred where disturbance coincided with eutrophication. Disturbance damage to the indigenous dominants (particularly *Festuca ovina*) was an important determinant of seedling establishment by the sown invaders. Large seed size was identified as an important characteristic allowing certain species to establish relatively evenly across the productivity—disturbance matrix; smaller—seeded species were more dependent on disturbance for establishment. Successful and unsuccessful invaders were also distinguished to some extent by differences in germination requirements and present geographical distribution.

Brady, N. C., and R. R. Weil. 1999. *The Nature and Properties of Soils*. 12th Edition. Prentice Hall, Upper Saddle River, NJ.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. 11. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56:10-15.

Studies were conducted during 1979 growing season to examine how North American bison (*Bison bison*) use prairie dog (*Cynomys ludoviciana*) colonies in Wind Cave National Park, South Dakota. Objectives included 1) determining whether bison selected for prairie dog towns parkwide; 2) characterizing in greater detail bison use patterns of a 36-ha colony in Pringle Valley as a function of time since prairie dog colonization; and 3) relating these bison use patterns to measured changes in structure and nutritional value of vegetation on and off the dog town. During mid-summer, prairie dog towns were one of the most frequently used habitats by bison parkwide. Day-long observations at Pringle Valley revealed that bison exerted strong selection (nearly 90% of all habitat use and feeding time) for the dog town, which occupied only 39% of the valley. While there, they partitioned their use of the colony by grazing in moderately affected areas (occupied <8 years by prairie dogs) and by resting in the oldest area (>26 years occupation). Prairie dogs

facilitate bison habitat selection for a short-grass successional stage in this mixed-grass community by causing a broad array of compositional, structural, and nutritional changes in the vegetation.

Dahlgren, R. and M.J. Singer. 1991. Nutrient cycling in managed and unmanaged oak woodland grass ecosystems. Symposium on Oak Woodlands and Hardwood Rangeland Management. Gen. Tech. Rpt. PSW-126. USDA Forest Service Pacific Southwest Research Station, Albany, CA.

Dudley, D.M., K.W. Tate, N.K. McDougald and M.R. George. 2002. Factors influencing soil-surface bulk density on oak savanna rangeland in the southern Sierra Nevada foothills. Pp. 131-138 in: Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. USDA Forest Service Pacific Southwest Research Station Gen. Tech. Report PSW-184. Berkeley, CA.

The objectives of this study were to compare soil-surface bulk density between rangeland pastures not grazed since 1935, 1975, and 1995 to grazed areas with a 15-year record of light (>1,000 lbs/acre RDM), moderate (600-800 lbs/acre RDM) and heavy (<400 lbs/acre RDM) grazing by beef cattle; and to determine the influence of oak canopy, topographic position, and livestock concentration activities on bulk density. The study was conducted on sandy-loam soils on oak savanna at the San Joaquin Experimental Range in Madera County, CA. A total of 1047 bulk density samples were collected. Soil-surface bulk density was 19% lower under oak canopy than in adjacent open grasslands. Livestock grazing at all levels increased bulk density above that in areas excluded from grazing for 5, 25 and 65 years, while there was no significant differences among enclosures. Areas with light grazing had lower bulk density than moderately and heavily grazed sites, which were not different from each other. RDM recommendations at or above 800 lbs./acre will likely lead to reduced soil surface bulk density on these soils series. Livestock concentration areas were the most compacted sites in the study.

Egerton-Warburton, L.M. and E.B. Allen. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10:484-496.

We evaluated arbuscular mycorrhizal (AM) species diversity and abundance in nine locations along an anthropogenic nitrogen deposition gradient in coastal sage scrub (CSS) vegetation in southern California. The primary pollutants were nitrogen oxides derived from vehicular emissions. Extractable soil N on the gradient ranged from 5 to 87 $\mu\text{g/g}$ during the summer months. For comparative purposes, we also assessed AM communities in nitrogen-fertilized (60 kg $\text{N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and unfertilized plots. Nitrogen enrichment induced a shift in AM community composition. In particular, an increasing input of nitrogen was associated with the displacement of the larger-spored species of *Scutellospora* and *Gigaspora* (due to a failure to sporulate) with a concomitant proliferation of small-spored *Glomus* species (e.g., *Glomus aggregatum*, *Glomus leptotichum*). A subsequent reduction in species richness and diversity (as measured by Shannon-Wiener index) accompanied eutrophication. Nitrogen enrichment also significantly reduced spore abundance, modified the timing of AM spore production in the most eutrophied site, and reduced hyphal and vesicular root infection. The fertilization experiment yielded similar patterns to those found along the gradient, and hence nitrogen input most likely explains the relationship between anthropogenic pollution and shifts in the AM communities. Such changes also indicated that AM species were sensitive indicators of nitrogen enrichment. The CSS is currently undergoing a conversion to Mediterranean annual grasslands, especially in the more urban polluted areas, and the shifts in the mycorrhizal fungal community may facilitate grass dominance in this system.

Firestone, M.K. 1995. Nutrient cycling in a managed oak woodland-grass ecosystem. Final Report to the Integrated Hardwood Range Management Program, University of California, Davis, CA.

Floate, M. J. S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems In: F. E. Clark and T. Rosswall (eds.). *Terrestrial nitrogen cycles*. *Ecological Bulletin* 33: 585-601.

Most ecosystems rely wholly or partly on the flow of nitrogen from soil to plant and back to soil, either as plant residues or as animal excreta. Cropping systems involve large nutrient removals, whereas grazing systems may have

equally large nutrient throughput but smaller removals in animal products. Nutrient cycling via grazing animals is therefore important in the maintenance of soil fertility. Grazing practice varies in intensity from very extensive use of rangeland to highly intensive use of high production pastures under rotation management. There is a resultant range in the extent of animal influence on nitrogen cycling. Direct effects of grazing include consumption of herbage, trampling of soil and spoilage of herbage, excretion of dung and urine, and removal of N by the sale of animal products. Indirect effects may be defined as the secondary results of these primary influences. These indirect effects include grazing selection and modification of botanical composition and sward structure, alteration in the proportion and distribution of N-return to the soil via plant and animal pathways, with resultant effects on decomposition and mineralization rates, and the extent of losses which may occur. The magnitude of these effects depend on five independent variables – initial state of soil and vegetation, climate, animal agent and the distribution in time and space of both vegetation and animals. The influences of grazing processes in different ecosystems and management practices on the total N supply and on fast and slow cycling pools is discussed. It is concluded that one of the main objectives of management should be to obtain and maintain the maximum amount of N in the fast-cycling pool.

Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6(3): 324-337.

See abstract / annotation under section I.

Holechek, J. L., R. D. Pieper, and C. H. Herbel. 1998. ***Range Management: Principles and Practices***. 3rd Edition. Prentice Hall, Upper Saddle River, NJ.

Frank, A.B., D.L. Tanaka, L. Hofmann, and R.F. Follett. 1995. Soil carbon and nitrogen of northern Great Plains grasslands as influenced by long-term grazing. *J. Range Management* 48(5): 470-4.

Holland, E.A. and J.K. Detling. 1990. Plant response to herbivory and below-ground nitrogen cycling. *Ecology* 71:1040-1049.

Plant responses to herbivory and links to belowground nitrogen cycling were investigated at Wind Cave National Park, South Dakota. Laboratory estimates of net nitrogen mineralization were highest in soils from the more altered areas of prairie dog colonies (*Cynomys ludovicianus*) and lowest in the adjacent, lightly grazed, uncolonized grassland. The ratio of CO₂: net nitrogen mineralized, as index of immobilization, was highest in the uncolonized grassland and lowest in the altered core areas. Soil moisture was an important modifier of in situ field estimates of net nitrogen mineralization. Root biomass, an important carbon source for decomposers in perennial grasslands, was lowest in the altered core area and highest in the adjacent uncolonized grassland. Decreased nitrogen immobilization and increased net nitrogen mineralization in the laboratory incubations likely resulted from decreased root carbon inputs in grazed areas, which limited carbon availability to decomposers. Such increases in plant—available nitrogen may partially explain the frequently reported grazing—induced increases in shoot nitrogen concentrations. These studies suggest that carbon allocation to roots is a key link determining nitrogen—cycling responses to herbivory.

Ingham, R. E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecological Monographs* 55:119-140.

The most common system responses attributed to microfloral grazers (protozoa, nematodes, microarthropods) in the literature are increased plant growth, increased N uptake by plants, decreased or increased bacterial populations, increased CO₂ evolution, increased N and P mineralization, and increased substrate utilization. Based on this evidence in the literature, a conceptual model was proposed in which microfloral grazers were considered as separate state variables. To help evaluate the model, the effects of microbivorous nematodes on microbial growth, nutrient cycling, plant growth, and nutrient uptake were examined with reference to activities within and outside of the rhizosphere. Blue grama grass (*Bouteloua gracilis*) was grown in gnotobiotic microcosms containing sandy loam soil low in inorganic N, with or without chitin amendments as a source of organic N. The soil was inoculated with bacteria (*Pseudomonas paucimobilis* or *P. stutzeri*) or fungus (*Fusarium oxysporum*), with half the bacterial microcosms inoculated with bacterial—feeding nematodes (*Pelodera* sp. or *Acrobeloides* sp.) and half the fungal microcosms inoculated with fungal—feeding nematodes (*Aphelenchus avenae*). Similar results were obtained from both the unamended and the chitin—amended experiments. Bacteria, fungi, and both trophic groups of nematodes were more abundant in the rhizosphere than in nonrhizosphere soil. All treatments containing nematodes and bacteria had higher

bacterial densities than similar treatments without nematodes. Plants growing in soil with bacteria and bacterial—feeding nematodes grew faster and initially took up more N than plants in soil with only bacteria, because of increased N mineralization by bacteria, NH_4^+ —N excretion by nematodes, and greater initial exploitation of soil by plant roots. Addition of fungal—feeding nematodes did not increase plant growth or N uptake because these nematodes excreted less NH_4^+ —N than did bacterial—feeding nematode populations and because the N mineralized by the fungus alone was sufficient for plant growth. Total shoot P was significantly greater in treatments with fungus or *Pelodera* sp. than in the sterile plant control or treatments with plants plus *Pseudomonas stutzeri* until the end of the experiment. The additional mineralization that occurs due to the activities of microbial grazers may be significant for increasing plant growth only when mineralization by microflora alone is insufficient to meet the plants' requirements. However, while the advantage of increased N mineralization by microbial grazers may be short—term, it may occur in many ecosystems in those short periods of ideal conditions when plant growth can occur. Thus, these results support other claims in the literature that microbial grazers may perform important regulatory functions at critical times in the growth of plants.

Lauenroth, W.K., D.G. Milchunas, J.L. Dodd, R.H. Hart, R.K. Heitschmidt, and L.R. Rittenhouse. 1994. Effects of grazing on ecosystems of the Great Plains. In: M. Vavra, W.A. Laycock, and R.D. Pieper, eds. *Ecological Implications of Livestock Herbivory in the West*. Society for Range Management, Denver, CO.

Mathews, B.W., L.E. Sollenberger, V.D. Nair and C.R. Staples. 1994. Impact of grazing management on soil nitrogen, phosphorus, potassium and sulfur distribution. *J. Environ. Qual.* 23: 1006-13.

Parton, W. J., and P. G. Risser. 1980. Impact of management practices on the tallgrass prairie. *Oecologia* 46: 223-234.

The ELM ecosystem-level grassland model simulates the flow of water, heat, nitrogen and phosphorous through the ecosystem and the biomass dynamics of plants, consumers and decomposers. The model was adapted to a tallgrass prairie site in northeastern Oklahoma, USA, the Osage Site of the U.S. International Biological Program Grassland Biome. Several range management manipulations were simulated by the model and the results compared to field data and literature information: 1) altering the grazing intensity, grazing system and grazing time period; 2) adding nitrogen and phosphorous to the grassland; 3) adding water during the growing season; and 4) spring burning of the prairie. The model showed that cattle weight gain per head, above-ground and below-ground plant production, transpiration water loss, standing dead biomass, and the net nitrogen balance decrease with increasing grazing intensity, while soil water content and bare soil water loss increase. A moderately stocked year-round cow-calf grazing system is more beneficial to the grassland than a more highly stocked seasonal steer grazing system because the former increases the above- and below-ground primary production and the plant nutrient uptake rates. Range manipulations, such as fire, which stimulate uniform grazing of a pasture, increase primary production, cattle weight gains, and nutrient uptake of plants and animals. Model results indicated that adding fertilizer was the best strategy for increasing cattle weight gains per head, while adding water would produce the greatest increase in primary production. Simulation of yearly and triennial spring burns suggests that these treatments increase primary production, plant nutrient uptake, and cattle weight gain per head. Burning increases the nitrogen losses from the system; however, these losses are greater with annual burns. The model results also suggest the spatial grazing pattern of cattle must be considered to correctly represent the impact of grazing on the prairie. The model is used to describe the behavior of the tallgrass prairie ecosystem, evaluate alternative management strategies, and identify future scientific research and management studies.

Patra, A.K., L. Abbadie, A. Clays-Josserand, V. Degrange, S.J. Grayston, P. Loiseau, F. Louault, S. Mahmood, S. Nazaret, L. Philippot, F. Poly, J.I. Prosser, A. Richaume and X. Le Roux. 2005.

Effects of grazing on microbial functional groups involved in soil dynamics. *Ecological Monographs* 75(1): 65-80.

Enhancement of soil nitrogen (N) cycling by grazing has been observed in many grassland ecosystems. However, whether grazing affects the activity only of the key microbial functional groups driving soil N dynamics or also affects the size (cell number) and/or composition of these groups remains largely unknown. We studied the enzyme activity, size, and composition of five soil microbial communities (total microbial and total bacterial communities, and three

functional groups driving N dynamics: nitrifiers, denitrifiers, and free N₂ fixers) in grassland sites experiencing contrasting sheep grazing regimes (one light grazing [LG] site and one intensive grazing [IG] site) at two topographical locations. Enzyme activity was determined by potential carbon mineralization, nitrification, denitrification, and N₂ fixation assays. The size of each community (except N₂ fixers) was measured by the most-probable-number technique. The composition of the total soil microbial community was characterized by phospholipid fatty acid analysis (PLFA), and the genetic structure of the total bacterial community was assessed by ribosomal intergenic spacer analysis. The genetic structures of the ammonia-oxidizing, nitrate-reducing, and N₂-fixing communities were characterized by polymerase chain reaction and restriction fragment length polymorphism (PCR-RFLP) or by polymerase chain reaction and denaturing gradient gel electrophoresis (PCR-DGGE) targeting group-specific genes. Greater enzyme activities, particularly for nitrification, were observed in IG than in LG sites at both topographical locations. The numbers of heterotrophs, nitrifiers, and denitrifiers were higher in IG than in LG sites at both topographical locations. The amplitude of changes in community size was higher than that of community enzyme activity. Phospholipid and nucleic acid analyses showed that the composition/structure of all the communities, except nitrate reducers, differed between IG and LG sites at both locations. For each community, changes in activity were correlated with changes in the occurrence of a few individual PLFAs or DNA fragments. Our results thus indicate that grazing enhances the activity of soil microbial communities but also concurrently induces changes in the size and composition/structure of these communities on the sites studied. Although the generality of our conclusions should be tested in other systems, these results are of major importance for predicting the effects of future disturbances or changed grazing regimes on the functioning of grazed ecosystems.

Ruess, R. W. 1984. Nutrient movement and grazing: experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. *Oikos* 43:183-188.

The effects of simulated grazing and nitrogen source on the assimilation of essential nutrients were examined in *Kyllinga nervosa*, a sedge from the Serengeti short grass plains. Clipping and nitrogen source both had significant effects on forage quality and the rates of nutrient uptake. Clipping increased green leaf nutrient concentrations and specific root uptake of nutrients an average of 18.2% and 77.7%, respectively. Ammonium-grown plants had higher green leaf nutrient levels of potassium, phosphorous, copper, manganese, sodium, zinc, and iron; while nitrate-grown plants had higher green leaf levels of calcium and magnesium/ Specific root uptake of all elements except magnesium were greater in ammonium compared with nitrate-grown plants. Green leaf nutrient levels of laboratory-grown *K. nervosa* were nutritionally unbalanced for ungulates, and both clipping and ammonium aggravated the potential toxicity of the species.

Savory, A. 1999. *Holistic Management*. Island Press, Washington, D.C.

Tiedemann, A.R., H.R. Sanderson, and N.J. Cimon, 1986. Future site productivity considerations of short-duration, high intensity grazing. In: J.A. Tiedemann Ed. *Short Duration Grazing*. Washington State Univ., Pullman, WA.

Tisdale, S.L., W.L. Nelson, J.D. Beaton. 1985. *Soil Fertility and Fertilizers* 4th edition. Macmillan Publishing, New York, NY.

Warren, S.D. 1987. Soil hydrologic response to intensive rotation grazing: a state of knowledge. In: Y.S. Fok Ed. *Infiltration Development and Application*. Proceedings of the International Conference on Infiltration Development and Application. Water Resources Research Center, University of Hawaii, Honolulu, HI.

Warren, S.D., T.L. Thurow, W.H. Blackburn, and N.E. Garza. 1986a. The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. *J. Range Man.* 39(6): 491-5.

Warren, S.D., M.B. Nevill, W.H. Blackburn, and N.E. Garza. 1986b. Soil response to trampling under intensive rotation grazing. *Soil Sci. Soc. Am. J.* 50(5): 1336-41.

Warren, S.D., W.H. Blackburn, and C.A. Taylor, Jr. 1986c. Soil hydrologic response to number of pastures and stocking density under intensive rotation grazing. *J. Range Management* 39(6): 500-4.

Watkins, B.R., and R.J. Clements. 1978. The effects of grazing animals on pastures. Pages 283-289 in J.R. Wilson, editor. *Plant Relations in Pastures*. CSIRO, East Melbourne, Australia.

No abstract or summary available.

IV. LIVESTOCK GRAZING, FUEL AND FIRE REGIMES

Allen, B.H. and J.W. Bartolome. 1989. Cattle grazing effects on understory cover and tree growth in mixed conifer clearcuts. *Northwest Science* 63: 214-220.

A long-term study of cattle grazing effects on shrub and herbaceous cover and tree growth in mixed conifer clearcuts began at Blodgett Forest Research Station on the west slope of the Sierra Nevada (California, USA) in 1977. Until that time, no studies had quantified the relationships between cattle grazing and reduction in non-tree vegetation, and grazing damage to tree regeneration. Yet, with the ban on use of herbicides in Federal forest management, alternative tools for reducing unwanted vegetation were needed. Cattle grazing reduced shrub and herbaceous canopy cover to 8 percent six years after harvesting, and 31 percent eight years after harvesting on two mixed conifer clearcuts. These cover levels were within timber management objectives for tree growth. No significant trampling damage occurred and browsing damage to white and Douglas-fir seedlings was primarily caused by deer. Tree seedlings showed no significant differences in height or basal diameter growth under any treatment. Thus, cattle grazing appears to be a viable tool for meeting brush/grass objectives in forest plantations.

Anderson, H.E. 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, General Technical Report INT-122. Intermountain Forest and Range Experiment Station, Ogden, UT.

This report presents photographic examples, tabulations, and a similarity chart to assist fire behavior officers, fuel management specialists, and other field personnel in selecting a fuel model appropriate for a specific field situation. Proper selection of a fuel model is a critical step in the mathematical modeling of fire behavior and fire danger rating. This guide will facilitate the selection of the proper fire behavior fuel model and will allow comparison with fire danger rating fuel models. The 13 fire behavior fuel models are presented in 4 fuel groups: grasslands, shrublands, timber, and slash. Each group comprises three or more fuel models; two or more photographs illustrate field situations relevant to each fuel model. The 13 fire behavior fuel models are crossreferenced to the 20 fuel models of the National Fire Danger Rating System by means of a similarity chart. Fire behavior fuel models and fire danger rating fuel models, along with the fire-carrying features of the model and its physical characteristics, are described in detail.

[Bachelet D.](#), [Lenihan J.M.](#), [Daly C.](#), [Neilson R.P.](#) 2000. Interactions between fire, grazing and climate change at Wind Cave National Park, SD. *Ecological Modelling* 134 (2-3): 229-244.

Projected changes in global climate have important ramifications for the future of national parks and other reserves set aside to conserve ecological uniqueness. We explored potential implications of climatic changes on lifeform distribution and growth at Wind Cave National Park (WCNP), South Dakota, which lies on a climatically determined ecotone between grassland and forest. Fire, promoted by healthy grasslands, is a negative feedback limiting tree development because it kills seedlings and consumes live foliage thus reducing tree growth and survival. Historical records show that fire suppression has enhanced forest expansion. On the other hand, livestock grazing reduces grass biomass and fuel loads thus indirectly reducing fire frequency and enhancing the expansion of forests or woodlands. Natural fires and moderate grazing by native herbivores have maintained the coexistence of trees and grasses but climatic variations affecting the area's water resources can lead to dominance by either lifeform. We used a dynamic vegetation model (DVM) MC1 to simulate the interactions between climatic changes, natural fire regime, and grazing pressure and their impact on the biogeographical and biogeochemical characteristics of the park. We used one future climate projection (HADCM2SUL) which simulates warmer weather by the end of the next century: the temperature increase would constrain the growth of trees that rely on the availability of deep water, favor shrub and grass

development and promote a shift from forests to woodlands. Woody encroachment of shrubs in grasslands areas, enhanced by grazing, was only held in check by frequent natural fires in the simulation.

Bartolome, J.W. and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madrono* 28(3): 172-184.

We present information clarifying the past and present role of the native perennial grass *Stipa pulchra* in the California grassland. *Stipa pulchra* occupies a diverse array of habitats in northern and central California, as shown from information collected on more than 1500 plots by the State Cooperative-Soil-Vegetation Survey. *Stipa pulchra* did not increase in density over a 20 year period in ungrazed areas on the Hopland Field Station in northern California and was replaced by other perennial grasses and annuals on some plots. *Stipa pulchra* germinated more slowly than associated annual plants and *S. pulchra* seedlings apparently did not survive the period of rapid spring growth in annual grassland. In pot trials fewer *S. pulchra* germinated and plants grew poorly when grown with high densities of *Bromus mollis* and *Festuca megalura*. High densities of *B. mollis* limited *S. pulchra* growth more dramatically than high densities of *F. megalura*. We suggest that *S. pulchra* is the most common California native grass not because the species dominated the original California grassland, but because it is favored by disturbances common now. Disturbances that reduce associated annuals are important for colonization by *S. pulchra*.

[Belsky A.J.](#) and D.M. [Blumenthal](#). 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. *Conservation Biology* 11 (2): 315-327.

Many ponderosa pine and mixed-conifer forests of the western, interior United States have undergone substantial structural and compositional changes since settlement of the West by Euro-Americans. Historically, these forests consisted of widely spaced, fire-tolerant trees underlain by dense grass swards. Over the last 100 years they have developed into dense stands consisting of more fire-sensitive and disease susceptible species. These changes, sometimes referred to as a decline in "forest health," have been attributed primarily to two factors: active suppression of low-intensity fires (which formerly reduced tree recruitment, especially of fire-sensitive, shade-tolerant species), and selective logging of larger, more fire-tolerant trees. A third factor, livestock grazing, is seldom discussed, although it may be as important as the other two factors. Livestock alter forest dynamics by (1) reducing the biomass and density of understory grasses and sedges, which otherwise outcompete conifer seedlings and prevent dense tree recruitment, and (2) reducing the abundance of fine fuels, which formerly carried low intensity fires through forests. Grazing by domestic livestock has thereby contributed to increasingly dense western forests and to changes in tree species composition. In addition, exclosure studies have shown that livestock alter ecosystem processes by reducing the cover of herbaceous plants and litter, disturbing and compacting soils, reducing water infiltration rates, and increasing soil erosion.

Bond, W. J. and B. van Wilgen. 1996. *Fire and Plants*. Chapman and Hall, New York, New York.

A textbook on fire and plant ecology. Aimed for upper division or graduate level ecology students, it is international in scope, and the time scales considered are evolutionary.

Borman, M.M. 2005. Forest stand dynamics and livestock grazing in historical context. *Conservation Biology* 19(5): 1658-1662.

Livestock grazing has been implicated as a cause of the unhealthy condition of ponderosa pine forest stands in the western United States. An evaluation of livestock grazing impacts on natural resources requires an understanding of the context in which grazing occurred. Context should include timing of grazing, duration of grazing, intensity of grazing, and species of grazing animal. Historical context, when and under what circumstances grazing occurred, is also an important consideration. Many of the dense ponderosa pine forests and less-than-desirable forest health conditions of today originated in the early 1900s. Contributing to that condition was a convergence of fire, climate, and grazing factors that were unique to that time. During that time period, substantially fewer low-intensity ground fires (those that thinned dense stands of younger trees) were the result of reduced fine fuels (grazing), a substantial reduction in fires initiated by Native Americans, and effective fire-suppression programs. Especially favorable climate years for tree reproduction occurred during the early 1900s. Exceptionally heavy, unregulated, unmanaged grazing by very large numbers of horses, cattle, and sheep during the late nineteenth and early twentieth centuries occurred in most of the U.S. West and beginning earlier in portions of the Southwest. Today, livestock numbers on public lands are substantially lower than they were during this time and grazing is generally managed. Grazing then and grazing now are not the same.

Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M. DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2005. Effects of invasive alien plants on fire regimes.

Plant invasions are widely recognized as significant threats to biodiversity conservation worldwide. One way invasions can affect native ecosystems is by changing fuel properties, which can in turn affect fire behavior and, ultimately, alter fire regime characteristics such as frequency, intensity, extent, type, and seasonality of fire. If the regime changes subsequently promote the dominance of the invaders, then an invasive plant–fire regime cycle can be established. As more ecosystem components and interactions are altered, restoration of preinvasion conditions becomes more difficult. Restoration may require managing fuel conditions, fire regimes, native plant communities, and other ecosystem properties in addition to the invaders that caused the changes in the first place. We present a multiphase model describing the interrelationships between plant invaders and fire regimes, provide a system for evaluating the relative effects of invaders and prioritizing them for control, and recommend ways to restore preinvasion fire regime properties.

Campbell, R.R. 1954. Fire in relation to forest grazing. *Unasylva* 8: 154-158.

No abstract or summary available.

Detling, L.E. 1961. The chaparral of southwestern Oregon with considerations of its post-glacial history. *Ecology* 42: 348-357.

The chaparral formation of the Pacific Northwest is confined to the Rogue River watershed and a few small areas in the south Umpqua Valley, Oregon. Floristically it is related to the chaparral of central and northern California, with *Ceanothus cuneatus* and *Arctostaphylos* spp. as its chief shrub constituents. The most significant climatic features of the chaparral belt of the Rogue and Shasta Valleys are: (1) Mean annual precipitation between 312-742 mm, (2) summer precipitation from 17-28 percent of annual total, (3) mean winter minimum temperatures from -5.8 to 0.7 degrees C, and (4) mean summer maximum temperatures from 29.9 to 33.7 degrees C. In southwestern Oregon chaparral is the most xeric in requirements of all the vegetation types, and in most situations is subclimax to oak woodlands or ponderosa pine forest. Relict occurrence of *Ceanothus cuneatus* and the distribution patterns of the Rogue River chaparral associates indicate that chaparral once extended northward almost to Puget Sound. Judging from known climatic requirements of the present California and Oregon chaparral, a decrease of about 230 mm in annual rainfall below the present means, accompanied by a rise of at least 1.0 degrees C in winter maximum and 5.0 degrees C in summer maximum temperatures must have occurred to cause such an extension of the formation. During such a xerothermic phase chaparral also occupied the Klamath Basin east of the Cascade Mts. Many of the associated species migrated through the Columbia Gorge and mingled with what was probably a grassland formation in the mid-Columbia region.

Evanko, A.B. and R.A. Peterson. 1955. Comparison of protected and grazed mountain rangelands in southwestern Montana. *Ecology* 36: 71-83.

Comparisons of five areas, each with parts open to and protected from grazing, were made in the Idaho fescue-bluebunch wheatgrass type in southwestern Montana. Various elements of the vegetation and water absorption by the soils were measured to determine effects of grazing and protection treatments. Measurements which could have been affected directly by current grazing, such as height growth and yield, were restricted to ungrazed plants. Detailed findings from the study were: 1) While all test areas were located within a 1 and ½ mile radius of each other, composition of vegetal cover within and outside the enclosures varied substantially among areas. 2) The following trends were observed in vegetation cover relative to treatment: a) Unpalatable forbs and shrubs were more common on the grazed than on protected counterparts. Differences were small but consistent. No particular species appeared to stand out as having high indicator value. b) Total grass cover was slightly greater on the protected than on the grazed portion. Idaho fescue provided less cover on the grazed portions of those areas where it was dominant. Bluebunch wheatgrass showed a similar but less pronounced trend. Only Sandberg bluegrass was persistently most abundant on the parts of the areas open to grazing. c) Variations were so great among areas that no common compositional pattern could be defined for the type. 3) Leaf heights, basal area per clump, and herbage yield per pland and per square centimeter for the major forage species were, with one exception, greatest on the protected portions in each of these comparisons. Comparatively close correspondence of these characteristics existed within treatments among areas, especially for Idaho fescue and bluebunch wheatgrass. 4) Calculated yield of the most common forage species was usually greatest on the protected areas. 5) Litter on the soil surface and rate of water absorption by the soil were, in most cases, substantially less on the grazed portion of the areas. They varied considerably between areas within treatments. 6) In a comparison between a lightly used and a protected area, amount and kind of cover and frequency of plant occurrence did not reflect the light use. Measurements of height, clump basal area, yield per clump, and yield per

square centimeter showed less difference in this comparison than where protected and more heavily grazed areas were compared. On this mountain bunchgrass type, it was found that leaf height, plant area, and yield per clump and unit of plant area of individuals of important forage species appear to furnish more reliable and usable criteria for evaluating range condition than do cover estimates. Strategically located exclosures may provide the range administrator with a standard for evaluating, in a relatively simple manner, the degree to which the grazing treatment has affected certain characters, especially those associated with vigor of plants.

[Hemstrom M.A.](#), [Korol J.J.](#), [Hann W.J.](#) 2001. Trends in terrestrial plant communities and landscape health indicate the effects of alternative management strategies in the interior Columbia River basin. *Forest Ecology and Management* 153 (1-3): 105-126 Sp. Issue.

Current and potential future conditions of terrestrial plant communities and landscape health were modeled for three alternative public land management strategies in the interior Columbia River basin. Landscape health was defined as an integration of the degree to which vegetation and disturbance conditions resemble native patterns and support levels of human activity. The range of vegetation and disturbance variability for a period before the middle 19th century was used as a basis for comparison of current and future regimes to the "historical" system. Departure from the "historical" regime in wildland environments was found to be related to altered disturbance patterns, especially changed fire regimes, forest insect and disease levels and excessive livestock grazing effects. Overall, mid-seral forests are currently more prevalent than they were in the past and old forests, especially single-layer structural types, are less abundant. Non-native plant species and altered plant community composition conditions exist across broad areas of rangelands. Landscape health has declined substantially in many areas. Proposed management strategies that emphasize maintenance and restoration activities in a hierarchical landscape approach should generate improved landscape health conditions over the next 100 years. However, the massive scale of changes to disturbance and vegetation patterns from historical to current times and the cost of implementing restoration activities make dramatic improvement unlikely.

[Heyerdahl E.K.](#), [Brubaker L.B.](#), [Agee J.K.](#) 2001. Spatial controls of historical fire regimes: A multiscale example from the interior west, USA. *Ecology* 82 (3): 660-678.

Our objective was to infer the controls of spatial variation in historical fire regimes. We reconstructed a multicentury history of fire frequency, size, season, and severity from fire scars and establishment dates of 1426 trees sampled on grids in four watersheds (64 plots, over 1620 ha each) representative of the Blue Mountains, Oregon and Washington, USA. The influence of regional climate, a top-down control, was inferred from among-watershed variation in fire regimes, while the influence of local topography, a bottom-up control, was inferred from within-watershed variation. Before about 1900, fire regimes varied among and within watersheds, suggesting that both top-down and bottom-up controls were important. At the regional scale, dry forests (dominated by ponderosa pine), burned twice as frequently and earlier in the growing season in southern watersheds than in northern watersheds, consistent with longer and drier fire seasons to the south. Mesic forests (dominated by subalpine fir or grand fir) probably also burned more frequently to the south. At the local scale, fire frequency varied with different parameters of topography in watersheds with steep terrain, but not in the watershed with gentle terrain. Frequency varied with aspect in watersheds where topographic facets are separated by significant barriers to fire spread, but not in watersheds where such facets interfinger without fire barriers. Frequency varied with elevation where elevation and aspect interact to create gradients in snow-cover duration and also where steep talus interrupts fuel continuity. Frequency did not vary with slope within any watershed. The presence of both regional-scale and local-scale variation in the Blue Mountains suggests that top-down and bottom-up controls were both important and acted simultaneously to influence fire regimes in the past. However, an abrupt decline in fire frequency around 1900 was much greater than any regional or local variation in the previous several centuries and indicates that 20th-century fire regimes in these watersheds were dramatically affected by additional controls such as livestock grazing and fire suppression. Our results demonstrate the usefulness of examining spatial variation in historical fire regimes across scales as a means for inferring their controls.

[Keeley, J.E.](#) in press. Fire management impacts on exotic species invasions in the western United States. *Conservation Biology*.

Fire management practices affect alien invasion in diverse ways. I considered the impact of six fire management practices on alien invasions: fire suppression, forest fuel reduction, prescription burning in crown fire ecosystems, fuel breaks, targeting noxious aliens, and postfire rehabilitation. Most western United States forests have had fire successfully excluded for unnaturally long periods of time and this appears to have favored the exclusion of alien plant species. Forest fuel reduction programs have the potential for greatly enhancing forest vulnerability to alien invasions. In part this is due to the focus on reestablishing pre-Euro-American fire regimes on a landscape that differs from pre-Euro-American landscapes in the abundance of aggressive non-native species. We may be forced to choose between restoring "natural" fire regimes or altering fire regimes to favor communities of native species. Intensive grazing in

many western forests may exacerbate the alien problem after fire and temporally decoupling grazing and fire management may reduce the alien threat. Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural, high-intensity crown fire regime that is less amenable to forest restoration tactics. Historical use of prescribed fire for type conversion of shrublands to more useful grazing lands has played some role in the massive annual grass invasion that threatens these shrublands. Fuel breaks pose a special invasive plant risk because they promote alien invasion along corridors into wildland areas. Use of prescription burning to eliminate noxious aliens has had questionable success, particularly when applied to disturbance dependent annuals, and success is most likely when coupled with ecosystem restoration that alters the competitive balance between aliens and natives. Artificial seeding of alien species as a form of postfire stabilization appears to cause more problems than it solves and may even enhance alien invasion.

Keeley, J. E. 2001. Fire and invasive species in Mediterranean-climate ecosystems of California. Pages 81-94 in K.E.M. Galley and T. P. Wilson (eds.). *Proceedings of the Invasive Species Workshop: the role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.*

Within the Mediterranean-climate region of California and adjacent regions, invasive plants are largely concentrated in the lower elevation valleys and foothills. Fire has historically been an important part of the ecology of many of these ecosystems; however, anthropogenic disruptions of natural fire regimes have contributed to the widespread invasion of certain communities. Throughout the Coast Ranges and foothills of the Sierra Nevada and Cascades, high fire frequency has contributed to the type conversion of shrublands and closed woodlands to annual grasslands dominated by alien grasses and forbs of Mediterranean Basin origin. Returning these landscapes to their former closed-canopy state is the only likely means of reducing the presence of non-natives. Valleys and other sites with deeper clay soils, which formerly were perennial grasslands, also have been type-converted to nonnative annual grasslands by intensive grazing and ploughing. There is evidence that spring burning may be an appropriate management tactic for shifting the balance away from the annual alien grasses towards increased native cover, but only on sites with an existing perennial bunchgrass presence. This tactic, however, may not be an appropriate community restoration technique because it inhibits native annuals as well. Currently, the vast majority of grasslands in the state lack native bunchgrass, and on these sites different burning prescriptions may alter species composition; however, there is no convincing demonstration that fire alone is an effective technique for diminishing the dominance of nonnative annuals. Prescription burning is increasingly used to control invasion of particularly noxious weeds that are typically targeted because they alter the functioning of ecosystems, e.g. making rangelands unpalatable to livestock or wildlife. Such use of prescription burning may enhance resource benefits from some stakeholders, but generally burning of annual grasslands does not greatly alter the native to nonnative composition, unless accompanied by active native plant restoration. Several aspects of current fire management practice may contribute to the increase in alien plants. Limited success in fire prevention is 1 key element because increasing populations density has continued to add fire on the landscape, and this has contributed to continued type-conversion from native woody vegetation to nonnative herbaceous associations. Pre-fire fuel manipulations may likewise contribute to this trend; for example, use of prescription burning on sites that currently have higher than natural fire frequencies potentially favors aliens. Also fuel breaks contribute to enhanced survivorship of alien seed banks, resulting in source populations poised for invasion of adjacent burned sites. Post-fire site "rehabilitation" is responsible for widespread introduction of alien species at a time when elevated soil nutrients may favor aliens over natives. Of most concern is the potential for these aliens to alter fuels in a way that increases fire frequency, which further increases expansion of the aliens.

Keeley, J.E., D. Lubin and C.J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13(5): 1355–1374.

Patterns of native and alien plant diversity in response to disturbance were examined along an elevational gradient in blue oak savanna, chaparral, and coniferous forests. Total species richness, alien species richness, and alien cover declined with elevation, at scales from 1 to 1000 m². Blue oak savannas were heavily dominated by alien species and consistently had more alien than native species at the 1-m² scale. All of these aliens are annuals, and it is widely thought that they have displaced native bunchgrasses. If true, this means that aliens have greatly increased species richness. Alternatively, there is a rich regional flora of native annual forbs that could have dominated these grasslands prior to displacement by alien grasses. On our sites, livestock grazing increased the number of alien species and alien cover only slightly over that of sites free of livestock grazing for more than a century, indicating some level of permanency to this invasion. Blue oak savannas are an important propagule source for alien species because they maintain permanent populations of all alien species encountered in post-fire chaparral, and because

the vegetation mosaic in this region places them in close proximity.

Mack, M., and C. M. D'Antonio. 1998. Impacts of biological invasion on disturbance regimes. *Trends in Ecology and Evolution* 13:195-198

The evidence clearly indicates that individual invasive species have altered ecosystems by changing disturbance regimes. Indeed, invasive species have changed disturbance regimes in both disrupted and intact systems. The authors focus on three common mechanisms by which this happens. Many invaders change the amount of physical disturbance, by enhancing or suppressing fire, or by increasing or decreasing soil disturbance. Other invaders (primarily animals) have themselves become disturbance agents. Finally, certain invading species act either to intensify or ameliorate the effects of disturbance on the system. Most of the studies reviewed demonstrated that altering disturbance regimes promotes invasive species and contributes to the demise of at least a portion of the native biota. In their conclusion, the authors caution that the continued movement of species around the globe by humans will only compound the negative effects of disturbance and invasions on ecosystems.

Madany, M.H. and N.E. West. 1983. Livestock grazing – fire regime interactions within montane forests areas of Zion National Park, Utah. *Ecology* 64(4): 661-667.

Major differences were found between the vegetation structure of ponderosa pine-dominated communities on the Horse Pasture Plateau and those on the nearby but isolated Church and Greatheart Mesas in Zion National Park. The Horse Pasture Plateau was heavily grazed by livestock in the late 19th and early 20th centuries, while the mesas were never grazed. Conditions on the mesas now approximate the pre-European situation of the region as described in the earliest written accounts. Pine, oak, and juniper sapling density and cover were much higher on the formerly grazed plateau than on the relict mesas. Herbaceous species dominated the ground layer in mesa ponderosa pine savanna stands, while grass and forb cover was low on analogous sites of the plateau. Age-class distributions of major tree species further substantiated that major physiognomic changes have occurred on the plateau since the arrival of European man. Analysis of fire scars showed that prior to 1881, the mean fire-free interval for ponderosa pine stands on the plateau was 4 to 7 yr, while the interval for Church Mesa was 69 yr. Since there were no recorded fires on Church Mesa between 1892 and 1964, and yet no corresponding increase in sapling density, the increased understory density of plateau stands should not be attributed primarily to cessation of fires. Instead, heavy grazing by livestock and associated reduction of the herbaceous ground layer promoted the establishment of less palatable tree and shrub seedlings. Fire, however, played an important secondary role in maintaining savanna and woodland communities.

Mensing, S. A. 1998. 560 years of vegetation change in the region of Santa Barbara, California *Madrono* 45: 1-11.

Pollen evidence from two sites in the Santa Barbara region show evidence of vegetation changes following European settlement in California. In the Santa Barbara coastal region, oak woodland populations (dominated by *Quercus agrifolia*) remained stable during the pre-European period; however, in the last century woodland densities have increased. At higher elevations along the oak woodland/pine forest ecotone, pines are becoming dominant. Reduction in fire frequency has probably been the main factor contributing to density increases. The pollen record does not show any evidence of an expansion of chaparral over the last 200 years; however, there is weak evidence for an increase in coastal-sage scrub since the early 1800's. The transformation of the California grassland appears to have begun particularly early with the invasion of *Erodium cicutarium* in the region even before the first Spanish settlement in California.

Mitchell, J.E. and D.R. Freeman. 1993. Wildlife-livestock-fire interactions on the North Kaibab: A historical review. USDA Forest Service Rocky Mountain Research Station Gen. Tech. Report RM-222.

No abstract or summary available.

Norman, S.P. and A.H. Taylor. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. *Forest Ecology and Management* 215 (1-3): 51-68.

Type conversions of vegetation are often triggered by changes in one or more limiting environmental factors. Such changes are particularly evident along montane forest-meadow ecotones, where historical changes in fire, grazing and climate have occurred. In this paper, we reconstruct spatial and temporal variation in climate, livestock grazing and fire

for 11 meadow inclusions in the pine-dominated forest of northeastern California, USA. We then compare this environmental variation to temporal patterns of tree invasion by dating the establishment of 1420 trees, saplings and seedlings. Invasive trees included ponderosa pine (*Pinus ponderosa* Laws.), Jeffrey pine (*Pinus jeffreyi* Grev and Balf.), lodgepole pine (*Pinus contorta* var. *murrayana* Loudon (Grev and Balf.)) and western juniper (*Juniper occidentalis* Hook.). Before the arrival of Euro-Americans in 1849, fires burned with a median interval of 11 years based on 1–3 ha composite records from multiple trees, and 14 years using records from individual trees. There was substantial variation in the date of the last recorded fire within and among meadows, but fire was rare after 1905. The onset of tree establishment varied among meadows, but followed the reduction and removal of fire. Livestock grazing also varied among meadows, and the highest establishment rates occurred when grazing was moderate. Mean tree establishment was 22.9 trees/ha/decade during the late 19th century when grazing was unregulated, 62.6 trees/ha/decade when sheep were present, but regulated, and 40.7 trees/hectare/decade after sheep were replaced with cattle. Ponderosa and Jeffrey pine established during a range of temperature and precipitation conditions, but establishment was greater when summer precipitation was below normal, annual temperatures were normal and springs were cool. Although changes in disturbance and climate were associated with tree establishment, the persistence of trees at the meadow edge is best explained by continued fire exclusion. With the long-term absence of fire the local effects of different disturbance histories are being lost.

Odion, Dennis C., Frank W. Davis. 2000. Fire, soil heating, and the formation of vegetation patterns in chamise chaparral. *Ecological Monographs* 70: 149-169.

We documented patterns of surface heating associated with chaparral fire to characterize fundamental scale variation in the intensity of this stand-replacing disturbance. To test how this variation may influence community structure, we studied its effect on the soil seed bank and the distribution of seedlings and resprouts that emerged after fire. To evaluate the long-term significance of initial patterns, we monitored vegetation development for 4–5 yr, thereby encompassing the dynamic portion of the chaparral fire cycle. We studied two stands on level uniform terrain before, during, and after fall fires. Stands were dominated by chamise (*Adenostoma fasciculatum*), a postfire seeder/sprouter. Nonsprouting *Arctostaphylos* and *Ceanothus* spp. were also present. Preburn vegetation, seed populations, soil heating, and postburn plant growth were analyzed along transects of contiguous 1-m² plots, so that we could block them together incrementally to identify scale dependence of patterns. In addition, we directly compared heating effects under the fuel array with those just outside by establishing plots in canopy gaps, under the adjacent canopy, and in gaps created and eliminated by reciprocally translocating fuel. Pre- and postburn seed populations were estimated in soil samples collected from all plots. The proportion of seed that survived above and below 2.5 cm in the soil was determined in a subset of plots.

The amount and distribution of canopy fuel that collapsed during fire and smoldered on the ground caused pronounced spatial variation in total surface heating. The strength of relationships among patterns of soil heating, preburn canopy, surviving seeds, and seedlings and herbaceous resprouts was consistently most pronounced in blocks 3–5 m long. At this scale, postburn patterns were strongly negatively associated with the amount of preburn canopy and the pattern of soil heating this fuel created. Seedlings or herbaceous resprouts of numerous species were abundant where soil heating was relatively low, most notably in natural and created canopy gaps. Conversely, areas where dense canopy occurred before fire, especially gaps displaced by fuel addition, were barren except for occasional *Arctostaphylos* and *Ceanothus* seedlings. These obligate postfire seeders, along with the subshrub *Helianthemum scoparium*, had more deeply buried seeds, and some of them were able to survive where soil heating was prolonged. However, *Helianthemum* did not emerge from depth. Seedlings of *Arctostaphylos* and *Ceanothus* nearest *Adenostoma* burls survived significantly better when *Adenostoma* failed to resprout. This was common in one burn where heating was relatively high and burl size was small. Seed mortality prevented *Adenostoma* seedling emergence from occurring where its seeds were most abundant prior to fire, which was in proximity to its burls. *Adenostoma* seedlings did emerge in areas of lower soil heating, but their survival was inversely related to the density of *Helianthemum* seedlings. No shrub seedlings emerged after the first year following fire because their seed banks were exhausted by fire-induced mortality and/or germination. After 4–5 yr, few young *Adenostoma* remained. The combination of seedling and resprout regeneration allowed this shrub to maintain dominance, but to a lesser extent in the older stand. Our results support a vegetation pattern–process model in which local species distributions after fire in *Adenostoma* chaparral are antecedently linked to the physical and chemical properties of the canopy. These control the nature of combustion, the soil heating that results, and the distribution of seeds and resprout tissues that survive. The vegetation develops entirely from these sources, so fire-induced patterns are manifest in the long-term structure of this vegetation.

Odion, D. and C. Tyler. 2002. Are long fire-free periods needed to maintain the endangered, fire-recruiting shrub *Arctostaphylos morroensis*(Ericaceae)? *Conservation Ecology* 6(2): 4. [online] URL: <http://www.consecol.org/vol6/iss2/art4>

Morro manzanita (*Arctostaphylos morroensis*) is a distinctive shrub restricted to a small area along the coast of California, USA. This endangered species faces two opposing fire-related extinction risks: (1) adults are killed by fire,

and (2) recruitment opportunities only occur with fire. These strongly limit the capacity of this, as well as other obligate-seeding species, to recover from a population decline, which may result if there is an inadequate amount of time between fires for replenishment of sufficient seed populations. Using a prescribed burn, we tested whether the size of the seed bank that had accumulated in a 40-yr-old stand would prove adequate for maintaining *A. morroensis* population sizes through fire. Prior to the burn, we found ~11,000 seeds/m² in the soil, mostly in the top 5 cm. However, the number of viable seeds was substantially lower (334 seeds/m²), and less than one-third of these survived the experimental fire (99 seeds/m²). Germination occurred only in the first two wet seasons after the fire, and may have been adequate to replace the number of *A. morroensis* present before the burn. However, most seedlings did not survive their initial summer drought. After three years, the new population of *A. morroensis* was less than half the size of the parent population. Further mortality is expected because the remaining seedlings are highly clumped. We conclude that *A. morroensis* may require considerably longer than 40 years to establish an adequate seed bank to compensate for mortality and prevent population decrease or local extinction. This prolonged risk is perhaps explained by specialization of this species to a historic regime of relatively infrequent fire. There are many obligate-seeding species in fire-prone shrublands that may not be resilient to a regime of fire more frequent than that with which they evolved.

Paine, R.T., M.J. Tegner, and E.A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535-545.

All species have evolved in the presence of disturbance, and thus are in a sense matched to the recurrence pattern of the perturbations. Consequently, disturbances within the typical range, even at the extreme of that range as defined by large, infrequent disturbances (LIDs), usually result in little long-term change to the system's fundamental character. We argue that more serious ecological consequences result from compounded perturbations within the normative recovery time of the community in question. We consider both physically based disturbance (for example, storm, volcanic eruption, and forest fire) and biologically based disturbance of populations, such as overharvesting, invasion, and disease, and their interactions. Dispersal capability and measures of generation time or age to first reproduction of the species of interest seem to be the important metrics for scaling the size and frequency of disturbances among different types of ecosystems. We develop six scenarios that describe communities that have been subjected to multiple perturbations, either simultaneously or at a rate faster than the rate of recovery, and appear to have entered new domains or "ecological surprises." In some cases, three or more disturbances seem to have been required to initiate the changed state. We argue that in a world of ever-more-pervasive anthropogenic impacts on natural communities coupled with the increasing certainty of global change, compounded perturbations and ecological surprises will become more common. Understanding these ecological synergisms will be basic to environmental management decisions of the 21st century.

Rummell, R.S. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. *Ecology* 32(4): 594-607.

A study of ungrazed Meeks Table and Grazed Devils Table in central Washington provided evidence that parts of the virgin ponderosa pine forest contained dense mats of herbaceous understory vegetation and sparse stands of tree reproduction. Pinegrass (*Calamagrostis rubescens*) dominated and elk sedge (*Carex geyeri*) was a minor part of the understory virgin flora. Densities of herbaceous understory vegetation on ungrazed Meeks Table were 183 percent to 254 percent of the densities on grazed Devils Table. Herbage yields of pinegrass were strikingly different between the two Tables. Pinegrass beneath open ponderosa pine produced 850 pounds of air dried herbage per acre on Meeks Table compared to only 240 pounds on Devils Table. While the timber overstories on the two Tables were similar, Meeks Table had only a very few small trees but Devils Table had 3,291 small trees per acre. The high density of herbaceous understory vegetation on Meeks Table contributed substantially to the deficiency of advance tree reproduction. Heavy grazing of the herbaceous understory vegetation, rather than exclusion of fire, appeared to be the prime factor in explaining the dense advance tree reproduction on Devils Table.

Sampson, A. W. 1944. Plant succession on burned chaparral lands in northern California. University of California, Agriculture Experiment Station Bulletin 685.

A detailed monograph on fire effects and management of chaparral and rangelands in northern California.

Savage, M. and T.W. Swetnam. 1990. Early 19th century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71: 2374-2378.

The coincidence of fire decline and early sheep herding on the Navajo Reservation, 45-70 years before the same association in the rest of the region, lends strong support to the hypothesis that heavy livestock grazing played a significant role in reducing fire frequency in ponderosa pine forests.

Swiecki, T.J., Barnhardt, E. 2002. Effects of fire on naturally occurring blue oak (*Quercus douglasii*) saplings. Pages 251-259 in Standiford, R.B.; McCreary, D.; Purcell, K.L., technical coordinators. Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. 2001 October 22-25; San Diego, CA. USDA Forest Service, Pacific Southwest Research Station, Gen. Tech. Rep. PSW-GTR-184, Albany, CA.

We studied the survival and regrowth of naturally-occurring blue oak saplings burned in a September 1996 arson fire in Vacaville, California. The saplings (pre-fire height 33-353 cm) were burned in a rapid, low-moderate intensity fire. Of 67 blue oak saplings surveyed, 4 failed to resprout after the fire and 2 more died within the following 5 years (9 percent mortality overall); all mortality was among saplings less than 100 cm tall. Saplings which were completely topkilled (51/67) were significantly smaller on average than those which were only partially topkilled (12/67). Saplings taller than 201 cm, or with a stem diameter greater than 5.6 cm at 30 cm height, were only partially topkilled. Only 20 percent of the completely topkilled saplings had regained both their post-fire height and diameter by 5 years after the fire. Height growth of new shoots from completely topkilled saplings was highest in the first year after the fire, but declined in succeeding years. High levels of vole damage in resprouted topkilled saplings has adversely affected growth and shoot survival. Our observations indicate that fire negatively impacts small blue oak saplings and does not favor blue oak regeneration, as has been suggested by other authors.

Thomas, P.H. 1971. Rates and spread of some wind-driven fires. *Forestry* 44: 155-175.

This paper describes the rate of spread of fires in cribs in laboratories and in experimental fires in gorse and heather in which fuel bulk density was altered. The mathematical relationships among factors affecting spread rates were calculated and found to be consistent in the lab and field. The conclusions were: 1) There was an inverse relation between fuel loading per unit volume and rate of spread. 2) There was a roughly linear increase in the rate of spread with wind speed up to 4 m/s. 3) The heating of the unburnt fuel includes contributions from the radiation from solids in the fuel bed, from the flames, and from convection. The correlation between laboratory fires and fires in the field is instructive in showing the limitations to which theory or measurements are subject in discussing field data and it demonstrates that a judicious mixture of theory and empiricism allows idealized model experiments to represent the main features governing this kind of wildfire.

Tyler, C.M., D.C. Odion, and R.M. Callaway. 2007 (in press). Dynamics of woody species in the California grassland. Chapter 10, in Stromberg, M., Corbin, J. and D'Antonio, C., editors. *Ecology and Management of California grasslands*. University of California Press, Berkeley, Ca.

Though by definition grassland is dominated by herbaceous vegetation, woody species can be common associates within all five of California's grassland vegetation types. In addition, grassland, shrubland, and woodland communities often become intermixed where they overlap. Interior valley grasslands merge with oak woodland and chaparral in the foothills, and with saltbush scrub in the southwestern edges of the San Joaquin Valley. In the moist northwestern regions of the state, coastal prairie "exists in a continuum" with coastal scrub and forms a mosaic with mixed evergreen forest. In the coastal areas of southern California, grassland extends into coastal sage scrub. This patchwork of vegetation types is dynamic. Grasslands in California, as in many parts of the world, can replace or be replaced by shrub- or tree-dominated vegetation. The boundaries and relative abundance of grassland and woody vegetation in landscapes can shift over time and space. These patterns are influenced by both physical and biological factors, including fluctuating climate, disturbance, and changes in native and non-native herbivores. Climate, soils and geologic substrate exhibit the broadest controls on the distribution of grasslands and co-occurring woody vegetation. Grasslands tend to occupy fine textured soils, but there is potential for woody vegetation in all but the finest textured soils and where climate and soil lead to the most extreme summer water deficit. On sites where different community-types are possible, what determines whether grassland or woody vegetation will dominate at a particular point in time? In this chapter, we describe first the dynamics between grasses and shrub vegetation. We focus on factors that lead to transitions between grassland and shrublands, such as disturbance, and the stabilizing feedbacks and reproductive processes that maintain them. We then discuss the dynamics at the grassland - oak savanna interface. We define oak savanna as grassland habitat with widely spaced oak trees whereas oak woodland is comprised of nearly closed, or closed-canopy stands of trees with sparse herbaceous vegetation in the understory. These habitats realistically form a continuum of oak canopy coverage. Here we focus on constraints over the recruitment of oaks into grassland settings

because this is an area of active interest to managers and scientists and then describe the ways in which oaks modify understory vegetation and productivity once they are established into grassland.

Tyler, C.M. and M. Borchert. 2003. Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae) in relation to fire.

Zigadenus fremontii is often a striking component of the flora following fire in the chaparral. Like other geophytes, it produces large numbers of flowers in the first spring after a burn. Although these plants are most conspicuous in the early postfire environment, the question that remains is, how do they persist in the interval between fires? To address this we investigated differences in the growth and reproduction of *Z. fremontii* in burned and unburned chaparral. We monitored marked individuals for nine years at three sites: two that were burned in 1990 and one in the same area that was in unburned mature chaparral. We measured leaf area, and production of flowers and fruits. We also conducted seed experiments in the field to determine the rates and timing of germination. We found that reproduction occurs only in the immediate postfire period: flowering and production of fruits and seeds in the first year following fire, and seedling establishment by year 3. There was a cost of reproduction; plants that flowered (in the burn area) had negative growth rates the following year. In contrast, plants in unburned chaparral, which did not flower, had positive growth rates over the same period. Moreover, plants that produced the most flowers had the lowest growth rates. In the unburned chaparral site, plants were not dormant as predicted from previous literature; instead they produced leaves nearly every year. In most years the average leaf area per plant was greater than that in the burned sites. Our results indicate that postfire reproduction depends on growth and carbohydrate storage in the inter-fire period. We also suggest that this species is relatively long-lived for a herbaceous perennial.

Wagner, F.H. 1989. Grazers, past and present. Pp. 151-162 In L.F. Huenneke and H.A. Mooney, (eds.) *Grassland Structure and Function: California Annual Grasslands*. Kluwer Academic Publishers, Boston, MA.

This paper presents a review of the herbivorous fauna that prevailed in, and influenced, the California grassland during its formation, during its existence in prehistory, and during the changes it has undergone since European colonization. The California grasslands sustained heavy grazing pressures from a diverse herbivorous fauna during the late Pleistocene, and possibly up to the start of the recent epoch ca. 10,000 B.P. The first Europeans arriving in 16th century A.D. encountered large numbers of three ungulate species – black-tailed deer, pronghorn antelope and tule elk – none is an obligate grazer. Livestock herds were first developed by the Spaniards along the coast, subsequently in the Central Valley by Indians and large numbers of feral horses and cattle. The ranching industry did not develop until after the gold rush. Beef cattle numbers reached 1.8 million by 1860, declined by over half by 1870 due to drought, then increased to all-time highs (2.9 million on rangelands) in the last half of the century. Sheep numbers peaked around 1880 at 6 million, and have declined since to a contemporary total of less than half a million. Grazing pressures on public rangelands have stabilized for several decades, but might be at an all-time high on private ranges. By the 16th century, California perennial bunchgrass vegetation might have been a relict of a previous, more favorable climate. Its survival might have been abetted by a depauperate ungulate fauna comprised only of browsers which protected it from competition by woody species.

Wright, H. A. and A. W. Bailey. 1982. Fire ecology—United States and Southern Canada. John Wiley and Sons, New York, New York, USA.

Standard, early fire ecology text for temperate North America.

Zedler, P.H., C.R. Gautier and G.S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California USA chaparral and coastal scrub. *Ecology* 64:809-818.

This study describes changes in the abundance of shrub species after 2 fires in 1979 and 1980 on Otay Mountain in San Diego County, California. The 1979 fire burned a large area of dense chaparral and coastal sage scrub. The 1980 fire burned a portion of the 1979 fire area that had been seeded with annual ryegrass (*Lolium multiflorum*) as an erosion protection measure. Changes in the vegetation caused by the 1979 fire alone were similar to those commonly seen in chaparral wildfire, but the reburning of the vegetation in 1980 caused drastic changes in some areas. *Ceanothus oliganthus* was almost completely eliminated from the area of the 1980 burn. *Adenostoma fasciculatum*, the most abundant shrub at the study site, was reduced in density by up to 97%. Even *Xylococcus bicolor*, which normally resprouts with complete success after fire, suffered substantial mortality with reburning. The changes brought about by the 1980 fire will certainly persist for many decades. While sudden shifts in vegetation composition probably occurred

without human intervention, human activity (especially after the introduction of aggressive annual grasses 200 yr ago) has apparently caused an increase in the instances of abrupt change.

[Zimmerman G.T.](#) and [Neuenschwander L.F.](#) 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir/ninebark habitat type. *Journal of Range Management* 37(2): 104-110.

Influences of livestock grazing on community structure, fire intensity, and normal fire frequency in the Douglas-fir/ninebark (*Pseudotsuga menziesii*/*Physocarpus malvaceus*) habitat type were studied at the University of Idaho's experimental forest in northern Idaho. Livestock grazing caused increased tree numbers, decreased production, cover, and frequency of major palatable grasses, and altered dominance of shrub and forb species. Grazing influences on community structure were increased accumulation of downed woody fuel in every size class, increased forest floor duff, and decreased herbaceous fuels. Livestock grazing influences were discussed in light of their significance in potential fire intensity and fire frequency in Douglas-fir forest communities.