Ecology and Restoration of California Grasslands with special emphasis on the influence of fire and grazing on native grassland species

Carla D'Antonio*
Susan Bainbridge*
Coleman Kennedy*
James Bartolome[t]
Sally Reynolds*

***Department of Integrative Biology**
[t]Department of Environmental Science, Policy and Management
University of California
Berkeley, California
94720

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Introduction

The grasslands of California's Mediterranean climate region are unique because they occur within a region where precipitation falls only during the cold part of the year, they have a very strong representation of annual species in their flora and they have undergone a large-scale replacement of native species by European ones over the past 150 years. Today, they occupy approximately 10 million ha either as open grassland or as understory in oak-dominated savannas and woodlands (Heady et al. 1992). Forage from these lands provides the grazing resource for range livestock production, a leading agricultural commodity in the State. In addition, California grassland and oak savanna ecosystems are extremely important as wildlife habitat (Guisti et al. 1996) and as a center of high native plant diversity. Indeed, around 90% of species listed in the Inventory of Rare and Endangered Species in California (Skinner and Pavlik 1994), occur within California grassland settings. Despite the value of California grasslands for both range production and native biological diversity, this habitat is increasingly reduced in acreage and quality due to conversion for cropland, residential and urban development and exotic species invasion. As a result, intact native grassland today is among one of the state’s most threatened ecosystems (Noss et al. 1995).

Factors proposed to be responsible for the current state of California grasslands include livestock grazing and other land use histories, climate and the prevalence of seed of non-native species. The most abundant plants in California grassland and understory of associated oak savannas and woodlands are annual species introduced from the Old World (Baker 1989, Heady et al. 1992). Although several weedy species, including the abundant Eurasian annual forb, *Erodium cicutarium* (filaree) (Mensing and Bynre 1998), were present in California before settlement in 1769, the vast majority spread in the late 18th and early 19th century (Hendry 1931). The composition and structure of California grasslands at the time of European colonization is generally not known and although there is a general assumption that it was a perennial dominated prairie, there is little evidence to support this claim (Hamilton 1997, Schiffman 1997).

While there is general agreement that the habitat has undergone a radical transformation in the last 150 years (Clements 1934, Heady 1977, Wester 1981, Baker

1989, Hamilton 1997), reconstructing the pre-contact state of the California grassland and the causes and trajectory of change are difficult due to the dearth of scientific observations from this period. Before the arrival of Europeans, perennial bunchgrasses likely dominated wetter areas whereas drier sites were dominated by annual grasses, forbs, and perhaps shrubs (Hamilton 1997, Schiffman 1997). These 'original' grasslands were likely subjected to herbivory by native ungulates (Tule elk, pronghorn and black-tailed deer) and small mammals (Wagner 1989), soil disturbance by abundant small mammals (Schiffman 1997, 2000) and burning by native-Americans (see Blackburn and Anderson 1993). With the arrival of Spanish settlers, large numbers of livestock (i.e. cattle, horses and sheep) were introduced and simultaneously, Mediterranean-region grasses and forbs arrived (Burcham 1956).

The decline of native grassland species has been attributed to several causes. The absence of comparably heavy grazing pressure in the pre-contact California grassland (Heady 1977, Heady et al. 1977, Mack and Thompson 1982) in contrast to the extensive history of intensive livestock grazing in the Old World region from which the invading exotic plants originated (Jackson 1985) could have played a role in favoring European species as livestock production intensified. Also it has been proposed that exotic annual grasses are competitively superior to many native species with or without livestock grazing and thus could have replaced them solely through competition and greater seed production (Heady et al. 1977, Bartolome and Gemmill 1981, Murphy and Ehrlich 1989). Other factors that potentially contributed to the decline of the native grassland include a lengthy drought during the mid 1800s (Burcham 1956), and tillage for crop agriculture (Stromberg and Griffin 1996). Crop agriculture, which spread widely after 1850 (Burcham 1957), is an important predictor today for presence/absence of native perennial grasses (Stromberg and Griffin 1996) suggesting its very strong role in the decline of native grassland cover.

Regardless of which factors were responsible for the decline of native-dominated grassland, it is clear that in many regions of the state today, native species are a minor component of the grassland flora. Several noxious weeds such as *Centaurea solstitialis* (yellow star thistle), *Taeniatherum caput-medusae* (medusa-head grass), and *Aegilops triuncialis* (barbed goat grass) have recently expanded into enormous areas of California and further degraded the quality of grasslands for native species, livestock grazing and recreation. Other threats to this habitat include development, vineyard conversion, alteration of grazing and fire regimes and lack of regeneration of oaks (Reiner et al. 2001). Thus, despite the overwhelming importance of grassland and oak savanna habitat in California and concern for its condition, it is a habitat in peril today.

Currently, restoration of native species in California grasslands is a conservation goal in many parks, reserves and agency land-holdings. Until recently it has not been a livestock production goal because little is known about the ability of annual exotic- versus native perennial-dominated grasslands to support livestock production. Early range scientists both learned to adapt livestock management practices to annual-dominated ranges in California (Bentley and Talbot 1951) and attempted range improvements with seeded exotic perennials (Love and Jones 1947). Only recently have livestock production groups or individual ranchers and conservation groups such as The Nature Conservancy begun to work together towards goals of sustained livestock production and enhancement of native perennial grass cover and native grassland diversity. Yet the scientific basis upon which decisions regarding the intensity and seasonality of grazing and/or the use of fire to manage species composition and productivity is weak and a comprehensive survey of the successes and failures of grazing and fire manipulations is long overdue.

Restoring native plant diversity and abundance [or dominance] in California grasslands to their full potential requires the definition of restoration targets and the application and testing of workable management practices. Although invasion by exotic species and climatic fluctuations probably played important roles in the loss of native species, these factors are neither controllable nor testable at appropriate scales. By contrast, livestock grazing and fire regime, two factors whose alteration probably contributed significantly to the destruction of the original grassland, are manageable both in an experimental context and as practical restoration tools today (Dyer et al. 1996, Hatch et al. 1999). Scientific investigations in California and elsewhere have shown that grazing and fire have complex effects on grassland structure. Currently, both are being used and promoted as a means of enhancing native grassland diversity in different parts of the state (fire—DiTomaso et al. 1999, Meyer and Schiffman 1999; grazing--Edwards

1995, 1996, Reeves 2001). Their effects likely vary with climatic and edaphic factors and it is with the goal of understanding the context-specificity of these effects that we have put together the following review.

This paper presents an up-to-date evaluation of the impacts of grazing and fire on the composition of grasslands in California with specific emphasis on their effects on the remaining populations of native forbs and perennial grasses. We intend that the findings will help to refine the scope of potential management regimes that might be applied to California rangeland systems to enhance the richness and abundance of native grassland species. The review is also intended to help identify gaps in our understanding of the interaction of management practices with climatic and soil variability and to help direct future experimental work in this area.

Background: What is the California Grassland?

The California grassland has long been divided into two major community types, the Coastal Prairie and the Valley Grassland (Munz and Keck 1959, Heady 1977). This division is based on perceived differences in abundance of native perennial grasses and in the relative dominance of annual versus perennial plants. The coastal prairie, found within a belt extending from the coast a few km inland, usually contains significant amounts of both native and exotic perennial species (Heady et al. 1977). A characteristic species in the northern and more coastal part of this prairie is *Danthonia californica* (California oatgrass). *Nassella pulchra* (purple needle grass) is abundant throughout the region. The more extensive and usually annual plant-dominated valley grassland occurs in inland valleys and inner coast range slopes (Heady 1977). In the limited areas where native perennial grasses are present, *Nassella pulchra* (purple needle grass*), Elymus glaucus* (blue wildrye)*,* and *Poa secunda* (one-sided bluegrass) are among the more common valley grassland species, although other species may be locally abundant (e.g. *Sporobolus airoides* [alkali sacaton] in seasonally wet, alkali soils in the southern Central Valley).

The coastal prairie and valley grassland intergrade spatially and temporally with each other and with shrub and tree-dominated communities, forming a heterogeneous habitat with pronounced variability on local and regional scales. Indeed, the division of the California grassland into these two types is somewhat simplistic. For example, within the relatively discrete coastal prairie grasslands of the Santa Cruz Mountains alone, Johnson (2000) distinguished 10 distinct types of prairie communities based on plant composition. Likewise in other areas of the state Heady (1956, 1958) and Beetle (1947) noted that the grasslands were extremely varied within relatively short distances. Jackson and Bartolome (in press) suggest a third grassland type be separated from the Valley Grassland. At least some of the variability in composition is related to the presence of an oak canopy, which can have an important but contingent effects on understory production and composition (Callaway et al. 1991, Frost et al. 1997). Other sources of variation in composition have received little attention from researchers.

Factors that may contribute to the variation in species composition among sites include soils [edaphic conditions], regional and local climate, past and current land use [especially the history of use for crop and livestock production) and the history of fire. Overall we know very little about the relative importance and interaction of these factors. Those few quantitative studies that exist of grassland composition across environmental and soil gradients tend to be focused on a single county or region (e.g. Johnson 2000-Santa Cruz Mountains, Hektner and Foin 1977-North Coast Prairie in Mendocino, Stromberg and Griffin 1996-Carmel Valley) or on comparisons of adjacent serpentine and non-serpentine grasslands (e.g. McNaughton 1968, Kruckeberg 1984, Harrison 1999). Climatic variation has also been cited as one of the primary determinants of community composition in California annual grassland (Talbot et al. 1939, Heady 1956, 1977, Bartolome et al. 1980, Jackson and Bartolome in press) and is recognized as contributing to statewide patterns of native perennial grass diversity (see discussion in Johnson 2000). Yet we know remarkably little about the interaction of climatic variability, soil composition and land management activities in affecting the occurrence of native perennial grasses and native forb species in the California grassland.

Ecological Constraints to Restoration of Native Grassland Species-State of our Knowledge.

Numerous sources of evidence suggest that removal of pressures such as intensive livestock grazing and/or tillage that were thought to have contributed to the decline of native grassland species in California, do not lead to increased native dominance even after several decades (White 1967, Bartolome and Gemmill 1981, Stromberg and Griffin 1996). For example, 40 years of monitoring populations of the native grass *N. pulchra* within two grazing exclosures at the Hopland Field Station (Mendocino County) revealed no increase in *N. pulchra* density and continued dominance by exotic annual species (Bartolome and Gemmill 1981, Merenlender et al 2001). Likewise, Stromberg and Griffin (1996) surveyed numerous grassland sites that had not been grazed or farmed for many decades and most were still dominated by European annual species. Such observations demonstrate that without directed management activity, recovery of native species is unlikely. In the following sections, we review what is known about those factors that might limit abundance of native grassland species. We believe this information is directly relevant to management because it suggests treatments that might aid in promoting native species.

Importance of interspecific competition:

In California grasslands today, native species always co-occur within a matrix of exotic species, and because seedlings of these exotics usually greatly outnumber native seedlings, the environment for native seedling establishment is potentially highly competitive (Biswell 1956, Heady 1956, Macdonald et al. 1988, Heady et al. 1992). One seedling may have several hundred to several thousand neighboring individuals within a 10 cm radius (Major and Pyott 1966, Young and Evans 1989). The potential for species interactions to limit recruitment of native plants is considered to be the primary reason why restoration projects that rely solely on seeding native grasses without the reduction of exotic annual species have low success (Evans and Young 1972, Dyer et al. 1996, Stromberg and Griffin 1996, Dyer and Rice 1997, 1999). The perceived competitive dominance of European over native grassland species has spurred recent investigation of interactions among native perennial grasses and European annual grasses (Nelson and Allen 1993, Dyer et al. 1996, Dyer and Rice 1997, Eliason and Allen 1997, Dyer and Rice 1999, Hamilton et al. 1999, Dyer et al. 2000). While interspecific interactions are likely important for native forbs as well, there have been very few studies on this topic (Cook 1965, Carlsen et al. 2000).

Competition from exotic annual grasses has been demonstrated to be important during all stages of the life cycle of the native perennial grass, *Nassella pulchra* (Hamilton et al. 1999), yet most evidence from California grassland studies points to the seedling stage as the period of highest interference from exotic annuals (Bartolome and Gemmill 1981, Jackson and Roy 1986, Dyer et al. 1996, Dyer and Rice 1997, 1999), a result supported by grassland studies elsewhere (Grubb 1977, Weiner and Thomas 1986, Foster 1999). Once established, native perennial grasses in California appear to be successful competitors and can survive in a diverse grassland community for many years (White 1967, Jackson and Roy 1986, Dyer and Rice 1997, Corbin and D'Antonio unpublished). However, failure to establish in the presence of competing annuals represents a major limitation for populations of native perennial grass species.

Physiological differences in germination, growth rate, nutrient and water uptake, and reproductive allocation between exotic annual and native perennial grasses all likely contribute to the difficulty in establishing native perennial grasses among competing exotic annuals. In a field experiment conducted in a Coast Range grassland, germination of native perennial species was delayed by 2-5 days compared to annual species (Jackson and Roy 1986). Likewise, in a greenhouse study, Reynolds et al. (in review) found that seeds of exotic annual grasses germinated much more rapidly than those of several species of native perennial grasses collected from a coastal prairie site. Another greenhouse study also found that *N. pulchra* seeds germinate more slowly and attain a lower density when sown with exotic annuals than when sown alone (Bartolome and Gemmill 1981). On the other hand, Robinson (1971) found field germination of *N. pulchra* seeds to be unaffected by the presence of non-native annual grasses.

Once seeds have germinated, native grass seedlings have a slower winter growth rate and greater belowground biomass allocation relative to exotic annuals (Jackson and Roy 1986, Holmes and Rice 1996). At the end of one growing season, Holmes and Rice (1996) found the exotic annual grass *Bromus diandrus* (ripgut brome) to have twice the above-ground dry weight of *N. pulchra*. The faster aboveground growth rate of annuals results from their rapid uptake of available resources and results in a reduction in light for native seedlings. With their earlier development, exotic annuals may also effectively deplete soil resources before seedlings of native species have a chance to do so (Ross and

Harper 1972, Bartolome and Gemmill 1981, Fowler 1986, Hamrick and Lee 1987, Fossum 1990, Facelli and Pickett 1991, Dyer and Rice 1999). Dyer and Rice (1997, 1999) found that seedling survival, growth and culm production in *N. pulchra* were negatively affected by a range of exotic annual species densities. They demonstrated that by spring, exotic annual species are large enough to significantly decrease both available light and soil moisture (down to 30 cm). Other studies have shown that the presence of exotic annual grasses negatively influences reproduction of native perennials in California grasslands by reducing inflorescence number and seed output (Gordon and Rice 1992, Hamilton et al. 1999, Carlsen et al. 2000).

While the mechanisms of exotic and native grassland species competition may be of greater academic than applied interest, the negative effects of exotic annual grasses on native establishment are such that reducing the vigor of the annuals seems crucial for the successful establishment of native perennial grasses. Thus, restoration efforts can benefit from continued investigation of competitive interactions. For example, experimental studies testing the minimum density of the annual neighborhood necessary for competitive release of perennials or the optimal season for weeding or herbiciding annuals may reduce management costs. Also, a primary shortcoming of current studies in the California grassland is the persistent focus on a single native species, *N. pulchra*. Other native plants may respond differently from *N. pulchra* to competition with non-native annual grasses. The existing studies are also of limited geographic scope.

Seed limitation:

Even in grasslands where native species persist, native seedling recruitment is generally very low (Bartolome and Gemmill 1981). Although this may be due to factors such as competition, seed supply may also be a limiting factor. Very few studies have tested the importance of seed limitation in the success of California grassland restoration efforts. However, data from unseeded control plots in restoration projects can be used to determine if a seed supply is present or not (Bugg et al. 1997). Hamilton et al. (1999) directly tested whether seed supply, from either the seed bank or seed rain, is a limiting resource for *N. pulchra* seedling establishment in a southern California grassland. Small plots (10 x 10 cm) were established in a mixed native/exotic grassland and assigned to one of four seed addition treatments (control, seed addition (+ 50 *N. pulchra* seeds/plot), litter removal followed by seed addition, and seed addition combined with added water). Plots with added seed had on average 5.1 ± 0.8 seedlings / 100 cm^2 which was five times more seedlings than plots without seed addition. Neither litter removal nor water addition had a significant effect on seedling recruitment without added seeds, suggesting that *N. pulchra* seedling recruitment is strongly limited by available seed.

In some cases, removal of non-native vegetation may have resulted in recruitment from the soil seed bank or from adjacent vegetation. Several studies in California grasslands show that native annual forbs may increase in abundance and sometimes dominate sites the year after fire (Hervey 1949, Meyer and Schiffman 1999, DiTomaso et al. 1999, others) or after the removal of noxious weeds (Thompson et al. 1993) suggesting the presence of a native soil seed bank. Similarly, observations from a restoration project in San Francisco suggest that viable seed or dormant bulbs of some native perennial species (*Elymus glaucus, N. pulchra, Festuca rubra* [red fescue], *Bromus carinatus* [California brome]*, Allium dichlamydeum* [wild onion], *Chloragalum pomeridianum var. divaricatum* [soap plant]) may persist in the soil at some sites. After the removal of the exotic perennial grass *Cortaderia jubata* (pampas grass), Pitschel and Clinebell (1988) observed the emergence of native perennial seedlings belonging to species that had not been observed to reproduce on the site for 15 years. In a coastal-terrace prairie project involving removal of dense stands of the African perennial succulent *Carpobrotus edulis* (Hottentot fig), native grasses recovered quickly from seed (Connors 1986). This particular Coastal Prairie, located on Bodega Bay Marine Reserve, contains healthy stands of native grasses and many more native species than Valley Grasslands throughout the Central Valley. As native species were abundant immediately adjacent to the iceplant-infested restoration sites, potential seed sources were abundant.

A broad range of data supports the generalization that exotic annual seeds comprise a larger proportion of grassland seed banks than seeds of native perennial species (Champness and Morris 1948, Major and Pyott 1966, Dyer et al. 1996, Holl et al. 2000, Alexander 2001). However, relatively little work has been done that identifies specific native grassland species with the potential to survive dormant in the soil (but see (Bakker et al. 1991, Bartolome 1979). A 1966 study of the seed bank of both grazed and ungrazed prairie vegetation dominated by *N. pulchra* in Yolo County revealed a poor correlation between the relative number of seeds in the soil and the composition of the established vegetation (Major and Pyott 1966). Although the perennial grass species *N. pulchra* and *Aristida hamulosa* (hook three-awn) dominated the aboveground vegetation, neither they nor any other perennial species had viable seed present in the seed bank. Seeds of exotic annual species, however, were quite abundant, with *Bromus hordeaceous* (soft chess), *Avena spp.* (wild oats) and *Vulpia* (annual fescue) *spp*. having 1500, 300 and 800-2500 seeds/m^2, respectively. More recent investigation of California grasslands supports the hypothesis that seeds of exotic annual species are capable of maintaining relatively large seed banks compared to native perennial grasses (Maranon and Bartolome 1989, Stromberg and Griffin 1996, Alexander 2001).

Annual variation in climate:

Climatic variation has often been identified as the primary determinant of community composition in California *annual* grassland (Talbot et al. 1939, Heady 1958, 1977, Jackson & Bartolome in press) and its importance in influencing the composition of native grassland has been noted. It is widely recognized that native grasses tend to be more common in wetter regions of the state (Wester 1981, Hamilton 1997) and experimental work has demonstrated the importance of local scale variability in moisture for native perennial grass recruitment (Dyer et al.1996). Despite its recognized importance, very few studies have carefully examined how rainfall affects the composition of California's grasslands or the outcome of restoration actions within grassland settings. Hatch & Bartolome (in prep) concluded that the total amount of annual rainfall was not as important in affecting annual grass productivity and native perennial grass cover as was the duration of drought within a single growing season. Examination of rainfall patterns in coastal California over the past two decades suggests that the rainy season is characterized by drought periods of varying duration that typically occur 1 to 2 months after the first significant rains. In southern California Rich Minnich (personal communication) has found that because annual grasses are usually the first species to germinate with fall rains, early season droughts have a strong effect on their survival and abundance. The negative effect of drought periods within the rainy season can cancel out the positive effects of a season with high overall precipitation levels (George et al. 2001). Unfortunately, most grassland restoration studies have not explicitly considered the effect of climate on the success of restoration methods, despite its potentially strong effects on the outcome of management activities.

Effects of non-livestock mammals on restoration:

Recently Schiffman (1997, 2000) and Hamilton (1997) have argued that the pre-contact grassland in California was a highly disturbed environment with vast areas of soil regularly impacted by native mammal species. They argue that in drier or hotter regions of the state, this disturbance regime would have favored native annual plant species, pre-adapting the sites to invasion by weedy European annual species. Today it is clear that disturbance by native mammals can promote the entry of unwanted exotic species into California grasslands. For example, gophers and ground squirrels promote the invasion of Highway iceplant into coastal prairies (D'Antonio 1993, Vila and D'Antonio 1998), gophers promote invasion of north coast prairie by exotic perennial grasses (Peart 1989), and native kangaroo rats promote invasion of Carrizo Plains grassland by introduced forbs (Schiffman 1994). Because rodents are particularly abundant in California grasslands, they might make control of exotics a continual problem.

In addition, feral pig populations are increasing throughout many regions of California including grasslands. Their feeding activities result in enormous amounts of soil disturbance. Pigs can reduce cover of established native perennial grasses and could presumably disrupt restoration attempts by interfering with establishment of native perennial species. However, Kotanen (1995) found that although feral pigs reduced native perennial grasses in a North Coast Prairie, their activities caused an increase in both native and non-native species diversity by opening up space for establishment within the perennial grass matrix. Mark Stromberg (personal communication) has observed that feral pigs avoid grubbing directly under established native perennial grasses in the central California coast and at any particular locale they do not appear to decrease cover of native perennial grasses. Instead, they rototill enormous swaths of annual dominated grassland with unknown effects on native species diversity. It is likely that pig effects vary with climatic and edaphic factors and with the pool of species that is available for colonization. We believe that pigs have the potential to be an important and widespread structuring force in California grasslands with a strong influence on the outcome of restoration efforts, but controlled experiments are necessary to evaluate the factors that determine the outcome of grubbing activities.

Impacts of fire and grazing on composition of California grasslands

Methods for conducting this review:

We utilized the following computer databases to search the published literature for studies documenting the impacts of fire and grazing on California grasslands: BIOSIS (1985-2001), Web of Science (1945-2001), Current Contents, CAB, WORLDCAT, and Agricola (1970-2001). In addition, we checked MELVYL, Dissertations-On-Line and the individual libraries for University of California, and California State Universities for theses, dissertations and other literature. Subject keywords used to search these databases were "California" in combination with each of the following: grassland, prairie, *Stipa, Nassella, Elymus, Poa*, and *Danthonia*. The results of these searches were further refined with the subject words "fire", "burn", “grazing”, “livestock”. Additional studies were located from the references of these papers. To obtain access to unpublished studies, we surveyed ecologists from The Nature Conservancy's field offices in California, the National Park Service, State and County Parks, USDA, UC Cooperative Extension Offices and major consulting firms (see Contact List, Appendix A).

Initially we had hoped to gather enough studies to conduct a meta-analysis of the overall role of both grazing and fire in affecting rangeland composition in California. Meta-analysis synthesizes the results of multiple studies in order to statistically analyze the general outcome of a given treatment (Osenberg et al. 1999). A meta-analysis review involves the calculation of a standard treatment effect size that can be averaged across independent studies (Gurevitch and Hedges 1993). These analyses are particularly useful for ecosystem scale studies that are difficult to replicate in time and space (Bender et. al 1998). To do the meta-analysis, effect size is calculated for the variables of interest for each study. It is defined mathematically as natural log of the ratio $[X_{grazed}/X_{control}]$ where X represents cover, biomass or abundance of a species or group of interest in a given study that could be responding to the main treatments. We will refer to mean effect size as response ratios (lnRR). The average effect size is evaluated statistically within and among categorical groups based on attributes of the studies to determine if effect size is influenced by one or more predictor variables. “Qb” is a test statistic that indicates whether the treatment category you are examining (for example burned plots versus not burned plots) contributes significantly to explaining the variation in response found in the data set. Higher values correlate with greater explanatory power of the treatment of category in question. We conclude that a predictor variable is “significant” or that an effect size is greater than zero when there is at least a 95 % probability that we are correct in judging it. Statistical significance is presented in terms of P (probability) values where $P<0.05$ means that the probability of deciding a given factor or a given level of change is important when it is not, is less than five percent.

For inclusion in our meta-analysis, a study had to meet the following criteria: (1) Performed in the California floristic province in a grassland with at least some native species present, (2) Replication of treatments (i.e. $n>1$), (3) Use of an ungrazed or unburned control plot for comparison against the grazed or burned plots and (4) Collection (and availability) of data (i.e. means and variances) on the difference in abundance (as cover, biomass or frequency) of native plants in grazed or burned and ungrazed or unburned plots in order to provide a common metric of outcome (Fernandez-Duque and Valeggia 1994). Common problems we encountered were a lack of true replication and lack of data on variance among plots. For grazing, only six data sets met the criteria for inclusion in the meta-analysis. This sample size is prohibitively small for meta-analysis, and we present a qualitative rather than quantitative summary of the grazing studies we located in the following section (for details of all the studies we located see Tables 1 & 2). We did however, estimate an effect size in each of the grazing studies that met the meta-analysis criteria and present a discussion of the general direction of this ‘grazing’ effect for those studies.

For our review of fire impacts, we found 19 studies that fit the criteria for meta-analysis. While this also is not a large number, it was enough to conduct an analysis. Additional detail on methodology and results of this analysis are summarized in Appendix B.

Does livestock grazing matter?

Despite the position of some conservationists that livestock grazing is incompatible with native biodiversity preservation (Fleischner 1994, Painter 1995), managed grazing practices have been endorsed as a tool for promoting biodiversity in native grassland remnants and for restoration projects (e.g. Menke 1982, Edwards 1995, 1996, Reeves 2001). Reconciling these views in the context of the California grassland is complicated by the large climatic gradient encompassed by the habitat, pronounced inter-annual variation in weather patterns, strong topographic variation and regional variation in the species pool. At any one site, the impact of grazing arises out of the complex interaction of several variables including the history of land use (e.g. cultivation and grazing history), the current and recent management scheme (i.e. the timing, intensity and frequency of grazing), the abiotic environment (e.g. soil type, elevation, precipitation and temperature) and the species composition of the plant community (Heady 1984). Across sites, the interaction between climate and grazing in relation to native plant distributions is likely important but has not been rigorously examined (but see Dyer et al. 1996, Langstroth 1991, Jackson and Bartolome in press). Given the overriding role often attributed to climate in native bunchgrass distribution (Bartolome et al. 1980, Wester 1981, Hamilton et al. 1999), this interaction needs to be carefully addressed.

In theory, because plant species differ in phenology (e.g. early versus late-season annuals), the timing of grazing should differentially suppress or promote species by mitigating competitive interactions and/or reducing fecundity (Augustine and McNaughton 1998). For example, early spring grazing has been shown to suppress the faster germinating exotic annual grasses, thereby reducing the competitive suppression of perennial bunchgrasses whose seedlings germinate slightly later and grow more slowly early in the season (Love 1944, Langstroth 1991, Dyer et al. 1996). Similarly, reductions in the density and fecundity of the invasive forb *Centaurea solstitialis* have been achieved through application of grazing before seed maturation, with concomitant increases in elements of the native flora (Thomsen et al. 1993). The frequency and intensity of grazing influences the rate of live biomass accumulation on a site, thereby affecting the rate of competitive displacement in a multispecies community (McNaughton

1968, Noy-Meir et al. 1989). Additionally, grazing affects the amount of plant litter at the soil surface with important indirect effects on patterns of germination and seedling establishment (Heady 1956, Facelli and Pickett 1991). Grazing livestock also modify physical and chemical properties of soils with important implications for nutrient cycling, hydrology and plant composition (Weaver and Rowland 1952, Hobbs 1996, Jones 2000).

Grazing influences plant composition directly through herbivore selectivity (i.e. plant palatability) and indirectly via interspecific variation in tolerance to herbivory (Belsky 1986, Augustine and McNaughton 1998). Systematic investigations of native plant palatability and species responses to grazing have not been carried out in native California grasslands since the early studies of Gordon and Sampson (1939), but scattered anecdotal and experimental evidence is available. Based on observations of moist coastal grassland at Sea Ranch (Sonoma County), *Elymus glaucus* and *Calamagrostis nutkaensis* (reed grass) are thought to be unpalatable to livestock, resulting in their persistence on some grazed sites (Dwire 1984). A somewhat better-studied species is *Danthonia californica*, which has been observed to be both palatable and tolerant of moderate levels of grazing on coastal sites in northern California (Cooper 1960, Hatch et al. 1999). Several species of native forbs (e.g. *Iris* spp., *Orthocarpus* spp., *Ranunculus californica*, *Limnanthes* spp., *Orcuttia* spp., *Limnanthes floccosa*) may increase under light to moderate levels of grazing (Edwards 1995, Barry 1998), possibly due to the suppression of co-occurring exotic annual grasses.

The most thoroughly studied of the California grassland natives, *Nassella pulchra*, provides a case study of the difficulties inherent to generalizing about a species' response to grazing across environments. Huntsinger et al. (1996) and Dennis (1989) found substantial variation in response to defoliation among different populations, and exclosure studies have yielded equivocal results on the response of *N. pulchra* to both grazing and protection from grazing (Bartolome and Gemmill 1981, Stromberg and Griffin 1996, Hatch et al. 1999). Predictions of grazing impacts are further complicated in considering the larger community of California grassland plants due to the variable tolerances and diverse regeneration requirements represented in the native and exotic flora. For example, anecdotal evidence suggests that some species rely on microsites generated by cattle trampling for germination or reproduction (Barry 1998, Reeves 2001) whereas other plants may decline in the presence of grazing. Due to inter- and intraspecific variation in palatability and response to grazing, management plans intended to maximize native biodiversity will need to be calibrated to local conditions (Dennis 1989, Huntsinger et al. 1996). Rigorous studies of the response of native plant species to livestock grazing are necessary for the design of appropriate grazing plans.

General approach & issues in reviewing grazing studies in California

Our literature review was conducted with the goal of testing the hypothesis that livestock grazing changes the abundance of native California grassland plants. We had hoped to obtain enough studies to evaluate how geographic, edaphic and historical factors might influence the domain under which this hypothesis held true. However, this was not possible. Although an extensive literature documents the impact of grazing effects in California annual grasslands (e.g. Heady 1956, 1958, Pitt and Heady 1979, Rosiere 1987, Bartolome and McClaran 1992), relatively few studies have examined the impact of grazing on native plants (see Table 1, for a complete listing). Of the studies that have considered the native flora, many lack replication and control plots (Table 2), complicating the interpretation of their results and limiting their applicability to other sites. Moreover, studies of grazing and native plants suffer from a narrow taxonomic scope, often focusing solely on *N. pulchra.* Additionally, the spatial distribution of the existing studies is restricted to a small portion of the broad geographical range formerly occupied by California native grasslands (Table 3) so regional variation in grazing effects cannot be reliably detected.

Six studies that met meta-analysis criteria were used to determine the cumulative effect size of grazing on plant functional groups (Dyer unpublished, Dyer and Rice 1997, Jackson pers. comm., Marty unpublished b, Keeley unpublished, TNC 2000). Effect size is defined as natural log of the ratio [$X_{grazed}/X_{control}$] where X represents cover or biomass of the plant species or group of interest in a given study. These studies were conducted at 5 different sites during different years so data include at least some geographic and climatic variation. However, for most comparisons the number of studies required to change results from statistically non-significant to significant (referred to as the “fail-safe number”) is very small, indicating a danger in drawing any conclusions from this analysis. The number of studies recommended for obtaining a truly reliable result based on a small fail-safe number is 40 (5n+10; where n is the number of studies already used) (Rosenthal 1979). Accepting these limitations, the data do suggest a positive effect of grazing on native vegetation, particularly native perennial grasses, when all grazing regimes are lumped together (Table 4). Wet season and continuous grazing in particular appear to have a positive effect on native perennial grasses although differences between grazing regimes were not significant (Qb=0.9844, P=0.611, df=2). However, in contrast to claims of others (Thomsen et al. 1993, Kephart 2001), the effect of grazing on native forbs is negligible. Exotic grasses appear to be little affected by grazing in general but may benefit slightly from continuous grazing. Finally exotic forbs appear to benefit slightly from grazing, particularly in the dry season, but the effect was not statistically significant (Qb=4.1364, P=0.126, df=2).

Numerous other studies, while not useful for meta-analysis, offer valuable insights into the role of grazing in California grassland restoration. We identified three general categories into which the existing studies can be placed and discuss them separately in the following sections. They include: 1) Livestock exclosure studies, 2) Manipulative experiments that examine the response of established plants and early life stages to grazing treatments of particular timing and/or intensity, and 3) Controlled grazing of invasive, exotic plants in conjunction with native plant monitoring.

Livestock exclosure studies

Exclosure studies compare the community composition of actively grazed plots to plots that had been previously grazed for decades but subsequently protected from livestock for varying numbers of years. Many of these studies have unreplicated and/or uncontrolled experimental designs that limit the interpretation of their results (Table 2). The studies also measure grazing intensity in inconsistent ways (or not at all), precluding the standardization of grazing intensity across studies. Knowledge of the land use history of a site is imperative to the interpretation of experimental results. Because virtually all of the California grassland has been grazed by livestock at some point in time, there is no “pristine” grassland to serve as a baseline for comparison with grazed sites (Fleischner 1994). Additional issues to consider in interpreting experimental results include spatial scale (e.g. plant distribution patterns in an exclosure plot may be caused by different processes than patterns found at the landscape scale; Bartolome 1989a) short temporal scales (the initial response of a community to protection or release from grazing may not represent the long-term response) and the pool of species that are present or able to disperse to the protected area. Despite their shortcomings, exclosure studies are one of the few practical approaches to evaluating long-term grazing impacts (Bock et al. 1993, Fleischner 1994).

Native plants exhibit patterns of increase (e.g. *Deschampsia holciformis* [hairgrass] Foin and Hektner 1986), decrease (e.g. *Danthonia californica*; Hatch et al. 1999) or no change (*N. pulchra*; Stromberg and Griffin 1996) in response to protection from livestock grazing. The inconsistency in response is likely a result of variation in grazing tolerance and life history among native species and variation in experimental conditions and among years in which the studies were done.

Studies that have focused on the response of *N. pulchra* to grazing protection yield a picture of the complex response of this native bunchgrass to protection from livestock grazing. In inland sites at the Sierra Field Station, *N. pulchra* increased in abundance after protection from grazing (Hatch et al. 1991). By contrast, experiments from a coastal site (Pomponio Beach State Park, San Mateo County) found that *N. pulchra* and *N. lepida* (foothill needlegrass) declined or increased in abundance within exclosures (Hatch et al. 1999). These inconsistent findings could be due to ecotypic differentiation in grazing tolerance between coastal and inland populations (Huntsinger et al. 1996) or to regional variation in the effects of grazing. *N. pulchra* exhibited similarly inconsistent responses to grazing protection over 41 years in two permanent exclosures at the Hopland Field Station (Mendocino County; Bartolome and Gemmill 1981; Merenlender et al. 2001). In one exclosure, the density remained stable, whereas *N. pulchra* declined in the other exclosure over 21 years, and then returned to the original density after 41 years (Merenlender et al. 2001). However, this finding cannot be clearly attributed to the exclusion of grazers as no adjacent, grazed sites were sampled for comparison.

Other studies have shown that *N. pulchra* abundance was unchanged after protection from grazing. Two studies in coastal grassland within and around the Hastings

Natural History Reservation (Monterey County) found that *N. pulchra* abundance was similar between grazed sites and sites that had been protected from grazing for 27 years (White 1967) and 54 years (Stromberg and Griffin 1996). Time series data (covering 1971 to 1991) on *N. pulchra* frequency along permanent transects in ungrazed grassland at the Hastings show no significant change in distribution over time (Stromberg and Griffin 1996). The lack of consistency in these results suggests that site characteristics, regional variation, or intraspecific differentiation may be governing the response of *N. pulchra* populations to livestock grazing. Clearly, manipulative experiments that employ regional replication on sites of known land use history are required to establish a relationship between *N. pulchra* distribution and grazing.

Of more direct utility to restoration planning are studies that examine community-wide responses to protection from grazing. A study of 79 sites in the Outer Coast Range near Hastings (Monterey County) found that grazed and ungrazed sites differ in composition and relative abundance of species, but the differences were species-specific rather than generally favoring natives over exotics (Stromberg and Griffin 1996). Although community composition differed among plots with different periods of protection from grazing (based on canonical correspondence analysis), the patterns of plant community composition were relatively stable over time, indicating that native species as a group failed to return to dominance after livestock exclusion. While livestock grazing was not associated with any known local extirpation of native plants (with the possible exception of *Elymus glaucus*), the invasive exotic grasses *T. caput-medusae* and *Lolium multiflorum* (Italian ryegrass) exhibited higher densities on grazed than ungrazed plots (Stromberg and Griffin 1996). Native species that achieved higher densities on grazed sites included *Koeleria macrantha* and *Hordeum californicum* (California barley).

Harrison (1999) similarly found that native species did not dominate (as a proportion of the total species) sites protected from livestock grazing over a period of 13 years. In a study that compared 80 sites from four treatment groups (i.e. grazed and ungrazed sites on serpentine and non-serpentine soils) on the McLaughlin Reserve in the inner Coast Range (Napa and Lake Counties), native species richness did not significantly differ between grazed and ungrazed sites (Harrison 1999). As only species richness was reported, patterns of spatial dominance cannot be inferred, and the grouping of individual species into native and exotic categories masked any species-specific responses to grazing. Using the vegetation along adjacent sides of fencelines to assess potential grazing impacts, Safford and Harrison (2001) found that the effects of grazing were different depending on whether soils were influenced or not influenced by serpentine. On serpentine grassland sites native diversity was lower in grazed than ungrazed sites, but there were no clear effects of grazing in non-serpentine sites.

Another community-wide study measured changes in the grassland plant assemblage as cattle were gradually removed from coastal grassland in Mount Diablo State Park, Contra Costa County (Micallef 1998). Permanent transects were sampled at three dates (1982, 1992, 1996); the earlier sample dates recorded only the tallest plant at each point, whereas the last sampling date recorded both "tallest-only" data and all species at each point. The "tallest-only" data failed to accurately represent the understory vegetation (especially forbs), yielding very different results than the comprehensive (i.e. all species recorded) data (Micallef 1998). Plots were assigned into four grazing intensity classes (high, medium, low or ungrazed) and vegetation data were grouped into six categories for analysis: native or exotic forb or grass, and all native or all exotic plants. Across all three sampling dates, the exotic grass, all native and all exotic categories increased with decreasing grazing pressure, while other categories showed no significant response. While the 1996 data did not show any significant relationships with the grazing intensity categories, the most heavily grazed sites had significantly lower native forb abundance than sites released from grazing (Micallef 1998). Anecdotal evidence from photographic documentation and observations of particular species over the course of the study suggested a general trend of increase in native plant abundance with decreasing grazing pressure that was not apparent from the data analysis (Micallef 1998). Some native grasses decreased over the course of the study (*Bromus laevipes*, *Vulpia microstachys*) and a variety of native herbs and grasses increased (*N. pulchra*, *Melica californica*, *Elymus glaucus*, *Agrostis pallens*, *Achillea millefolium*, *Holocarpha heermanii*, *Clarkia purpurea*). Some exotic invasive plants also increased with declining grazing pressure (*C. solstitialis*, *Torilis nodosa*, *Cynosurus echinatus*).

An observational study performed in coastal grassland (Sea Ranch, Mendocino County) suggests that certain perennial exotic species may achieve dominance on sites protected from grazing. An unreplicated comparison of grazed and ungrazed sites (Foin and Hektner 1986) found that plots protected from grazing for 10 years had elevated densities of exotic perennial grasses (i.e. *Anthoxanthum odoratum* and *Holcus lanatus*). D'Antonio (unpublished) is observing increased abundance of exotic perennial grasses along transects in a coastal site (Marin County) that has been protected from livestock grazing for 30 yr but without grazed sites, we cannot say whether invasion would be faster or slower with grazing. However, these invasive perennial grass species have become dominant only in coastal areas, primarily in the northern and central parts of the coastal prairie, and may not represent a problem for native grassland restoration in more inland sites (C. D'Antonio, personal communication).

Common conclusions of exclosure studies are that native plants do not return to dominance after protection from livestock grazing, and exotic plants persist as a major element of the vegetation. One hypothesis to account for this finding is that livestock grazing explains less of the variation in plant distribution than site-specific factors such as land use history, climate and soils. Stromberg and Griffin (1996) note that many native grassland plants were absent from previously cultivated sites, independent of livestock grazing and that land cultivation, elevation, soil texture and aspect all explained patterns of community composition more effectively than grazing (Stromberg and Griffin 1996). Similarly, Harrison (1999) found that soil type (i.e. serpentine vs. non-serpentine) and aspect better accounted for patterns in plant species richness than did grazing effects. The importance of site-specific factors is also consistent with the variation in the response of native plants to protection from grazing. This variability underscores the need for studies that include previous site history as an experimental factor, employ sufficient replication to permit rigorous analysis and occur over a spatial scale that encompasses regional environmental gradients. Additionally, more information on the responses of particular native species to grazing will be needed to meaningfully interpret patterns of distribution and inform management plans.

Manipulations of grazing regime

The grazing regime applied to a site influences plant distributions and it has been suggested that some grazing regimes may enhance native biodiversity more so than others (WallisDeVries et al. 1998). Many manipulations of grazing intensity have been performed in California annual grassland sites with only negligible native plant cover (e.g. Pitt and Heady 1979, Rosiere 1987, Jackson and Bartolome in press). The species composition and relative abundance of annual grassland communities are largely unaffected by livestock grazing, and climatic variation is believed to be the primary control over composition (Heady 1977, Jackson and Bartolome in press).

The amount of plant litter (i.e. mulch or residual dry matter) on the ground has been used as a proxy for grazing intensity, with mulch density or biomass serving as a negative correlate of grazing intensity (Bartolome et a., 1980, Jackson and Bartolome in press). Mulch influences moisture, light intensity and temperature at the soil surface, with effects on germination and seedling establishment (Weaver and Rowland 1952, Heady 1956, Facelli and Pickett 1991). Estimates of mulch or residual dry matter cover are often used to determine when to remove livestock from a paddock and so are representative in a broad sense of how grazing intensity decisions are often made. Yet we know little about the science behind their use. Most mulch manipulations have been performed in annual grasslands, but Bartolome et al. (1980) examined the response of native perennial grasses to various levels of mulch application in three coastal grassland sites (Humboldt County). Native grass growth was most enhanced by the highest level of mulch application employed in the experiment (1,120 kg/ha), suggesting that a low grazing intensity is most appropriate for increasing cover of native bunchgrasses. However, the effects on species composition and relative abundance were not measured, nor was the mechanism behind the pattern identified. Savelle (1977) found that removing mulch from *N. pulchra* tussocks resulted in increased seed production, and other experiments suggest that mulch can inhibit *N. pulchra* seedling establishment (Dyer et al. 1996). The effects of mulch on different life stages of native plants should be evaluated in experiments that involve a variety of native species.

Other studies have employed specialized grazing regimes with the goal of increasing the native, perennial component in annual-dominated grasslands. These studies would be useful for designing grazing regimes for restoration purposes, but all studies to date suffer from serious design flaws (e.g. no control plots) that complicate their interpretation and limit their applicability beyond the study sites. Observations from coastal grassland in Humboldt County indicate that a change from a continuous, high-intensity cattle grazing regime to an intermittent, moderate-intensity grazing rotation led to a 10% increase in *D. californica* abundance and a concomitant 35% decrease in the abundance of the invasive exotic grass *Taneiatherum caput-medusae* over 3 years (Cooper 1960). *Danthonia californica* decreased in frequency and cover within grazing exclosures (relative to grazed plots) in a coastal grassland site in San Mateo County (Hatch et al. 1999). Reeves and Morris (2000) found that applying a grazing regime based on holistic management principles (Savory and Butterfield 1999) to grassland in San Benito County resulted in increased abundance of native perennial bunchgrass over three years, but their study design is unclear and lacks control plots. Kephart (2001) used sheep and goat grazing to reduce the dominance of aggressive exotic plants (e.g. *C. solstitialis*) in mixed grassland in San Mateo County. After two years of short-duration, intensive grazing, native species richness increased and cover increased only slightly. Exotic species richness was unchanged although cover of exotics increased substantially. Unfortunately, this experiment also lacked an ungrazed control.

Properly timed application of livestock grazing can enhance the establishment and growth of native grasses by suppressing annual grasses. An early study (Love 1944) in inland grassland (Sacramento County) compared the establishment of *N. pulchra* and *N. cernua* in plots that were grazed by sheep in early April versus late April. Love (1944) suggested that the greater success of the native grasses in the early grazed field was due to the removal of the taller annual grasses, resulting in the release of native perennials from competitive suppression. The later grazing treatment occurred as the wet-season ended and the perennial grasses were unable to develop sufficient root biomass to survive the dry conditions (Love 1944). A series of related experiments on livestock grazing and *N. pulchra* distribution compared the effects of grazing in the wet and dry seasons at the Jepson Prairie Preserve (Solano County; Fossum 1990, Langstroth 1991, Dyer et al.

1996). Seedling emergence and survival were higher in the wet-season grazing treatment (especially in combination with burning) compared to the dry-season grazing treatment and an ungrazed control (Fossum 1990, Dyer et al. 1996). The putative mechanism behind this result was that litter removal increased light levels at the soil surface and enhanced seedling survival (Langstroth 1991, Dyer et al. 1996). However, neither grazing nor burning had a significant effect on emergence when the experiment was repeated a year later, suggesting that the effects of the treatments were mediated by climatic conditions (Dyer et al. 1996). Only a tiny fraction of the seedlings that emerged survived after four growing seasons (99.99% mortality), possibly due to below average rainfall following the treatments (Dyer et al. 1996). Wet-season grazing decreased the basal diameter of individual plants but enhanced reproduction via plant fragmentation, leading to an increased density of *N. pulchra* plants relative to ungrazed plots. Though wet-season grazing improved the establishment and vegetative reproduction of *N. pulchra*, plant microsite (i.e. on top of or between Mima mounds) exerted stronger effects on plant responses than the grazing treatments (Dyer et al. 1996, Langstroth 1991).

The majority of evidence suggests that properly managed livestock grazing can be employed to increase native bunchgrass abundance in California grasslands in some situations. However, most of the existing studies suffer from serious shortcomings, including flawed experimental designs particularly the lack of any sort of control. Annual climate variation greatly limits the interpretation of studies without ungrazed controls and pseudoreplication constrains the applicability of individual studies beyond the particular site. Additionally, there is little information on the response of native forbs to grazing treatments that seem to enhance bunchgrass abundance.

Due to the variation in response to grazing that is found in the native grassland flora, it is reasonable to assume that no single grazing regime will be optimal for all native species. A management plan that varies the timing and intensity of grazing on a landscape scale may better enhance native plant diversity than the uniform application of grazing. Properly designed experiments that explicitly examine the response of native species assemblages to different grazing regimes (including complete protection from livestock) are necessary to determine the utility of grazing in restoration projects.

Effects of controlled grazing on invasive exotic plants

Several invasive exotic plant species (e.g. *C. solstitialis*, *Cirsium* spp., *Phalaris aquatica*) are capable of forming dense stands that exclude native vegetation in California grasslands. The control of such plants with domestic grazers has been effectively employed in a variety of grassland habitats (Popay and Field 1996). In California grasslands, the invasive annual forb *C. solstitialis* has been the focus of management efforts that employ grazing and herbicide application (Thomsen et al. 1993, Kephart 2001). Experiments at Arrowhead Ranch (Colusa County) and the UC Davis Agronomy Farm (Sacramento County) have aimed to determine the efficacy of different grazing plans to decrease the abundance of the *C. solstitialis* (Thomsen et al. 1993). Grazing by sheep, cattle and goats drastically reduced the density of *C. solstitialis* flowerheads and seedlings over two years at both sites (Thomsen et al. 1993). Furthermore, a concomitant increase in native annual forbs (i.e. *Lupinus bicolor*, *Calandrinia ciliata* and *Limnanthes douglassii*) was associated with the reduction in *C. solstitialis*. The timing of the grazing application in relation to *C. solstitialis* phenology was the most important determinant of the treatment's effectiveness (Thomsen et al. 1993). Kephart (2001) similarly reduced *C. solstitialis* density and enhanced native plant diversity with controlled grazing. Controlled grazing therefore appears to be useful in reducing the dominance of *C. solstitialis.* Its usefulness in controlling other exotic pest species needs to be experimentally explored. It may be useful in the initial stages of a restoration project, in controlling localized outbreaks of exotics and in situations where the use of herbicides is undesirable (Popay and Field 1996).

Importance of species of livestock

We had hoped that this review would turn up enough studies to evaluate whether or not some of the variation in livestock grazing impacts could be attributed to differences in the types of grazing animals on a site. However, very few individual studies compare the effects of different types of livestock using replicated experimental plots. Also, we found so few studies that met the criteria for use in a meta-analysis that is was not possible to quantitatively compare the effects of sheep, horses and cows on California rangeland structure across studies. One exception, Keeley (unpublished) compared impacts of horse grazing versus cattle grazing on a valley grassland community in the Sierra Nevada foothills. Pastures grazed by horses versus cows were also compared to pastures released from all livestock grazing. Two years after treatments were implemented, there were no significant differences between treatments in cover of exotic species although there was a trend (P<.09) towards decreased richness of exotic species in pastures released from all livestock grazing and but no difference between horse and cow grazed pastures. Cover of native perennial species did not differ among treatments. Other attempts to compare different types of livestock also suggest that there are not strong or consistent differences in their impacts or that factors such as timing of grazing were more important than the type of grazer (Thomsen et al. 1993).

Conclusions regarding livestock grazing impacts

The relationship between livestock grazing and California's native grassland plants has not been clearly established. The existing data show that the interactions among livestock, exotic plants and native plants are complex and variable across regions and years. Grazing has been shown to benefit some native plant populations but the positive response to grazing is not universal among native species or across locales for any one species. Further research that employs both extensive surveying of properties with different grazing histories over a range of environmental conditions plus properly designed experiments are necessary to clarify the role of grazing in shaping native grassland diversity and restoration efforts. Future studies need to examine the response of the entire native species assemblage to grazing treatments, particularly native forbs since they have been largely overlooked in previous work. The inconsistent results from previous studies suggest that site-specific factors (e.g. species pool, land use history) and regional climatic differences exert a strong influence on the response of native plants to grazing. Studies that examine the sources of variation in the relationship between livestock grazing and native plants can provide a general framework to guide development of prescriptions for the use of grazing in restoration projects.

In addition, we know almost nothing about the impact of livestock grazing on rangeland composition in the presence of an oak canopy yet enormous areas of California grassland include oaks. Further observational and experimental work must include comparisons between oak understory and open grassland if we are to make headway in understanding how to manage these extensive savanna environments. We therefore recommend a combination of extensive survey and experimental work across a range of grazed and ungrazed environments in California oak savanna environments. Lastly, because residual dry matter (mulch) standards are used by many land managers as an index of grazing intensity, we need further experimental manipulations of mulch across a broader range of habitats including oak woodland understory to better understand what various levels mean to community composition.

Influence of Fire on the California Grassland

Fire has been proposed to be one of the most important factors affecting the origin and distribution of North American grasslands (Sauer 1950, Stewart 1951, Wells 1962, Axelrod 1985). While there is debate over whether or not this is true (see Vogl 1974, Jacobs et al. 1999), fire is clearly a common natural disturbance in grasslands and most grassland species are tolerant of fire within the natural regime of frequency and season. In the pre-European California landscape, fire may have been important in structuring vegetation including maintaining open grassland within the oak woodland, scrub and grassland mosaic where grassland was not the edaphic climax community (Mensing 1998, Callaway and Davis 1993, Westman 1976, McBride and Heady 1968, Vankat and Major 1978, Sugihara et al. 1987). Within the pre-contact grassland community, fire may also have been important for maintaining taxonomic and structural diversity. Yet other than identifying lightning and Native Americans as the main sources of ignition, we know little about the specifics of grassland fire regimes prior to European settlement (Komarek 1967, Blackburn and Anderson 1993). Fire frequency presumably increased after human settlement (approximately 12,000 BP) but changed again with European settlement (150+ yr ago) (Parsons 1981, Bartolome 1989b). Native Americans used fire as a means of increasing the abundance or fecundity of geophytes, grasses and particular forbs that were used for food, medicine, and fibers, in addition to managing game species (see Blackburn and Anderson 1993) and in some areas, grassland sites may have burned every year (Aschmann 1977, Blackburn and Anderson 1993). Greenlee and Langenhem (1990) estimated a pre-contact fire frequency between 1 and 15 years for the grasslands of the central coast.

Today, fire has been used in contemporary California grasslands to manage rangelands for livestock production by increasing productivity and forage quality, and eliminating noxious weeds (Menke 1989). Most recently, prescribed fire has been used as a means of reducing the abundance of non-native species and restoring native plants to grasslands throughout California. Yet there has been no systematic evaluation of the success of these 'restoration' efforts, and we do not currently know when and where the use of fire achieves conservation goals in California grassland.

Why should fire change the balance between native and exotic species?

Fire can aid restoration efforts in California grasslands because if hot enough, it can directly kill seeds in the soil and on adult plants, thereby reducing the density of potential competitors for native perennial species. Fire can also directly stimulate the germination of native forbs and release nutrients for use by establishing seedlings. Conversely, the exotic annuals that dominate contemporary California grasslands are said to have great resilience to the effects of fire (Keeley 1981) and very high rates of biomass production (Menke 1989). Because fire can increase the production of grassland vegetation after the initial direct reduction of above ground biomass (Vogl 1974), it could stimulate exotic grass productivity which could interfere with efforts to establish native species. In addition, reductions in non-native annual grass biomass that many people claim to observe in the first season following fire are rarely sustained beyond the first year, so (as discussed below) short-term benefits to native species may be ephemeral.

Fire generally results in an increase in available nitrogen (N) and phosphorus (P), increased N mineralization rates, enhanced N fixation and altered microclimatic conditions. In the California annual grassland, both low and high intensity fires resulted in higher nutrients in the ash residue but also significant volatilization losses of N and S (Menke and Rice 1981). Most of these changes occur immediately after fire and are associated with short-term microclimatic changes, including increased soil temperature and light, and decreased soil moisture. Increased available nitrogen may have negative effects on species native richness by favoring just a few fast growing species (Foster and Gross 1998, Stohlgren et al. 1999) including some exotics. Frequent fires, however, have been proposed to have long-term negative effects on available soil N and grassland productivity because they cause repeated volatilization of N and increased root death. The latter results in higher soil carbon (C), which in turn could result in N immobilization by soil microbes (see Seasteadt et al. 1991). It is not clear how this would affect the balance between native and non-native species.

Plant phenology and the susceptibility of meristems (regions of active cell division in plants) to fire are important determinants of interspecific variation in fire tolerance among species. In the peak of the growth season, grasses and many forbs have shifted their resources above ground where they are vulnerable to fire. Because there is variation in the phenology of individual species even within a life form group (e.g. native perennial grasses), the timing of fire may damage one set of species and thereby elevate the other to dominance. Species with buds and meristems located within plant tissues or by the soil surface are more likely to survive an intense fire than those with exposed or vulnerable meristems. Fire may increase growth and reproduction in some perennial grasses but not others (Daubenmire 1968, Vogl 1974).

Fire generally shifts grassland community structure towards forbs (Antos et al. 1983, Kucera 1970, Graham 1956, Hervey 1949, Heady 1972). By reducing the accumulated litter layer fire in grasslands, fire increases the proportion of forb species (e.g. Heady 1956, Heady et al. 1999). The increased light availability and temperature at the soil surface enhances germination of forb seeds. Geophytes (bulb plants) also generally increase flowering after fire (Mitchelson 1993, Gill 1977, Stone 1951) as a response to increased light (Stone 1951). Germination in legumes and other species with physical seed dormancy may increase as a result of the direct effects of fire (heat scarification) rather than secondary effects such as light (Baskin and Baskin 1998).

Fire application can be manipulated temporally in order to correspond with the phenology of target species (native or non-native). Soil seed banks of non-native annual grasses are generally large (Major and Pyott 1966, Bartolome 1979). Seeds are more vulnerable to fire prior to dispersal because they are unprotected by soil and seed moisture content is higher (i.e moister seeds are more susceptible to death by heating).

Prescribed burning can effectively suppress these species if applied before mature plants disperse their seed in the spring (e.g. Pollack and Kan 1998). Conversely, burning after seed dispersal and before germination may increase the abundance of exotic species that have increased establishment on bare ground such as many forbs. Post-germination burning (such as during an early winter drought) may be effective in reducing the soil seed bank of non-native annual grasses by eliminating seedlings. However, such wet-season burning is also potentially dangerous to native species in the soil seed bank because seeds that may have already imbibed water are more susceptible to high temperatures than are dry ones (Parker 1987). Effects of fire on the grassland soil seed bank are expected to be variable because of differences among species in their tolerance of high temperatures and heterogeneity in the intensity and duration of fire on the soil surface. Menke and Rice (1981) found that soil seed density of the exotic grasses *Bromus hordeaceous* and *Taeniatherum caput-medusae* decreased 50% after a summer burn. However, Eller (1994) found no significant difference in soil seed bank density of native forbs, exotic forbs or non-native annual grasses after a spring and a fall burn in another California annual grassland. It is likely that differences in burn characteristics determine this variation in response among studies yet few studies quantify fuel moisture and fire characteristics.

Fire intensity can be manipulated to some extent by season of burn and pre-treatments that influence fuel load (including intensive grazing to reduce fuel or rest from grazing to increase fuel), and by ignition strategies (i.e. using a headfire [driven by wind] versus a backing fire [burning into the wind]). Intensity is also influenced by factors that cannot be controlled, such as slope, soil texture, and humidity and temperature (Daubenmire 1968). Controlled burns tend to be less intense than wildfires, and small fires less intense than large fires. There have been no studies that compare burn season *and* fuel load to vegetation response in California grasslands, although several studies compare burning in different seasons to each other or look at the interaction between fire and grazing.

Review of Fire Studies

We located 28 studies that quantitatively addressed the effects of fire on native and exotic plants in California grasslands (Table 1). Of these, 10 are in peer-reviewed journals, 12 are unpublished theses or dissertations and the remaining 6 are unpublished (in progress) data sets. The majority measured the effects of prescribed or experimental burns but a few report results from natural or unplanned fires (York 1997, Delmas 1999). The research objectives and design of each study are summarized in Table 5.

In order to statistically evaluate and synthesize the results of the burn studies, we used meta-analysis, as described above (and see Appendix B for a detailed description of methods and interpretation of meta-analysis used in this section). Nineteen of the 28 fire studies we located were suitable for inclusion in the meta-analysis. The other 9 lacked appropriate controls, replication or measures of variation among sample plots. We used abundance variables such as biomass and percent cover as measures of responses to fire and calculated mean response ratios across all appropriate studies by comparing the cover or biomass of the species or group of species of interest between burned and unburned plots (expressed as lnRR values= natural log of the ratio [$X_{burned}/X_{control}$]). When lnRR values are near zero it indicates that the species or group of plants showed very little response to the treatment. Negative lnRR values indicate a decrease in the species of interest relative to its abundance in control plots and positive values indicate an increase. When we say that there is no significant increase or decrease in the cover of a species it means that the lnRR cannot be distinguished from zero with at least 95% confidence. Few studies measured species richness or diversity, precluding the statistical evaluation of these parameters across experiments.

The meta-analysis addresses the following questions about the potential for fire to benefit native species in California grasslands:

1) Does fire consistently result in a decrease in non-native species and an increase in native species? If so, is this effect more significant for some life form groups (i.e. native perennial grasses, non-native annual grasses, non-native forbs, and native forbs) than for others? (If fire does have an effect, how long does this effect last?)

2) Does burn timing, frequency (e.g. single versus repeated burning), and/or grazing influence the effectiveness of fire for enhancing native species?
3) How do the length of the longest winter drought and total annual precipitation in the year following the burn interact with fire to affect native species?

Most quantitative studies on fire in California grasslands provide results for only the first year after fire. For perennial grasses, the number of studies that continued beyond the second and into the third post-burn years was inadequate for most quantitative analyses. Results are presented as either general fire effects (includes all burn treatments), or as one of four treatment types (ungrazed/single burn, grazed/single burn, ungrazed/annual burn [2-3 times], grazed/annual burn).

Cover of all species, native versus exotic vegetation. Across the studies we surveyed, there was high variability among studies in response of the vegetation to fire resulting in no significant increase in total biomass or total percent cover in burned plots in the first year after fire (lnRR=0.067). However, three years after fire, total cover and/or biomass was higher in burned areas. Although the magnitude of this increase is small (lnRR=0.262, N=60), it is significantly different from zero and the heterogeneity of average responses among studies was much lower.

When examined by treatment type, fire results either in a slight decrease or has no effect on total vegetative cover in the first year in all treatments except ungrazed, annually burned sites where there is a significant increase in year 1 (lnRR=0.4704, N= 27; Figures 1 and 2) which lasts through year 3. Oddly, in ungrazed/single burn sites, there is a large second year decrease in plant cover in burned plots but by the third post-fire year vegetative cover springs back and is greater than in unburned treatments. When plots are grazed, there is little difference between burned and unburned plots (response ratios not different from zero) at any time perhaps because grazing reduces fuel and therefore decreases fire intensity resulting in little impact from fire.

Plant species origin (native or exotic) affects the results of our analyses during the first post-fire year (Q=8.36, df=1, P=0.041) but not in subsequent years. Fire generally had a positive, although small, effect on abundance of native vegetation (Figures 1 and 2) and no overall effect on exotic vegetation (combining both exotic annual grasses and forbs). The fire effect on natives in the first year is small but significantly greater than zero and is greater in ungrazed, annually burned sites (lnRR=0.7997, N =12) than all other treatments. By the third year after fire, native vegetation is more abundant in burned than unburned sites (lnRR=0.19-0.45) except for grazed multiply burned sites. In these, response to past fire was not apparent at three years after the cessation of burning (lnRR= 0.03, N=8).

Precipitation had a significant negative influence on first year burn results for total native vegetation (slope=-0.0134, $P<0.05$, df=83) but the amount of variation in response that is explained by precipitation is small (R^2=0.049). Variation among years and sites in the precipitation received during this time ranged from 17 to 150 cm per year. One of the driest sites (Carrizo Plains, 17 cm in 96-97) had one of the highest increases in native cover with fire of any site. This was due to a large increase in native annual forbs. The length of the longest drought period within the growing season (Oct. to April) was negatively correlated with total native cover in the year following fire (slope= -0.0177, $P<.05$, df=83) but the power of drought to explain much of the variation in response among studies is weak (R^2=0.043). Actual burn day (analyzed as Julien day) did not account for a significant amount of the variation in response to burning among sites but comparisons between burn months were significant (Q=14.20, df=3, P=0.014). The strongest positive responses of native cover to burning occurred in June and July fires (lnRR=1.63, N=5).

Fire generally has a small negative or negligible effect on total exotic cover the first year (lnRR= -0.0552, N=265), with the exception of ungrazed, repeat burn sites where the effect of fire on exotics is slightly positive (lnRR= 0.2502, N=15). Burning in both grazed and ungrazed plots resulted in a decrease in exotic vegetation by the second year but this effect was gone by the third year (Figure 1). By the third year after fire, exotic species showed a much stronger positive response to fire in ungrazed (lnRR= 0.7208, N=7) compared to grazed sites (lnRR= 0.1025, N=27). Hence, grazing appears may dampen the increase in exotic vegetation that otherwise occurs with fire by the third year (Figures 1 and 2). The lack of strong effects of fire on total exotic cover may result from fire having opposite effects on exotic forbs as on exotic grasses (see below).

The longest drought period during the growing season and total wet season precipitation did not correlate with the magnitude of response of exotic cover to fire during the first post-fire year. Timing did however, affect the outcome of fire but only in the first year. The greatest change in exotic cover that occurred with fire was a decrease in cover that occurred with March burning (lnRR=-0.9200, N=3) although sample sizes for comparisons among months are low.

Our results also show that the benefit of fire to native vegetation does not correspond with proportional decreases in exotic vegetation cover, especially as the time since the last burn increases. Rather, fire generally either has no effect on or benefits (e.g. forbs) exotic species. Thus, there is often an increase in the total vegetation cover, with proportional increases in both native and exotic components, rather than an unequivocal release of natives from exotic suppression after fire. Nonetheless, the largest magnitude of total native vegetation increase due to fire, occurs in the second post-fire year for grazed, single-burn samples and in the first year after fire for ungrazed, multiple-burn sites. In both of these latter cases exotic vegetation was reduced or did not benefit from fire.

General outcome by life form group.

Response to fire varied among the different life form groups in all three years after fire (year 1 Q=92.09, df=3, P=0.001; year 2 Q=17.40, df=3, P=0.007; year 3 Q=34.99, df=3, P=0.001). Indeed more of the variation in response to fire can be explained by life form group than by fire treatment.

Native perennial grasses. More than half of the quantitative studies on the effect of fire on native perennial grasses included or focused on the response of *Nassella pulchra* or *Danthonia californica*. Most of those studies compared fire with grazing, or tested the interaction of fire and grazing. Ahmed (1983) and Langstroth (1991) conducted detailed monitoring of tillering or fragmentation of *Nassella pulchra* in response to grazing and burning treatments. Two studies focused on the effects of late season fire and grazing on *Nassella* recruitment and seedling survival and growth (Fossum 1990, Dyer et al. 1996, Dyer and Rice 1997). The remaining studies looked at the response of native grasses at the community level (% cover) in a single season after fire. Two of the studies included seeding with native perennial grasses (Garcia-Crespo 1983, Dyer et al. 1996) and two compared a single burn with repeated burning (Betts unpublished, DiTomaso et al. 1999). The results of some of these studies are summarized in Table 6.

Although we used meta-analysis to determine if there was a general effect of fire on native perennial grasses as a group and by individual species, the sample size was very low for perennial grasses and results even for *Nassella pulchra* should be interpreted with caution. The meta-analysis showed that fire decreases abundance of *Nassella pulchra* and native perennial grasses as a group the first year after burning but that the effect is negligible when sites are also grazed (Figures 3-6). Thus, *Nassella* may be less tolerant of isolated burns at ungrazed sites than of grazing/burning combinations. However, the effects of grazing alone, burning alone (burning once versus repeatedly), or various burning/grazing combinations are not significant for native perennial grasses as a group and existing data are insufficient to determine long-term effects of the various treatments.

While *Nasella pulchra* is negatively affected by fire in the first post-fire year, in single burn studies it rebounds after the first year to become almost twice as abundant in burn treatments compared to unburned treatments by the second post-fire year. However, the effect disappears by the third year (Figure 5). A possible mechanism for this pattern is that fire has a negative impact on *N. pulchra* the first year but causes overcompensation in the second year, resulting in a decline the third year. The data suggest that fire does not enhance growth of *N. pulchra*, contrary to some individual studies that suggested a positive response. For example, tussock basal area increased significantly in burned plots compared to control and mowed plants at Hopland Field Station (Ahmed 1983) although foliar cover and biomass did not increase significantly the first post-fire year. Abundance of *N. pulchra* was not significantly changed the year after two other late season (Fall) prescribed fires (Garcia-Crespo 1983, Hatch et al. 1999) but when response was monitored beyond the first year, cover increased significantly beyond unburned plots except when also summer grazed (Langstroth 1991). In another study, *Nassella pulchra* and native perennial grass cover appeared to increase after two consecutive years of June/July burns and even more after the third consecutive burn. However, the increase also occurred in the control site (DiTomaso et al. 1999) suggesting that weather might be more important than burning.

The meta-analysis suggests that like *N. pulchra*, *Danthonia californica* is also negatively affected by fire (Figures 5 and 6) and the magnitude of decrease (lnRR=-0.235, N=6) is similar to that observed for *N. pulchra*. This decrease occurred equivalently in all burn/grazing treatments. Unlike *N. pulchra* however, *Danthonia californica*, does not rebound at any time. In the perennial dominated grasslands of northwestern California, by the first post-burn year, cover and frequency of *Danthonia californica* significantly decreased (-93.1%) in June burn treatments (Arguello 1994) but late summer burning did not cause a significant decrease. Hatch et al. (1999) also saw no decrease in *D. californica* with late summer burning. Arguello (pers. comm.) claims that *Danthonia* eventually recovers if burning is terminated although there have been no long term studies involving this species. The benefit of burning grasslands with this vulnerable species present may be an increase in native forb richness (Arguello, pers. comm.).

Livestock grazing appears to negate the first year negative effect of fire on both *Danthonia californica* and *Nassella pulchra* (Figure 6) and differences in fire effects between grazed and ungrazed burn treatments and their controls are significant ($P<0.05$) for both species. This is probably due to decreased pre-burn biomass in grazed plots which in turn decreases fire intensity.

Overall our results suggest that with the exception of causing a first-year decline in cover, fire does not have a strong effect on *N. pulchra* over time and repeated burning did not affect *Nassella* abundance. The observation by Biswell (1956) that *N. pulchra* persisted in railroad rights-of-way burned annually is consistent with these results. But long-term observations of *N. pulchra* stands excluded from both fire and grazing demonstrate that lack of fire and grazing do not lead to declines in abundance (Bartolome and Gemmill 1981). Together these observations suggest that although *N. pulchra* may be tolerant of frequent fire, or some combination of grazing and burning, it does not require fire to persist at a site. We cannot draw the same conclusions yet about *Danthonia* because many fewer quantitative studies have been done on its relationship to fire and grazing. Also studies of other native perennial grass species are badly needed.

The influence of burn timing (month) for native perennial grasses as a group is significant the first post-fire year. The largest increase results from burning in June (lnRR=2.21, N=2) and the smallest decrease results from burning in September (lnRR=-0.03, N=9). In addition, the longest within season drought period has a significant but small positive effect on post-fire abundance of native perennial grasses (slope=0.02, R^2=0.02, P<0.05, df=32) but total precipitation does not. The only study to compare the effects of burn season on *N. pulchra* (Ahmed 1983) did not continue beyond the first post-fire year.

Microsite factors or community composition may have influenced the outcome of particular burn trials. For example in grasslands with mima-mound topography, the basal area of *Nassella pulchra* on intermounds increased significantly for early-season grazed/burned plants, early season grazed plants, and all burn treatments (Langstroth 1991). By contrast, on mounds the basal area of burned plants generally decreased. It is difficult to determine if this microtopography effect is the result of differences in moisture availability or fuel load in the two microhabitats. Overall, few studies provided information on fuel loading, moisture content or microscale variation in physical factors that might allow greater insight into mechanisms responsible for measured responses of native grasses to fire.

Non-native annual grasses. Non-native annual grasses dominate the grasslands of California, often occurring in densities of up to 15,000 individuals per square meter (Major and Pyott 1966, Young and Evans 1989). Hence controlling exotic grasses is likely the key to enhancing native cover in California grassland. The meta-analysis suggests that fire can be used to decrease exotic annual grass cover the first year regardless of previous burning or grazing treatments (Figures 3 and 4). Treatment type did however, have a significant effect on exotic grass abundance the first year after fire (Qb=11.79, df=3, P=0.031) with the effect of grazing (Qb=7.39, df=1, P=0.032) being slightly stronger than the effect of repeated burning (Qb=4.43, df=1, P=0.058). The depressant effect of fire on exotic grasses was short-lived: during the second post-burn year only sites that had been burned more than once were associated with decreased exotic grass cover (Q=3.46, df=1, P=0.019). By the third year after fire neither grazing nor repeated burning alone affected exotic grass cover.

Precipitation and longest drought period were not significant predictors of the response of exotic grasses to fire during the first post-burn year. The meta-analysis also suggested that burn timing (Julien day, month or 'season') do not significantly influence first-year burn results for exotic annual grasses. The lack of difference between spring and summer may be due to the arbitrary nature of assigning "spring" versus "summer" seasons. The difference between those seasons is assumed to be the stage of ripeness of the seed, seed moisture and whether or not seed has been shed from the plants. However, because of variation in growth conditions among years, burn date (either 'Julien day' 'month' or 'season') is a poor surrogate for phenology and seed moisture at time of burning. In two of the four studies in which it was compared, burn season did have a significant effect on exotic annual grass cover with greater reductions occurring in response to spring compared to fall burning (Eller 1994, Meyer and Schiffman 1999). The other two studies found burn season was not significant, or became important only after three consecutive burns (e.g. Parsons and Stohlgren 1989). For the latter study, repeated fall burning was more effective than repeated spring burning for reducing the abundance of non-native annual grasses in foothill grasslands in the southern Sierra Nevada. The authors surmised that moisture content may actually have been higher at the time of their late fall burns than it was during their late spring burns and hence caused more damage to the seed bed or germinating seedlings (Parsons and Stohlgren 1989). To truly understand how timing affects the outcome of fire, it would be necessary to collect data on moisture content of the seedbed immediately prior to fire. Because phenology is asynchronous among non-native annual grasses (Chiariello 1989) at a given site, each of the potentially important species should be evaluated separately. Variation in fuel moisture among community members will introduce variation in the intensity of fire within the site and needs to be considered when planning a controlled burn.

In some within site comparisons of burn frequency, abundance of non-native annual grasses in plots burned two or three times was significantly lower than in plots burned fewer times (Parsons and Stohlgren 1989, Delmas 2000), but in others, exotic grass abundance after repeated burning was not lower than after the first fire (Hansen

1986, DiTomaso et al. 1999). Hansen (1986) found that although repeat burning did not decrease non-native annual grasses as a group any more than did a single burn, responses were variable among species. For example, repeated burning increased the decline of *Hordeum leporinum* compared to its decline after just a single burn, whereas *Vulpia myuros* increased with repeated burning in at least three trials (Hansen 1986). Similarly, DiTomaso et al. (1999) found no significant effect of repeat burning on non-native grasses overall but the third burn resulted in a decrease for some species while others increased.

The lack of consistency between studies that examine burn season and repeat burning may be an artifact of species-specific tolerances to burn season and repeat burning. *Avena* spp. and *Vulpia* spp increased with fire in the majority of the studies where present but other annual grass species decreased. Hopkinson et al. (1999) suggest that for barbed goat grass (*Aegilops triuncialis*), repetitive burning using different seasons may be required to cause sustained reductions in abundance. Such a strategy may increase reductions of other non-native annual grass taxa in a multi-species community. Restoration practitioners could benefit from further exploration of this topic.

Among herbaceous dominated communities in the Mediterranean regions of the world, Keeley (1981) claims that the California annual grassland is one of the most fire-resilient. Our analysis supports the resilience of exotic annual grasses in California grassland despite the fact that fire caused a decrease in their abundance the first year. Abundance in the second year tended to increase and by the end of the second or third post-fire year exotic annual grasses had completely recovered. Because so few studies conduct repeat burning, it is not known whether recovery time after numerous burns (4+) will be as fast as recovery time after just a single burn. Hanson (1986) did see relatively rapid (within 2 yr) recovery of exotic grasses after the cessation of annual burning in an alkali valley grassland site but more studies like this are needed to understand the contingencies surrounding duration of fire effects. (See Table 6 for additional summaries of fire effects on exotic annual grasses).

While observed reductions of exotic annual grasses after fire appear to be short term, coupling fire with seeding of native species during the may allow native grasses to establish during the period when exotics are reduced. More work is needed exploring use of short-term reductions in exotic grasses combined with post-fire seeding of natives as a means of decreasing the competitive suppression of native species by the otherwise abundant exotic grasses.

Native and Exotic Forbs. Our meta-analysis showed a general increase in both native and exotic forbs with fire although exotic forbs are negatively affected by a combination of consecutive fires and grazing (Figures 3 and 4). Also, the effect of fire is not significantly different for native versus exotic forbs except during the third year after a single fire in ungrazed grassland. In that case, exotic forbs had increased abundantly relative to controls (lnRR=1.4030, N=4) while native forbs had decreased relative to controls (lnRR=-0.1643, N=4). With all other treatments (e.g. grazed grassland, repeat burning), fire has a positive effect on native forb abundance by the third post-burn year.

While native forbs are positively affected by fire in the first year after fire, this effect is not significantly influenced by treatment type (Qb=2.2046, df=3, P=0.274). The magnitude of increase is greatest in ungrazed, repeatedly burned sites (lnRR=1.2056, N=8) and lowest in grazed repeatedly burned sites (lnRR= 0.2983, N=13) although high variability kept these treatments from being significantly different from eachother. By the third year after fire, the effect of fire on ungrazed burn treatments is negligible (lnRR=-0.0986, N=4) and the direction of effect in grazed single and repeatedly burned sites is positive (lnRR=0.5311, N=6; and lnRr=0.5355, N=3 respectively). However because of high among site variability among the repeatedly burned sites, the overall response for this treatment is not significantly different from zero.

The amount of precipitation the year after the burn has a positive influence on native (slope=0.0247, R^2=.112, $P<0.025$) forbs during the first year after fire. In other words, native forb cover increased more relative to unburned control plots in wet years compared to dry years. Exotic forbs were not significantly influenced by post-burn precipitation. The length of the longest drought within the growing season however, did not significantly influence the outcome of fire for either group of forbs. Adding these climate variables to the analysis did not significantly influence the effect of fire on exotic forbs the third year after fire.

The meta-analysis also showed that fire season (defined either as burn day or burn month) did not significantly affect the outcome of fire for native forbs in any of the first three years. This contradicts individual studies in which fire season was compared within a site. For example, Meyer and Schiffman (1999) found spring burning resulted in a significantly higher abundance of forbs than did winter or fall burning, and most of the increase was due to native forb cover. In contrast to native forbs, the meta-analysis showed that exotic forbs are significantly affected by burn month (Qb=16.78, df=5, P=0.005) and burn day (Qb=6.41, df=1, P=0.011) for data from the first year after fire. Exotic forb cover was higher in sites burned in November compared to ones burned in March. The third year after fire, burn month was also a significant influence on abundance of exotic forbs with September burns resulting in a much higher abundance of exotic forbs (ln=1.6514, N=6) after three years than burns conducted during the other three months for which there are data (June, August, November).

Appropriately timed fire has been suggested as a means of effectively suppressing some noxious weeds such as yellow star thistle (*Centaurea solstitialis*). For any single such forb, there were not enough studies to conduct a meta-analysis. However individual studies do support the use of carefully timed fire for suppression of noxious forbs. For example, the soil seed bank and above ground cover of *Centaurea solstitialis* was nearly depleted after three successive burns timed to prevent seed set (DiTomaso et al. 1999). This burning regimen also resulted in a simultaneous increase in native forb cover. In contrast, *Centaurea melitensis*, although rare (<0.1%) in the pre-burn condition, increased drastically (to 46.3% of all biomass in the plots) after successive fall burning and moderately (to 2.4%) after successive spring burning (Parsons and Stohlgren 1989), suggesting it will be difficult to control with fire.

Not surprisingly, the response of forb species to fire was somewhat species specific. A series of studies on the reproductive output of native forbs in grasslands at Vina Plains found significantly higher reproductive output after fire in the geophyte *Zigadenius fremontii* (Mitchelson 1993) and the annual forb *Sidalcea calycosa* (Hunter 1986) but no effect on the perennial herb *Dodecatheon clevlandii* (Schlising 1996). In addition, the decline in abundance of *Clarkia purpurea* following fire may have been due to decreased seed production with summer burning (DiTomaso et al. 1999).

Furthermore, Travers (1999) showed that pollen performance of the native annual forb *Clarkia unguiculata* was significantly enhanced with fire.

Most Californian plant taxa noted for their fire stimulated recruitment or classic fire following behavior (sensu Hanes 1971) are not grassland taxa. However, Meyer and Shiffman (1999) found that germination of *Phacelia cilata* was significantly increased by exposure to open flame, and a large increase occurred in the field with late spring and fall burning in contrast to its complete absence in unburned treatments (control and mulch removal). In addition, in most cases, native species of annual legumes (*Lotus*, *Lupinus*, *Astragalus*, and *Trifolium*) increased after fire and many are known to need scarification such as would occur with heating for seed germination to occur. The native *Lotus subpinnatus*, increased with 1 to 3 successive fall burns as did the native *Trifolium microcephalum* and *Lotus subpinnatus* with 1 to 3 successive spring burns (Parsons and Stohlgren 1989). An additional native legume, *Lupinus benthamii*, benefited from a single burn but the increase was not sustained (Parsons and Stohlgren 1989). In another study, native legumes were among those species that showed the greatest increase with repeated burning (DiTomaso et al. 1999). In a few cases, non-native legumes (e.g. *Medicago* spp.) benefited from fire. By contrast, fire had no effect on the abundance of *Lotus humistratus* in any burn season at the Carrizo Plain (Meyer and Schiffman 1999), and a negative effect on legumes at the San Joaquin Experimental Range (Larson and Duncan 1982).

The introduced forb, *Erodium* spp., is considered by many restoration practitioners to be a species likely to increase with prescribed grassland fire. We found that in most of the studies for which there were data, *Erodium* spp. increased compared to controls as a result of spring or early summer burns (Meyer and Schiffman 1999, Parsons and Stohlgren 1989, DiTomaso et al 1999, Pollack and Kan 1998). Increases occurred regardless of repeated burning (Parsons and Stohlgren 1989, DiTomaso et al. 1999). By contrast, fall burning generally had no effect on *Erodium*'s abundance (Meyer and Schiffman 1999, Delmas 1999, Parsons and Stohlgren 1989, York 1997). In addition, post-fire seed banks of *Erodium cicutarium* were significantly higher after spring burns compared to controls but were unaffected by fall burns (Meyer and Schiffman 1999).

The results described above are based on abundance measures such as percent cover and do not represent richness or diversity of native forbs. Although some native forbs increased after either a fall or spring burn, other species only responded to burning in a particular season. Hence overall it is difficult to predict how the richness of native forbs will respond to burning and a combination of fall and spring burning may be needed for maximization of native forb diversity in the grassland community. More studies are needed that evaluate effects of fire on native forb richness.

Conclusions

Our overarching conclusion based on a quantitative evaluation of the existing data sets on fire in California grasslands is that fire does not result in a straightforward increase in native vegetation or a consistent decrease in exotic cover, though elements of the native vegetation can benefit in some contexts. We found that whether fire benefits native grassland vegetation depends on the burn frequency and the presence of livestock. Native forbs benefit most from annual burning but not a combination of annual burning and grazing. On the other hand, grazing sustains the positive effects of a single burn on native forbs into the third year. Climate, particularly total precipitation, is generally more important than the type of burning treatment in influencing the response of native perennial grasses and forbs to fire.

Although sample sizes are inadequate for reliably predicting the outcome of fire on native grasses, the initial results suggest that the long-term effect of fire on the abundance of native grasses is small. *Nassella pulchra* appears to be more tolerant of fire than *Danthonia californica* but more data are needed regarding the long-term effects of fire and the relative influence of climate. Few studies combined repeated burning with seeding of native perennial grasses so we do not know whether part of the weak response of these grasses to fire are also due to lack of a seed bank to aid in the regeneration process. In addition, we have almost no data on effects of fire on native perennial grasses other than *N. pulchra* and *D. californica*.

Like native forbs, exotic forb species increase after burning which is a clear negative effect of using fire in California grassland restoration. However, livestock grazing appears to reduce the benefit that exotic forbs gain. In ungrazed sites, the increase in exotic species that occurs with an initial fire lasts into the third post-fire year. By contrast, in grazed sites exotic forbs decrease over time since fire. At the same time livestock grazing appears to sustain the benefit that native species gain by a single fire.

It is important to note that our meta-analysis only examined the effect of fire on abundance of native versus exotic life form groups. Although fire may have a negligible effect on abundance of a given group of grassland plants, it may increase or help maintain native species richness in grassland communities but not enough studies were available to test the generality of this outcome. Future studies are needed that evaluate how fire effects vary with local and regional climatic patterns and how they interact with the history of livestock grazing at a site. The use of fire as a restoration tool can only be evaluated by considering multiple, interacting factors.

While fire has been shown to temporarily increase the cover of native species and suppress non-native species in some cases, information regarding the methods or combinations of management that maintain or increase the abundance and richness of native species is lacking. Clarification of the context in which prescribed (and natural) fire benefits native species is important for determining optimal conditions for using prescribed fire, predicting changes in fire effects and the natural fire regime due to climate change, and determining how fire can be used with grazing to sustain and promote native grassland species.

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Table 1. Summary of Location and Environmental Variables at California Grassland Fire and Grazing Study Sites

Reference	study type	site name	latitude	longitude	elevation	slope	aspect	grassland type	perennial grass present	adj. veg	Jepson region	soil texture	historic land use	current land use	last burn
Ahmed 1983	fire	Hopland Field Station	39N	123W	300 m	level	none	valley and foothill	NAPU	oak wdld	NCoRO	fine loam over clay	grazed until 1956	none	unk
Arguello 1994	fire	Redwood NP/ Hospital Pasture	41N	124W	700 m	<20%	sw	bald hills	DACA	oak wdld	NCo	fine loam	grazed until 1978	park/ preserve	unk
Bartolome et al. 1980; Jackson and Bartolome in press	grazing	various	various	various	various	various	various	annual, valley and foothill	NAPU, DACA, others	various	NCoR, SCoR	various	grazed	grazed	unk
Bartolome and Gemmill 1981	grazing	various	various	various	nd	nd	nd	various	NAPU, DACA, others	nd	various	nd	nd	nd	nd
Bettes unpublished	fire	Nunes Ranch	38N	122W	120-275 m	nd	nd	valley and foothill	DACA, NAPU	nd	SnFrB	nd	grazing	grazed	unk
Cooper 1960	grazing	Fort Baker	41N	124W	260-1350 m	gentle	various	coastal	DACA and others	oak wdld	NCoR	various	grazing	grazed	unk
Cox and Austin 1990	fire	Miramar NAS	33N	117W	144 m	level	none	vernal pool	no	chaparral	SCo	redding	grazing	park/ preserve	unk
Delmas 1999	fire	Vina Plains	40N	121W	65 m	level	none	wildflower field	no	open	ScV	loam	grazed until 1982	park/ preserve	unk
DiTomaso et al. 1999	fire	Sugarloaf State Park	38N	122W	145 m?	level	none	valley and foothill	NAPU	oak wdld	NCoRO	nd	grazing	park/ preserve	unk
Dyer and Rice 1997	fire and grazing	Jepson Prairie	38N	122W	5 m	level	none	vernal pool	NAPU	open	ScV	sandy loam over claypan	grazing	park/ preserve	recent
Dyer et al. 1996/ Fossum 1990	fire	Jepson Prairie	38N	122W	5 m	level	none	vernal pool	NAPU	open	ScV	sandy loam over claypan	grazing	park/ preserve	recent
Eller 1994	grazing	Lake Perris SRA	34N	117W	216-583m	0-15%	nd	annual grassland	no	interior sage scrub	PR	sandy loam	grazing	park/ preserve	unk

Elliot and Wehausen 1974	grazing	Point Reyes	38N	122W	ca. 60 m	level	none	coastal terrace	various	open	CCo	sandy	grazing	grazing or park	unk
Foin and Hektner 1986	grazing	Sea Ranch	39N	123W	22	level	none	coastal terrace	Calamogrostis nutkatensis	open	NCo	loam, sandy loam	grazing	park/ preserve	unk
Garcia-Crespo 1983	fire	Cuyamaca Rancho SP-meadow	33N	117W	1350m	level	none	valley and foothill	NAPU; MURI	chap/oak wdld/ypf	PR	gravelly loam; loam and clay	grazing	park/ preserve	unk
Graham 1956	fire	San Joaquin ES	37N	120W	350 m	5%	east-none	annual grassland-savanna	no	oak wdld	cSNF	sandy loam	grazing	grazed	unk
Hansen 1986	fire	Creighton Ranch	36N	119W	70-74m	level	none	alkali grassland	DISP, POSC, STCE, SPAI	open	SnJV	loam-clay loam	grazed until 1980	preserve	unk
Hansen 1986	fire	Pixley Vernal Pool Preserve	36N	119W	105-107m	level	none	alkali grassland-vernal pool	DISP, POSC, STCE, SPAI	open	SnJV	sandy loam-loam	grazed until 1964	preserve	1973
Harrison 1999	grazing	various	n/a	n/a	n/a	n/a	n/a	serpentine-forb	no	various	NoCRI	serpentine	grazed	grazed	unk
Hatch et al. 1991	fire and grazing	Sierra FS	39N	122W	nd	nd	nd	valley and foothill	NAPU	oak wdld	nSNF	nd	grazing	park/ preserve	unk
Hatch et al. 1999	fire and grazing	Pomponio Beach SP	37N	122W	150m	gentle	west	coastal terrace prarie	DACA, NAPU, NALE	scrub	CCo	loam to sandy loam	continuously grazed last decades	grazed by sheep and cattle	unk
Heady 1956	grazing	Hopland Field Station	39N	123W	300 m	level	none	valley and foothill	NAPU	oak wdld	NCoRO	fine loam over clay	grazed until 1956	none	unk
Hektner and Foin 1977	grazing	Sea Ranch	39N	123W	22	level	none	coastal terrace	Calamogrostis nutkatensis	open	NCo	loam, sandy loam	grazing	park/ preserve	unk
Jackson, unpublished	grazing and fire	Sather Gate	38N	122W	nd	nd	nd	valley and foothill	NAPU, DACA	oak wdld	SnFrB	nd	grazing	grazed	unk
Kelley unpublished	grazing	Sequoia National Park	36N	119W	440-670 m	3-27	various	blue oak woodland	no	oak wdld	sSNF	various	grazing	grazing	unk

Kephart 2001	fire and grazing	Russian Ridge	37N	122W	nd	nd	nd	valley and foothill	NAPU and others	oak wdld	SnFrB	nd	grazing	park/ preserve	unk
Kneitel 1997	fire	Carrizo Plain	35N	120W	600-700m	19-31 deg	various	valley and foothill	POSE, NAPU	open	SnJV	nd	grazing	not grazed during study	unk
Langstroth 1991	fire and grazing	Jepson Prairie	38N	122W	5 m	level	none	vernal pool	NAPU	open	ScV	sandy loam over claypan	grazing	grazed	recent
Larson and Duncan 1982	fire	San Joaquin ES	37N	120W	350 m	5%	east-none	annual	no	oak wdld	cSNF	nd	grazing	grazed	1956
Marty, unpublished a	fire	Valensin Ranch	38N	121W	2 m	0%	none	vernal pool	no	open	ScV	loam	grazing	grazed	unk
Marty, unpublished b	fire and grazing	Beale AFB	39N	121W	45 m	15-30	west	vernal pool	NAPU	oak wdld	nSNF	shallow loam	equestrian	equestrian	unk
Merenlender et al. 2001	grazing	Hopland Field Station	39N	123W	300 m	level	none	valley and foothill	NAPU	oak wdld	NCoRO	fine loam over clay	grazed until 1956	none	unk
Meyer and Schiffman 1999	fire	Carrizo Plain	35N	120W	600-700m	level	none	annual	no	open	SnJV	clayey	grazed since 1800's	grazed	unk
Micallef 1998	grazing	Mount Diablo State Park	38N	122W	200-1000 m	various	various	annual, valley and foothill	NAPU and others	oak wdld	SnFrB	various	grazed	park/ preserve	unk
Parsons and Stolhgren 1989	fire	Kaweah River	37N	119W	700m	gentle	east	annual	no	bow	sSNF	coarse sandy loam	grazed until ca. 1930	none	1960
Pollack and Kan 1998	fire	Jepson Prairie	37N	122W	5 m	level	none	vernal pool	NAPU	open	ScV	sandy loam over claypan	grazing	park/ preserve	unk
Porter and Redak 1996	fire	Santa Rosa Plateau	33N	117W	650 m	level	none	valley and foothill	NAPU	open	PR	nd	grazing	grazed	unk
Reeves and Morris 2000	grazing	Hollister Hills SVRA	37N	121W	nd	level	none	various	various	open	SCoR	nd	grazing	grazed	unk
Saenz and Sawyer 1986	grazing	Redwood NP and adjacent	41N	124W	850 m	nd	nd	bald hills, wdld	various	open, wdld	NCo	nd	grazing	preserve, grazing	unk
Stromberg and Griffin 1996	grazing	Hastings Reserve	36N	121W	533-808 m	5-50%	southerly	valley and foothill	NAPU	oak wdld	SoCRO	various	grazed until ca. 1937	preserve	unk

Thomsen et al. 1993	grazing	Arrowhead Ranch	39N	122W	400 m	level	none	annual	no	oak wdld	NoCRI	nd	grazing	grazed	unk
TNC 2000	fire and grazing	Vina Plains	40N	121W	65 m	level	none	wildflower field	no	open	ScV	loam	grazing resumed	park/ preserve	unk
White 1967	grazing	Hastings Reserve	36N	121W	533-808 m	5-50%	southerly	valley and foothill	NAPU	oak wdld	SoCRO	various	grazed until ca. 1937	preserve	unk
York 1997	fire	McKenzie TM	37N	119W	550m	level	none	annual grassland	no	oak wdld	sSNF	shallow, clay	grazed until ca. 1991	none	unk
Zavon 1977	fire and grazing	Hopland Field Station	39N	123W	198-700m	30-50%	none	annual grassland	no	oak wdld	NCoRO	fine to fine loamy clay	grazing	lightly grazed	unk

Table 2. Studies of the effects of livestock grazing on native California grassland plants: experimental designs

Citation	Study type	County	scale of treatment application*	measure of grazing intensity**	grazing agent (density)	season (duration in days)	sample years***	comments
Bartolome *et al*. 1980	Mulch manipulation	several	plot	RDM	simulated	late summer/early fall	5	
Bartolome and Gemmill 1981	Observational/release	Mendocino	pasture	qualitative	sheep (high)	nd	2, 3, and 23	
Cooper 1960	Observational	Humboldt	pasture	stocking rate?	cattle (ca. 1,000?)	winter, summer, or spring and fall (nd)	1	
Dyer *et al*. 1996****	Grazing manipulation	Solano	paddock	RDM/ stocking rate	sheep (15)	spring/wet vs. summer/dry (2-3)	1-4	grazed until 400-500 kg/ha
Elliott and Wehausen 1974	Observational/release	Marin	pasture	stocking rate	cattle (1.16-2.63 ha per cow)	nd	6 after release	ungrazed = 6 years release from grazing
Foin and Hektner 1986	Observational/release	Sonoma	pasture	stocking rate (qualitative)	sheep (nd)	continuous	1, 3, 5	observations 7 to 13 years after release from grazing
Harrison 1999	Observational/release	Napa and Lake	pasture	presence/ absence	cattle (nd)	nd	1-2	all sites historically grazed
Hatch *et al*. 1999	Grazing manipulation/release	San Mateo	paddock	stocking rate	cattle (15) and sheep (200)	continuous	1-2	
Hatch *et al*. 1991	Grazing manipulation/release	Yuba?	paddock	stocking rate	cattle (nd)	continuous	1-2	
Heady 1956	Biomass/mulch manipulation	Mendocino	plot	RDM	simulated	fall	1-3	clipped to fixed height and varying percentages returned
Jackson, unpublished	Grazing manipulation	Contra Costa	paddock	RDM	cattle, light to moderate	spring (7), summer (7), continuous	6	
Jackson and Bartolome, in press	Mulch manipulation	several	plot	RDM	simulated	late summer/early fall		
Keeley, unpublished	Observational/release	Tulare	pasture	presence/ absence	cattle and horses	winter-summer	1	long-term grazing
Kephart 2001	Grazing manipulation	San Mateo	paddock	stocking rate	goats (500)-yr 1; sheep (40) and goats (7)-yr 2	May (12)	1-2	grazed to bare mineral soil

Langstroth 1991	Grazing manipulation	Solano	paddock	RDM/ stocking rate	sheep (15)	spring/wet vs. summer/dry (2-3)	1-4	grazed until 400-500 kg/ha
Love 1944	Grazing manipulation	Sacramento	pasture	stocking rate	sheep (264-275 early; 83 late)	spring and summer or fall (20-30)	same	grasses seeded into disced pasture
Marty, unpublished b	Grazing manipulation	Butte	paddock	RDM and stocking rate	cattle	Jan and May or continuous over 6 mo.	2	
Merelander et al. 2001	Observational/release	Mendocino	pasture	qualitative	sheep	nd	43 years	followed permanent plots over 43 years after removal
Micallef 1998	Observational/release	Contra Costa	pasture	RDM/ stocking rate	cattle (nd)	nd	1, 20, 24	
Reeves and Morris 2000	Grazing manipulation (no control)	San Benito	pasture	stocking rate	cattle (nd)	nd	1-2	monitored increased stocking rate
Saenz and Sawyer 1986	Observational	Humbolt	pasture	qualitative	cattle (nd)	early-late (8 mo) vs late (4 mo)	1	no ungrazed control
Stromberg and Griffin 1996	Observational/release	Monterey	pasture	RDM (qualitative)	cattle (nd)	seasonal vs continuous (nd)	>23	ungrazed for 51 years prior to study except horse pasture
Thomsen et al. 1993	Grazing manipulation	Colusa/Yolo	paddock	RDM	cattle (18 cow-calf pairs); sheep then goats (20-40)	May and 2-3 follow up later in the season (<3 days)	3	
TNC 2000	Grazing manipulation	Tehama	paddock and pasture	RDM	cattle	rotated Nov.-April	3	cattle reintroduced after 11 years of release from grazing
White 1967	Observational/release	Monterey	pasture	presence/ absence	cattle, horses	nd	27	ungrazed for 27 years prior to study except horse pasture

nd=data not available; *plot = experimental unit gen <10 sq. meters; paddock = experimental unit gen<0.5 acres; pasture=existing unit, generally >0.5 acres;

** RDM = residual dry matter at end of treatment application, grazed or clipped until a given RDM is achieved; ***year data collected after initiation of treatment (or release from grazing)

**** Includes Fossum (1991) data and is same experiment as Langstroth

Table 3. Studies of the effects of livestock grazing on native California grassland plants: Summary of of results

Citation	Summary of results	Comments
Bartolome and Gemmill 1981	*Nassella pulchra* fairly constant 20 years after release at one site; decrease at other site but perennial grass cover constant overall with increase in *Elymus glaucus*	trend; no control
Cooper 1960	*Danthonia californica* increased after 1 year reduced stocking	trend; no control
Dyer et al. 1996***	location (mound/intermound) more important than grazing treatment; *Nassella* emergence significantly higher in wet-grazed treatments than ungrazed	
Elliott and Wehausen 1974	*Danthonia californica* highest in heavily grazed plot; *Deschampsia caespitsa*, *Bromus carinatus*, and *Elymus glaucus* highest in ungrazed; native spp. highest in ungrazed	trend; not replicated
Foin and Hektner 1986	increase in perennial grasses (non-native and native) with release but not much change in native perennial grasses (*Deschampsia holiciformis*) or natives in general	trend; not replicated; no control
Harrison 1999	grazing had no significant effect on native species richness (nor did the grazing-soil interaction)	
Hatch et al. 1999	significant *Danthonia californica* decrease on ungrazed plots and increase on grazed plots with some slope effect; No significant effect on *Nassella lepida*; weak slope by grazing interaction for *N. pulchra* (decrease on upper ungrazed slope)	
Heady 1956	*Lasthenia californica* showed only significant treatment difference (negative correlation with mulch)	not spatially replicated?
Jackson unpublished	general increase in perennial grasses over study period but greatest increase in ungrazed and unburned; highest density of *Danthonia californica* with summer or spring grazing	
Jackson and Bartolome, in press	site and climate more important than RDM in determining composition	
Kelley, unpublished	no significant differences in cover of exotic or perennial species between grazed (cattle or horse) and release from grazing; richness of exotics increased in pastures released from grazing	
Kephart 2001	trend show increase in cover and richness of native species, increase cover of non-native species, and decrease in *Centaurea solstialis*	no control; not replicated
Langstroth 1991	fragmentation of *Nassella* significantly increases with summer grazing; basal area increase significant only when also burned for mound plants; mortality differential with mound/inter-mound; early spring grazing decreases number of reproductive tillers on mounds; highest seedling densities with early spring and burn treatment; forb density greater and exotic grass cover less in early spring grazed compared to summer grazed	

Love 1944	highest survivorship of most non-native perennial grasses and forbs with early, intensive grazing; highest survivorship of *Nassella pulchra* and *N. cernua* with early, intensive grazing	trend; no control; not replicated
Marty, unpublished b	no significant effect of grazing on *Nassella pulchra* growth or mortality and trends unrelated to grazing; grazing significantly decreases number of *Nassella* culms	
Merelander et al. 2001	lack of directional change in the system; woodland understory responded more dramatically and consistently than open grassland	selection of replicates not random; no control?
Micallef 1998	significantly higher cover of 1) native forbs in ungrazed areas than heavily grazed areas but not compared to other grazing intensities; 2) non-native grass with no grazing compared to moderate and heavy grazing; 3) native vegetation with decrease in grazing	only sampled tallest vegetation
Reeves and Morris 2000	increase in perennial grasses and forbs (native and non-native?)	trend; no control; not replicated; native versus non-native not indicated
Saenz and Sawyer 1986	native perennial gramnoids more abundant in short-term grazed open grassland and oak woodland than long-term grazed; native annual forbs more common in grassland grazed for full season	no ungrazed control; possibly not replicated at the pasture level
Stromberg and Griffin 1996	uncultivated native perennial grasses stable regardless of grazing regime; other factors probably more important	
Thomsen et al. 1993	significantly less *Centaurea solstialis* in cattle and goat treatments compared to ungrazed; timing probably more important than grazer; significantly higher abundance of native forbs in grazed treatments	
TNC 2000	decrease in native plant cover at pasture scale unrelated to grazing; native plant cover slightly but significantly higher in grazed experimental paddocks	habitat in control paddocks potentially not comparable with experimental; control not replicated at pasture scale
White 1967	*Nassella pulchra* significantly smaller and more numerous in grazed plots but no significant difference in cover and biomass overall; other factors probably more important than grazing (e.g. slope and moisture)	selection of replicates not random

Table 4. Effect of grazing on grassland plant functional groups (based on a limited number of studies n = 5). Values are the Cumulative effect sizes (mean natural log of the response ratio [X_{grazed} /$X_{control}$] weighted by study variances); ± 95% C.I.; (n = # of effect sizes rather than number of studies). * abundance significantly different from control P<0.05

	all regimes	*wet season*	*dry season*	*continuous*
Native perennial grasses	2.5273* ± 1.9357 (n=8)	3.9768 ± 11.3908 (n=3)	-0.0089 ± 38.2674 (n=2)	2.4968 ± 10.6713 (n=3)
Native forbs	-0.0703 ± 0.4109 (n=13)	0.0690 ± 0.7103 (n=7)	-0.1174 ± 6.0581 (n=2)	-0.1840 ± 1.2531 (n=4)
Exotic annual grasses	0.0702 ± 0.2986 (n=6)	-0.0324 ± 1.9037 (n=2)		0.3186 ± 2.0245 (n=2)
Exotic forbs	0.2364 ± 0.3884 (n=9)	0.2870 ± 0.7301 (n=4)	0.5747 ± 4.4973 (n=2)	-0.0147 ± 1.1193 (n=3)
All native	0.9755* ± 0.9755 (n=21)	0.1603 ±3.7503 (n=4)	0.000 ± 19.4852 (n=2)	0.000 ± 6.4958 (n=3)
All exotic	0.1456 ± 0.2061 (n=15)	0.1687 ± 5.9115 (n=4)	0.000 ± 21.7721 (n=2)	-0.6707 ± 0.0678 (n=5)
All functional groups	0.5024* ± 0.3159 (n=26)	0.77340* ± 0.5453 (n=16)	0.0352 ± 0.8137 (n=8)	0.5495 ± 0.6413 (n=12)

NOTE: The number of samples used to calculate these effect sizes are inadequate to determine significance of grazing effect. The number of studies required to change results from significant to non-significant (fail-safe number) is very small (<<1) relative to sample sizes used in the above calculations indicating that many more studies are needed to confirm these results. However, the fail-safe number for the overall effect of all grazing regimes on native vegetation is higher than the sample size suggesting the number of samples used to calculate the mean effect size is adequate.

Table 5. Experimental Design Summaries for California Grassland Fire Effects Studies

Reference	fire treatment comparisons	none-fire treatments	statistical analysis	pre-treat data ?	control	block	# reps*	treatment area	treatment scale***	post-burn years monitored	burn year 1	burn date (# yrs repeated)	comments
Ahmed 1983	3 seasons; *Nassella* density	mowing (1 season)	y	y	y	y	"6"**	9 sq. m	plot	1 (2)	1981	June 11; August 3; September 16	
Arguello 1994	2 seasons	none	y	y	y	n	10	9 sq. m	plot	1	1991	June 17-18; November 7	
Bettes, unpublished	repeat burn, season (in grazed grassland)	none	u	n	y	y	3-12	various	plot	3-12	1993	June, August, November	same study as Bartolome and Bettes 2000, Bettes and Bartolome 2001
Cox and Austin 1990	single burn	none	n	y	y	y	5	vernal pool	plot	1	1986	October 1986	
Delmas 1999	unplanned fires, 2 seasons, 1 repeat	none	y	n	y	n	"3"	ca. 2,400 ha	landscape	1-4	1991	September 1991; July 1993	unplanned and prescribed fire
DiTomaso et al. 1999	repeat burns	none	y	n	y	n	"3"	14 ha/70 ha	landscape	3	1993, 1995	early July (3)	
Dyer and Rice 1997	interaction with grazing	weeding and grazing	y	n	y	y	3	400 sq m	large plot	3	1988, 1991	September 1, 3	
Dyer unpub.	interaction with grazing	grazing and seed addition	u	n	y	y	3	400 sq. m	plot	3	1988	September	same study as Dyer et al. 1996, Fossum 1990
Eller 1994	3 seasons	none	y	y	y	y	3	45 x 150 m (275 ha)	large plot	1	1990	December 1990; May, October 1991	
Garcia-Crespo 1983	1 season	seed, fertilizer, mulch	y	n	y	y	2 (per site)	4 sq. m	plot	1	1981	April	
Graham 1956	repeat burn	none	y	n	y	n	"1-3"	150 acres	landscape	2-3	1950	July	

Hansen 1986	2 seasons, repeat burn	none		y	y	nr	3	various	large plot	1-4	1982-1984	August-October	
Hatch et. al. 1991	grazing interaction	late grazing	n	y	y	y	nd	nd	large plot	3	1990	November	
Hatch et. al. 1999	grazing interaction	late grazing	y	y	y	y	3	18 m2	large plot	3	1990	November	
Jackson, unpublished	interaction with grazing	grazing (3 treatments)	u	n	y	y	2	9 sq. m	plot	2-5	1993	November	same study as Hopkins et al. 1999, Fehmi and Bartolme 2001a and b
Kneitel 1997	interaction w/ disturbance (gopher)		y	n	y	y	3	1,300 acres	landscape	2	1994	June	
Langstroth 1991	interaction with grazing	grazing (3 treatments)	y	n	y	y	3	400 sq. m	large plot	2	1988	September 1	
Larson and Duncan 1982	1 season	fire retardent	y	n	y	n	"3"	5 ha.	landscape	1	1974	October	same study as Larsen 1977
Marty, unpublished a	1 season	none	u	y	y	y	"5"	400 m2	landscape	1	2000	June	grazed?
Marty, unpublished b	interaction with grazing	grazing (3 treatments)	u	y	y	n	5	50 acres	large plot	2	1998	July	
Meyer and Schiffman 1999	3 seasons	mulch removal	y	y	y	y	5	36 m2	large plot	1	1995, 1996	Feburary 1996; September 1995	same study as Meyer 1996
Parsons and Stohlgren 1989	2 seasons, # yrs repeated	none	y	y	y	n	"5"	100 sq. m	large plot	3	1980	mid-June (1-3); October-Novmber (1-3)	
Pollack and Kan 1998	1 season	none	y	y	y	n	"3"	35 m2	large plot	2 or 3?	1995	June	
Porter and Redak 1996	2 burns, successive years	none	y	n	n	n	"3"	1 km sq.	landscape	1-3	1992	May 1992; April 1993	
TNC 2000	repeat burn	grazing	y	y	y	y?	3?	>500 sq. m	landscape	35433	1996	easrly spring	
York 1997	unplanned fire	none	y	n	y	n	0	5041 m2	landscape	1	1994	September	unplanned fire

Zavon 1977	2 seasons; grazing interaction	none	y	n	n	y	2	0.135 ha	large plot	1	1979	August 1979; September 1980

* non block design repelicates in quates where single treatment applications adjacent to control area except Pollack and Kan (control plots in a single application)
*Ahmed. lumped low, med and high Nassella density (n=2 each) so n =6
*Langstroth data dropped beacuse same as Dyer, Fossum and Rice
*** plot = fire apllied to <10 x 10 meter area or less; large plot = > 10 x 10 meter area
and < 500 sq. meters; landscape = > 500 sq. meters

Table 6. Summary of Prescribed Burn Effects on Perennial Grasses

			Abundance: Cover, Frequency, Biomass
Reference	treatment	taxa	Results
Ahmed 1983	three burn dates; Nassella density	*Nassella pulchra*	tiller number significantly higher (3-4 times) than control in all burns and significantly higher than mow; September burn significantly longer than others at low density and September and August burn higher than June at high density
Ahmed 1983	three burn dates; Nassella density	*Nassella pulchra*	tiller length significantly longer (2 to 3 times) in all burn treatments than control and higher than mow; not significant between burns dates except low density was higher for the September burn and high density for the August burn
Ahmed 1983	three burn dates; Nassella density	*Nassella pulchra*	peak live shoot biomass not significantly different among treatments and control but variable among densities; mowed plots consistently lower than control and burn treatments except at low density
Ahmed 1983	three burn dates; Nassella density	*Nassella pulchra*	tiller growth the 1st post-burn yr significantly lower in all low density burn and mow treatments but growth rate earlier in yr significantly higher than control; by the end of 2nd post-burn year tiller growth or growth rate not significantly different
Ahmed 1983	three burn dates; Nassella density	*Nassella pulchra*	basal diameter increase lowest in control; at low density, all burns significantly higher than mow and control; at medium density Sept burn significantly highest; and at high density June burn significantly highest
Ahmed 1983	three burn dates	*Nassella pulchra*	relative cover lowest in control but not significant
Arguello 1994	two burn dates	*Arrhenatherum elatius*	cover not significantly effected by burn although it may prevent increase
Arguello 1994	two burn dates	*Danthonia californica*	cover significantly less (and large) in 2nd year for June burn but not the November burn
DiTomaso et al. 1999	July burn and repeat burning	*Nassella pulchra*	cover increased after 2nd consecutive June or July burn and increased significantly after 3rd year (decreased yr 1) but parallell increase in control site
Dyer and Rice 1997	late season burn, grazing and weeding at various densities	*Nassella pulchra* (experimental seedling plantings)	basal diameter increase at low seedling density significantly greater when burned; increase in basal diameter was greatest on ungrazed burned mounds; weeding effect greater on burned plots than grazed; overall mean increase in burned 2x than unburned

Garcia-Crespo 1983	April burn and burn seeding with native grasses	*Nassella pulchra, Elymus glaucus, Poa secunda, Elymus multisetus, Muhlenbergia rigens*	biomass decreased significantly due to burning; burn and seeded treatments increased (for *Nassella pulchra* not *Muhlenbergia rigens)* but not significantly
Garcia-Crespo 1983	April burn and burn seeding with native grasses	*Nassella pulchra*	biomass, density and basal area were not significantly effected by burning even when combined with other treatments except seeding; basal area and density declined in 1981 but increased in 1982
Hansen 1983	August to October burn and repeat burning and temporal replicates	*Distichlis spicata* (mostly)	cover changes are not consistent but mostly increased after fire
Hatch 1999	late season burn and interaction with grazing	*Danthonia californica*	frequency and cover decreased but not significantly
Hatch 1999	late season burn and interaction with grazing	*Nassella lepida*	frequency and cover decreased but not significantly
Hatch 1999	November burn and interaction with grazing	*Nassella pulchra*	cover increased, frequency decreased but no significant change
Hatch 1999	November burn and interaction with grazing	all perennials combined	frequency and cover decreased but not significantly
Hatch 1991	November burn and interaction with grazing	*Nassella pulchra*	positive response to burning
Kephart 2001	August season burns with seeding	all perennials	Elymus was the most successful
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*	crown cover decreased significantly the first year in grazed burn plots; but significantly greater in burn plots than unburned two years after the burn (except summer grazed burn)

Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*	fragmentation increased significantly in burned mound plants but summer grazing decreased fragmentation on mounds;
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*	mortality highest in summer grazed burned plots and intermound plants in spring grazed burn plots
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*-intermounds	basal area and perimeter increased regardless of treatment but basal area only increased significantly for spring grazed burned plants and spring grazed unburned plants and the increase in basal perimeter was significant for all burn treatments
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*-mounds	basal area of burned plants decreased but significantly only for summer grazed plants; basal perimeter on mounds of burned plants increased; spring grazed burned plants increased significantly and summer grazed burn plants decreased
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*	ramet density (<10cm size class) increased significantly with fire especially if spring grazed; 10-20 cm diamter class had greatest densities on unburned mound but summer grazed plants increased on intermounds even when burned; total density was significantly higher on mounds when burned but highest increase was for spring-grazed burned plants
Langstroth 1991	September burn and interaction with grazing	*Melica californica, Distichlis spicata, and Phalaris lemmonii*	frequency not significantly effected by treatment
Pollack and Kan 1998	June burn	*Nassella pulchra*	small increase in number of plots dominated by *Nassella*

Seed production, seed bank density, germination and seedling survival

Ahmed 1983	three burn dates	*Nassella pulchra*	seed bank density not significant from pre-burn
Ahmed 1983	three burn dates	*Nassella pulchra*	germination was significantly higher from control at all densities but not significant from mowing
Ahmed 1983	three burn dates	*Nassella pulchra*	number of reproductive culms significantly higher from control at all densities and from mowing except at medium density; hiest for June burn except at high density
Ahmed 1983	three burn dates	*Nassella pulchra*	number of seeds significantly higher from control and from mowing at all densities; highest for June burn except at high density

Ahmed 1983	three burn dates	*Nassella pulchra*	N and P concentration
Ahmed 1983	three burn dates	*Nassella pulchra*	seedling survival
Dyer et al. 1996/ Fossum 1990	September burn and interaction with grazing	*Nassella pulchra*	seedling survival highest for early spring graze + burn, early spring graze and burn treatments and lowest for control and summer grazed; w/o burning or grazing no seedlings survived past yr 1
Dyer et al. 1996/ Fossum 1990	September burn and interaction with grazing	*Nassella pulchra* (experimental seedling plantings)	seedling emergence was significantly greater in plots burned several weeks before seeds were planted and than any other treatment the first year but not the second; seedlind emergence in plots burned
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*	seed production per plant was significantly less but seed weight was significantly higher for burned plants; reproductive tillers significantly decreased by burning; seed production per tiller was reduced by burning except when also spring grazed
Langstroth 1991	September burn and interaction with grazing	*Nassella pulchra*	seedling density highest on mounds with burning and intermounds if unburned

Table 7. Summary of Prescribed Burn Effects on Exotic Annual Grasses

Decreases or Significant decreases in Non-native Annual Grasses

Reference	treatment variables	taxa	response variable	years to recovery*	Results
Ahmed 1983	three burn dates; Nasella density	*Bromus hordeaceous*	peak live shoot biomass	no data	significantly lower in all burn treatments (esp. low density) except at high *Nassella* density but not significant between burn dates
Ahmed 1983	three burn dates	*Bromus hordeaceous*	relative cover	no data	all burns significantly lower than control and mowed but no significant differences between burn dates
Garcia-Crespo 1983	early season burn and burn seeding with native grasses	annual grasses	biomass	2	significant decrease the first year but recovered after the first year
Hansen 1983	repeat burning and temporal replicates	all native (mostly *Hordeum depressum*)	cover	2-3	lowest abundance the first year after burn; repeat burning did not result in lower abundancae than single burn; recovery slower than non-natives
Hansen 1983	repeat burning and temporal replicates	all non-native	cover	2	best results the year after burn across temporal replicates; repeat burns not necessarily better than single burn; *Hordeum leporinum* decreased in all treatments and did not recover
Hansen 1983	repeat burning and temporal replicates	*Bromus hordeaceous*	cover	2	best results first year after treatment, or after two or three burns; sometimes recovery beyond original abundance and control
Hansen 1983	repeat burning and temporal replicates	*Bromus rubens*	cover	5+?	lowest abundance after third burn, but large decreases after first year and second burn too
Hansen 1983	repeat burning and temporal replicates	*Hordeum leporinum*	cover	5+?	lowest abundance in first year after burn (except 1985) and after multiple burns
Kneitel 1999		all non-native	cover	2	significant decrease first year

Langstroth 1991	interaction with grazing	*Avena barbata*	freq	no data	all burning and grazing treatments significantly lower than control but no significant burn interaction with grazing
Langstroth 1991	interaction with grazing	*Bromus diandrus*	freq	no data	densities in burn and burn and grazing treatments signicantly lower than grazed and controls
Langstroth 1991	interaction with grazing	*Bromus hordeaceous*	freq	no data	all treatments significantly lower than control; early-grazed and burn treatment signifcantly lower than other treatments and control
Langstroth 1991	interaction with grazing	*Hordeum leporinum*	freq	no data	burn and early-grazed and burn treatments lowest but not significant
Langstroth 1991	interaction with grazing	*Loliium multiflorum*	freq	no data	burn and early-grazed and burn treatments lowest but not significant
Langstroth 1991	interaction with grazing	*Taeniatherum caput-medusae*	freq	no data	all burn treatments significantly lower than control and summer graze (except spring graze and burn); burn only treatment significantly lower than both burn and graze treatments
Larson and Duncan 1982	single burn	all non-native grasses	biomass	2	shifted dominace from *Bromus hordeaceous* and *Vulpia megalura* to *Bromus hordeaceous*
Larson and Duncan 1982	single burn	*Vulpia megalura*	biomass	2	absent in burn area but 50% of cover in unburned
Pollack and Kan 1998	single burn	non-native annual grasses	cover	no data	significant decrease on both mound and intermound habitats; shift from Bromus, Lolium and Taenatherum to Erodium and Juncus bufonius
York 1997	late summer, unplanned fire	non-native annual grasses	cover and frequency	no data	cover and frequency less (ca. 50%) in burned area; largest decrease was *Bromus hordeaceous*

Significant decreases and differences between treatments in Non-native Annual Grasses

Delmas 1999	repeat burning and temporal replicates	native and non-native annual grasses	density	2-3	significant differences between burn treatments; lowest grass densities in twice burned areas
Eller 1994	three burn dates	*Avena* spp.	frequency	no data	non-significant decrease for Spring and Fall burns
Meyer and Schiffman 1999	3 burn season; mulch removal	*Bromus madratensis*	cover	2	significant lower in all burn treatments than control or mulch removal; winter burn sigificantly lower than Fall burn but late spring not significantly different than Winter or Fall burn

Meyer and Schiffman 1999	3 burn season; mulch removal	*Hordeum murinum*	cover	2	significant lower in Fall and late Spring burn from other treatments and control
Meyer and Schiffman 1999	3 burn season; mulch removal	all non-native grasses	cover	2	late Spring burn treatment significantly lower than other treatments and control; fall burn significantly lower than mulch and control; and winter burn significantly lower than control but not mulch removal
Eller 1994	three burn dates	*Bromus* spp. and other annual grasses	frequency	no data	significant decrease for spring burn and non-significant decreasefor other burns
Parsons and Stohlgren 1989	sesaon, repeat burns	non-native annual grasses	biomass	>3	significantly lower from control only after 3rd fall burn; decreases in all treatments and control except single spring burn
Parsons and Stohlgren 1989	sesaon, repeat burns	*Avena fatua*	biomass	no data	reduced to 5.4% of total biomass after 3rd fall burn and 12.4% after 3rd spring burn
Parsons and Stohlgren 1989	sesaon, repeat burns	*Bromus diandrus*	biomass	no data	reduced to 0.2% of total biomass after 3rd fall burn and 1.3% after 3rd spring burn

No apparent change in Non-native Annual Grasses

Parsons and Stohlgren 1989	sesaon, repeat burns	*Bromus hordeaceous*	biomass	no data	not significantly effected
DiTomaso et al. 1999	repeat burning and temporal replicates	non-native annual grasses	cover	no data	not significantly effected
Ahmed 1983	three burn dates	other non-native annual grasses	relative cover	no data	not significantly effected

Post-fire Increases in Non-native Annual Grasses

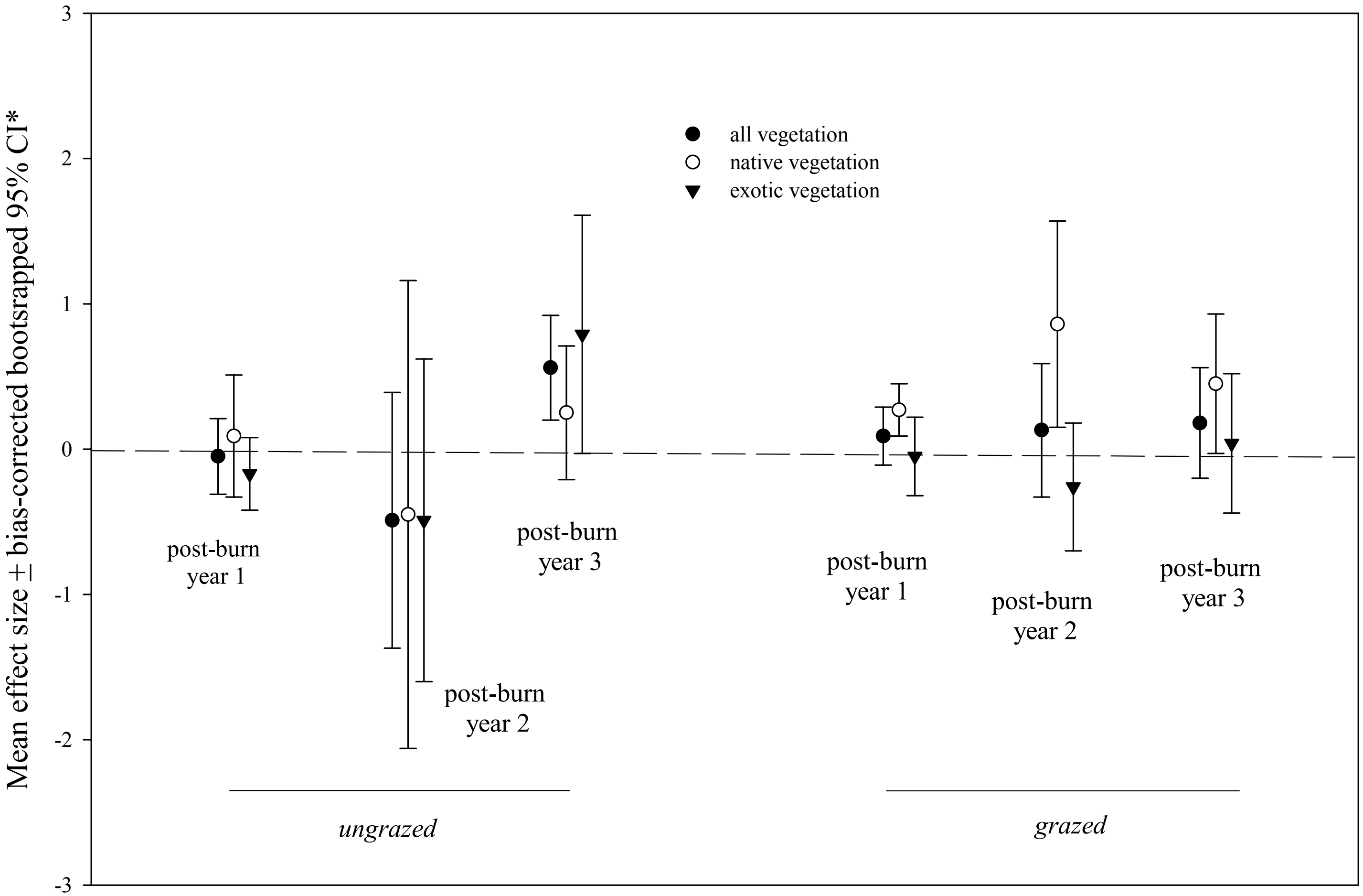
DiTomaso et al. 1999	repeat burning and temporal replicates	*Avena fatua*	cover		increased after each burn treatment
Meyer and Schiffman 1999	3 burn season; mulch removal	*Avena* spp.	cover	2	highest but not significantly in burn treatments and lowest in mulch removal
Eller 1994	three burn dates	*Avena* spp.	frequency	no data	non-significant increase for Decemebr burn
Larson and Duncan 1982	single burn	*Bromus diandrus*	biomass	2	slightly higher in burn area
Larson and Duncan 1982	single burn	*Bromus hordeaceous*	biomass	2-3	highest in burned area (200% of control)
York 1997	late summer, unplanned fire	native annual grasses	cover and frequency	no data	cover and frequency higher in burned area for all native species
Langstroth 1991	interaction with grazing	*Vulpia* spp.	freq	no data	density significantly higher in burn and late graze burn treatments
Parsons and Stohlgren 1989	sesaon, repeat burns	*Vulpia myuros*	biomass	no data	increased to 6.2% relative biomass after 3rd spring burn
Hansen 1983	repeat burning and temporal replicates	*Vulpia myuros*	cover	2	most burn treatments had higher abundance than controls and highest abundance after 3rd burn

Non-native Annual Grasses Seed banks

Eller 1994	three burn dates	*Avena* spp.	seed bank	no data	no significant differerence as a result of burn
Eller 1994	three burn dates	*Bromus* spp.	seed bank	no data	no significant differerence as a result of burn
Eller 1994	three burn dates	*Bromus hordeaceous*	seed bank density	no data	significant decrease from pre-burn

Ahmed 1983	three burn dates	other non-native annual grasses	seed bank density	no data	significant decrease from pre-burn
Ahmed 1983	single burn	annual grasses	seed bank density	no data	large decrease follwing summer burn
Menke and Rice 1981	3 burn season;mulch removal	annual grasses	seed bank density	no data	greatest in control and February-burned plots
Meyer and Schiffman 1996	3 burn season;mulch removal	all non-native grasses	seed bank density	no data	significantly lower in Fall and late Spring burn treatments
Meyer and Schiffman 1999	3 burn season;mulch removal	*Avena* spp.	seed bank viability	no data	Fall significantly lower than control and late Spring significantly lower than Fall
Meyer and Schiffman 1999	3 burn season;mulch removal	*Bromus madratensis*	seed bank viability	no data	significantly lower in Fall and late Spring burn treatments
Meyer and Schiffman 1999	3 burn season;mulch removal	*Hordeum murinum*	seed bank viability	no data	not significantly lower in burn treatments

Figure 1. Post-burn abundance mean effect size of all, native, and exotic vegetation, after a single fire, in grazed and ungrazed grassland. CI not overlapping zero are considered significant.



*CIs are bootstrapped because meta-analysis data generally do not conform to normal distribution criteria. CI are repeatedly calculated from a series of randomly chosen set of studies in order to generate a distribution of possible values. The bootstrapped values are corrected if more than 50% of the values are above or below the original value. See Rosenberg et al. (2000) for more details.

Figure 2. Post-burn abundance mean effect size of all, native, and exotic vegetation, after 2-3 annual burns, in ungrazed and grazed grassland.

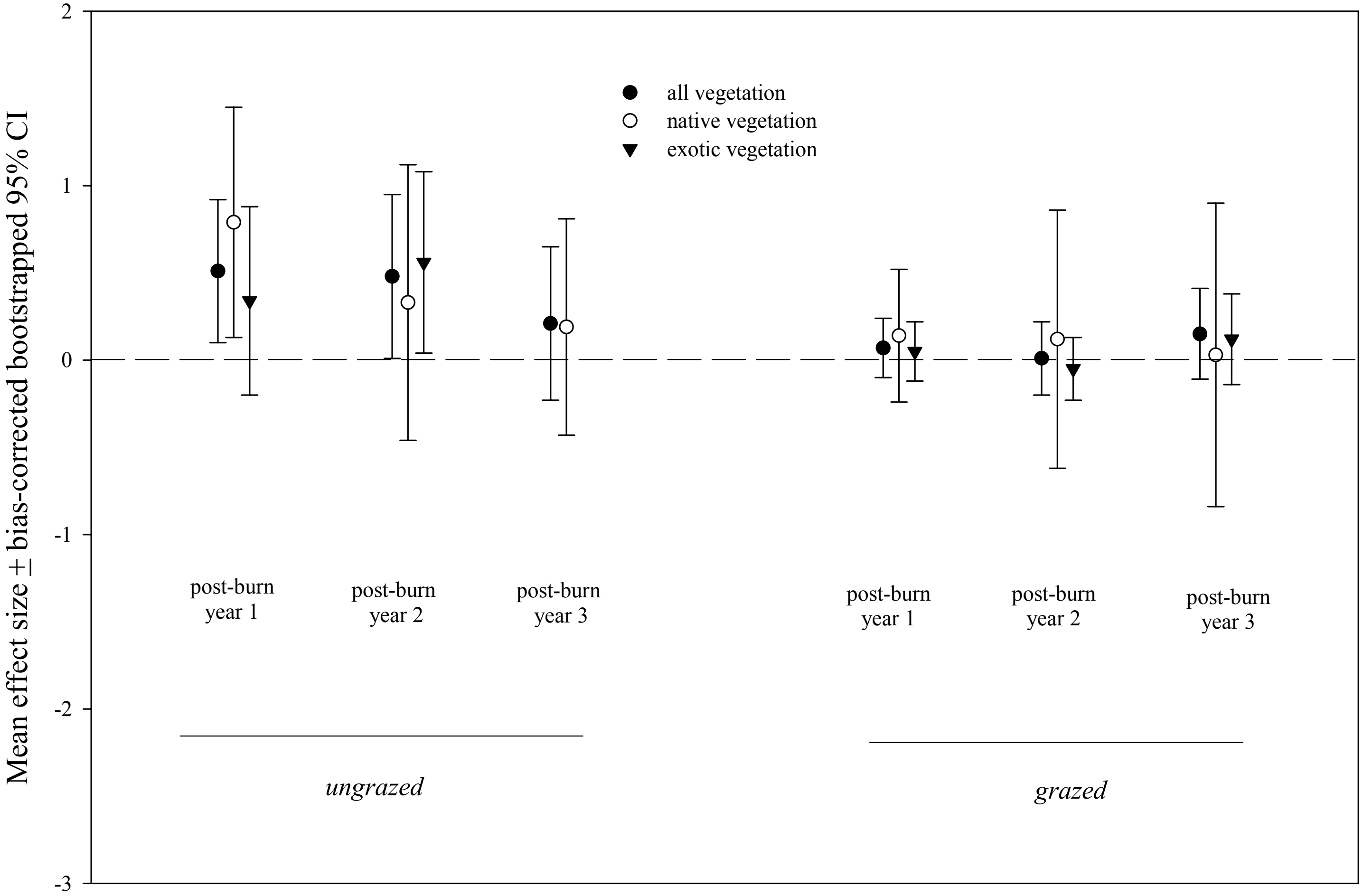


Figure 3. Post-burn abundance mean effect size of life form groups, after a single fire, in grazed and ungrazed grassland.

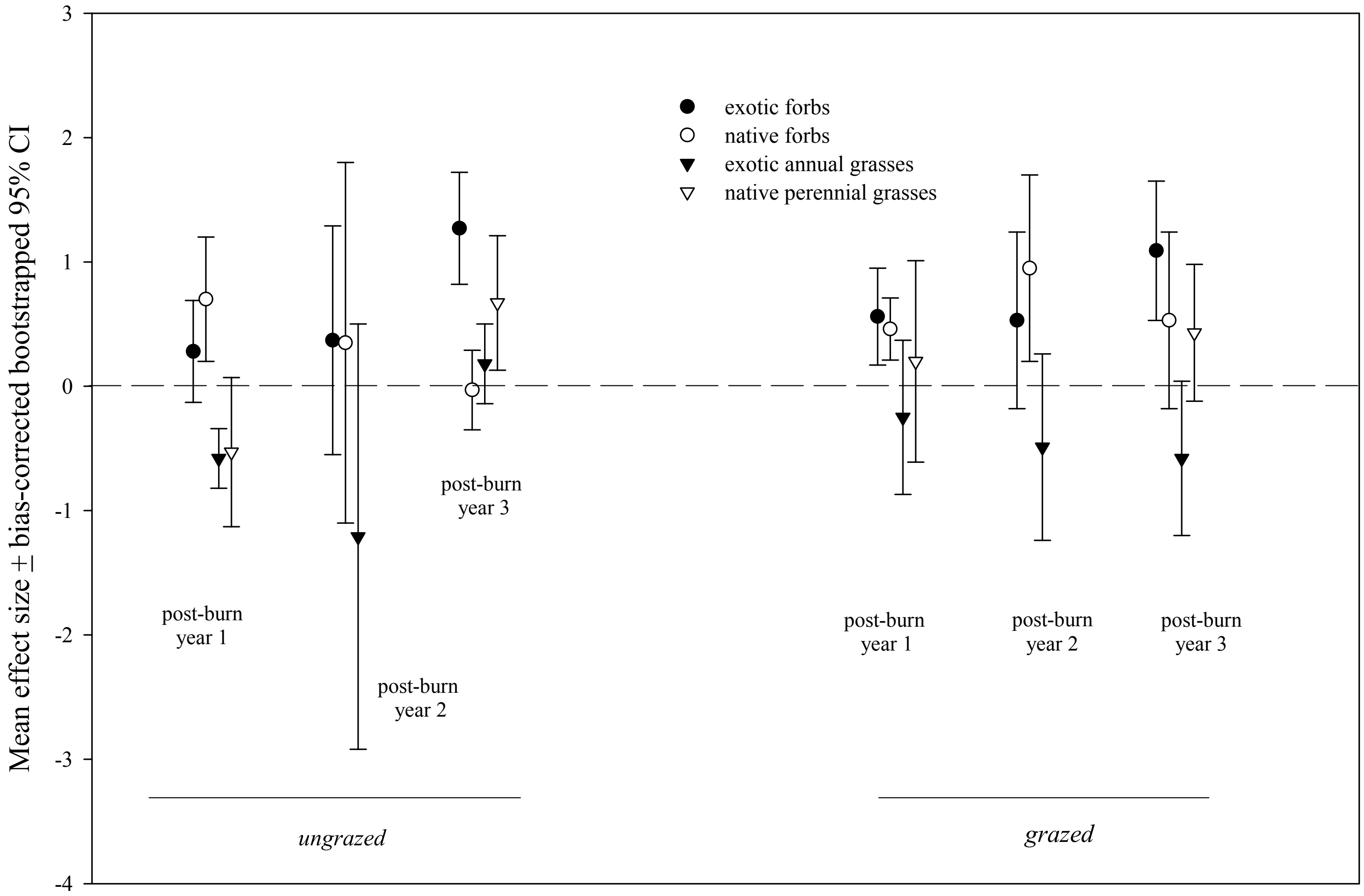


Figure 4. Post-burn abundance mean effect size of life form groups, after 2-3 annual burns, in grazed and ungrazed grassland.

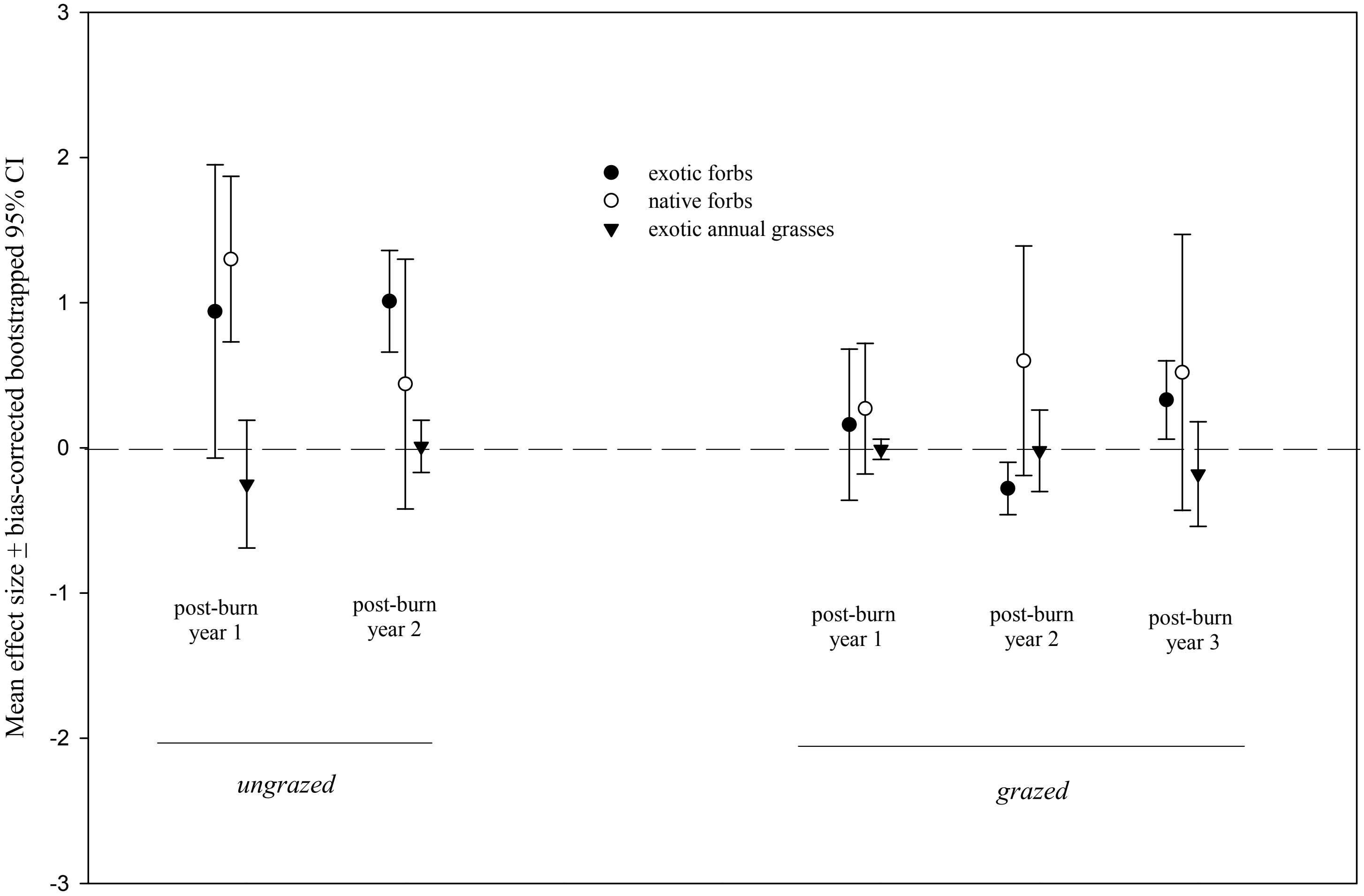


Figure 5. Post-burn abundance mean effect size of *Nassella pulchra* and *Danthonia californica,* all fire treatments 1-4 years after fire.

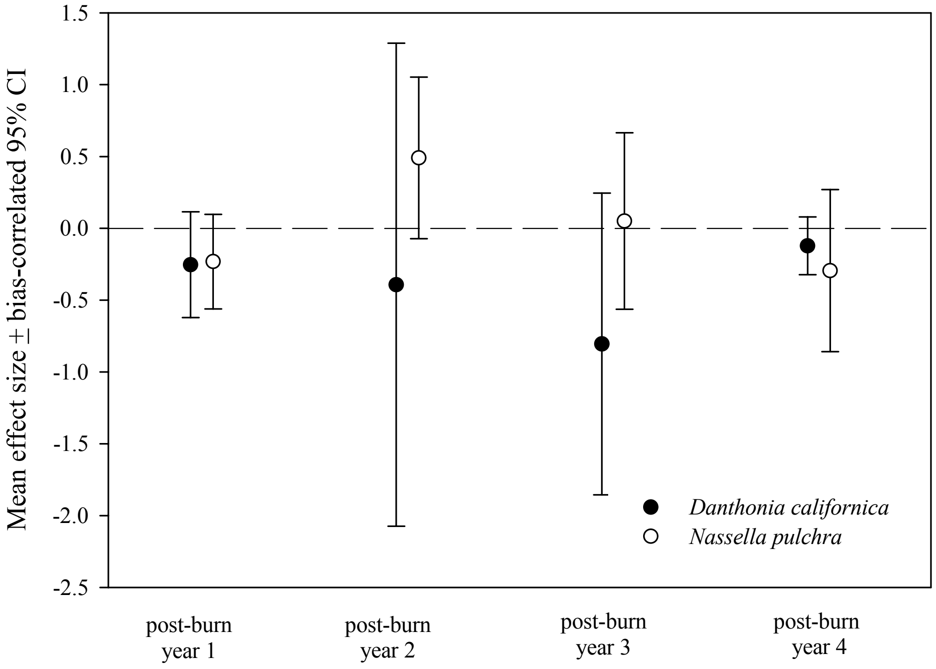
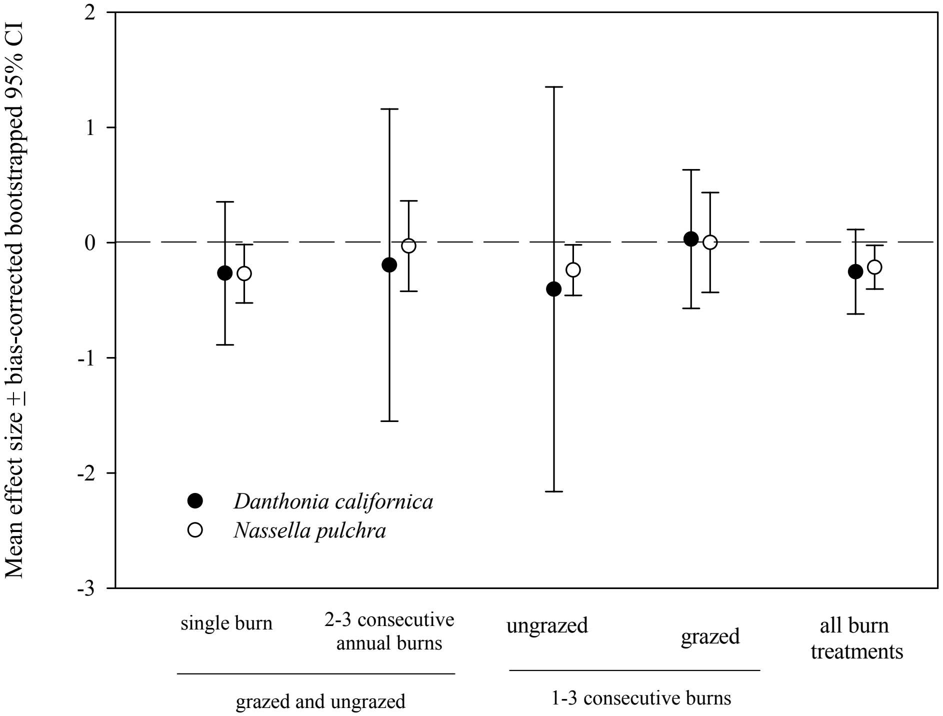


Figure 6. First post-burn year abundance mean effect size of *Nassella pulchra* and *Danthonia californica* by burn treatment type.



Appendix A-- Contacts for California Grassland Restoration Review.

The following were either sent a letter or email soliciting information reagrding grassland restoration, or were contacted by telephone. Included are researchers and land managers including agency biologists, academics, consultants and nurseries.

Contact name	Institution/Company	phone number/email
Aimee Betts	UC Berkeley	abetts@nature.berkeley.edu
Albert Beck	Eco-Analysts	530-342-5991
Andrew Dyer	University of South Carolina, Aiken	andyd@aiken.sc.edu
Andy Delmas	BLM, Boise, ID	208-384-3401
Ann Dennis	CalFlora	anndennis@ix.netcom.com
Ann Francis	NRCS	ann.francis@ca.usda.gov
Berta Youtie	TNC, Oregon	LaGrande, OR
Bill Davilla	Ecosystems West	831-429-6730
Bill Halvorson	US Geological Survey	bill_halvorson@usgs.gov
Bob Hornback	Muchas Grasses	707-874-1871
Bob Miller	Kamprath Seed Co.	209-823-6242
Bob Timme	Hopland Research Station	rmtimm@ucdavis.edu
California Specialty Gardens	JoAnn R. Morgan	209-527-5889
Carol Bornstein	Santa Barbara Botanic Gardens	805-682-4726
Charlie Danielson	Native Here Nursery	charlid@pacbell.net
Charles A. Patterson	private consultant	510-938-5263
Chris Sauer	Napa Native Plant Nursery	707-253-7783
Christian Kiillkkaa	Kiillkkaa Group Landscape Artisans	415-931-9079
Chuck Vaughn	Hopland Research Station	szcevaug@mailbox.ucdavis.edu
Chuck Williams		707-462-8984
Craig Dremann	The Reveg Edge	650-325-7333
Craig Martz	Department of Fish and Game	cmartz@dfg.ca.gov
Dan Osborne, Betsy Flack	Osborne, Daniel R., AIA, ASLA	415-777-3553
Daphne Hatch	NPS, GGNRA	415-561-4938
Daryl Peterson	TNC, Sacramento River Project	530-897-6370
Dave Magney	CNPS	805-6461545
David Amme	CalTrans	seed@tdl.com
David Gilpin	Pacific Coast Seed, Inc.	925-373-4417
David Kaplow	North Coast Native Nursery	707-769-1213
David Parsons	Aldo Leopold Wilderness Research Institute	djparsons@fs.fed.us
David Zippin	Jones & Stokes	San Jose, California
Deb Hillyard	Department of Fish and Game	dhillyard@ dfg.ca.gov
Diane Renshaw	private consultant	415-728-5845
Donna Vaiano	Moon Mountain Wildflowers	805-772-2473
Dudek Associates, Inc.		tfoster@dudek .com
Earl Lathrop	Loma Linda University, retired	909-687-8101
Edith Read	Psomas & Associates	714-751-7373 x7933
Elizabeth Gray	TNC, Hamilton Range	415-777-0487
Ellen Bauder	San Diego State University	ebauder@sunstroke.sdsu.edu
Eric Aschehoug	TNC, Santa Cruz Island Preserve	805-488-8840
Eric Porter	UC Irvine	eporter@ea.oac.uci.edu
Everett Butts	Wapumne Native Plant Nursery Co.	916-645-9737
Fred Nick	Nick Range Management	805-438-5852
George Cox	San Diego State University, retired	Geowcox@aol.com
Georgia Stigall	Native Habitats	Woodside, CA
Go Native Nursery		650-728-2286
Grey Hayes	UC Santa Cruz	grey@cats.ucsc.edu
Guy Kyser	UC Davis	gbkyser@ucdavis.edu

H.T. Harvey Associates		408-263-1814
Harold Appleton	Prunuske Chatham, Inc.	707-874-0100
James Barry	Calif. DPR, Headquarters, Sacramento	JBARR@parks.ca.gov
Jamie Kneitel	Florida State University	jkneitel@garnet.acns.fsu.edu
Jaymee Marty	TNC, Cosumnes River Preserve	916-684-2816
Jeanne Larson	San Joaquin Experimental Range, retired	mforvet@macol.net
Jeff Chandler	Cornflower Farms	916-689-1015
Jim Barry	State Parks and Recreation	jbarr@parks.ca.gov
Jim Dice	Department of Fish and Game	jdice@dfg.ca.gov
Jim Gorter	Karleskint-Crum, Inc	805-543-3304
Joan Stewart		Tori2toli@aol.com
JoAnn R. Morgan	California Specialty Gardens	209-527-5889
Joanne Kerbavaz	State Parks, San Francisco	jkerb@parks.ca.gov
Joe DiTomaso	UC Davis	ditomaso@vegmail.ucdavis.edu
John Anderson	Hedgerow Farms	530-662-4570
John Menke		qvredangus@sisqtel.net
John Rieger	John Rieger & Associates	619-263-2712
Jon Keeley	USGS	jon_keeley@usgs.gov
Joni L. Janecki	Joni L. Janecki & Associates, Inc	831-423-6040
Joshua Fodor, Kirk Dakis	Nurseries, Seed Suppliers	408-459-0656
Joshua Fodor, Kirk Dakis	Nurseries, Seed Suppliers	408-459-0656
Judith Lowry	Larner Seeds	415-868-9407
Julie Hooper	Circuit Rider Productions, Inc.	707-838-6641
Karen Sullivan	Lake County Natives	707-279-2868
Kathey Purcell	San Joaquin Expt. Range/Forestry Sciences Lab	559-868-6233
Kathleen Murrell	UC Davis graduate student/grazing Sierran meadows	530-752-2644
Ken Poerner	Solano Land Trust	707-432-0105
Ken Reeves		
Kenneth Whitney	Foothill Assocaites	Roseville, CA
Kevin Rice	UC Davis	kjrice@ucdavis.edu
Kevin Shaffer	Department of Fish and Game	kshaffer@dfg.ca.gov
Kim Marsden	Department of Fish and Game	kmarsden@dfg.ca.gov
Larry Saslaw	Bureau of Land management	Lawrence_Saslaw@ca.blm.gov
Leo Arguello	Redwood NP	Leonel_A._Arguello@nps.org
Louise Lacey	Growing Native Research Institute	510-232-9865
LSA Associates		916-630-4600
LSA Associates		949-553-0666
LSA Associates		510-236-6810
LSA Associates		909-781-9310
Marc Meyer	UC Davis	mdmeyer@ucdavis.edu
Mark Heath, Noah Booker	Shelterbelt Builders, Inc.	510-841-0911
Mark Stromberg	Hastings Reserve	stromber@socrates.berkeley.edu
Mary McClanahan	California State University, Fresno	Fresno, CA
Mary Meyer	Department of Fish and Game	mmeyer@dfg.ca.gov
Mary Price	UC Riverside	mary.price@ucr.edu
Megan Lulow	UC Davis	melulow@ucdavis.edu
Michael Lansdale	Martha Blane Associates	619-471-1245
Micki Miller	Wetland Research Associates	415-454-8868
Mikay Fugebsuto	Army Corp. Engineers	916-557-7271
Mike Conner	TNC on Army Corp project	916-449-2853
Mike Evans	Tree of Life Nursery	949-728-0685
Mike Wood	Sycamore Assoc.	Walnut Creek, CA
Mission Hill Nursery		619-295-2808
Nancy Gilbert	California Nursery & Design	916-692-1186

Nathaniel Benesi	Humbolt State University	njb8@humboldt.edu
Native Revival Nursery		408-684-1811
Pam Muick	Solano Land Trust	707-432-0105
Paul Albright	Albright Seed Company, Inc.	805-987-9021
Paul Kephart	Rana Creek Habitat Restoration	408-659-3811
Paul Reeberg	National Park Service	paul_reeberg@nps.gov
Paula Schiffman	California State University	Northridge, CA
Peter Hujik	TNC, Lassen Foothill Project	530-527-4261
Ramsey Seed, Inc.		800-325-4621
Randall Jackson	UC Berkeley	rjackson@nature.berkeley.edu
Rhonda, Bob or Michael Mark	Mark Seeding Services, Inc.	209-745-0491,
Rich Lis	Department of Fish and Game	rlis@dfg.ca.gov
Rich Reiner	TNC, Lassen Foothill Project	530-897-6370
Richard Nichols	EIP Associates	415-362-1500
Rick Storre	Freshwater Farms Northcoast Seed Bank	707-444-8261
Rob Hansen	Sequoia Community College	559-627-5473
Rob Preston	Jones & Stokes	Sacramento, California
Robert Matheny	Valley Transplant	209-368-6093
Robert Stephens, Jean Ferreira	Elkhorn Native Plant Nursery	831-763-1207
Robin Wills	National Park Service	robin_wills@nps.gov
Ruth Birch-Stephens	Heritage Ranch Nursery	209-665-2171
S & & Seeds	Vic Schaff	ssseeds@silcom.com
S. Gruman	BioNett, LLC	831-582-3477
San Dimas Expt. Station	USDA, Forest Service	626-963-5936
Scott Stewart	Conservaseed	916-775-1676
Shelia Barry	UC Cooperative Extension, Santa Clara	408-299-2635 ext. 1005
Sherry Teresa	Center for Natural Lands Management	steresa@cnlm.org
Sherryn R. Haynes	California Straw Works	916-453-0139
Sierra View Landscape	Jasper Swift	916-344-4943
Stephen Knutson	Stover Seed Company	213-626-9668
Steve Nawrath	Bitterroot Restoration	916-434-9596
Susan Clark		661-634-9228
Susan Harrison	UC Davis	spharrison@ucdavis.edu
Susan Shettler	Greening Assoc	408-336-1745
Terry Thomas	Presidio Trust	415-561-4481
Toms Stohlgren	US Geological Survey	toms@nrel.colostate.edu
Tony Caprio	Sequioa-Kings Canyon NP	Tony_Caprio@nps.gov
Trish Smith	TNC, Irvine Co. Open Space Reserve	714-832-7478
Tyson Holmes	Ecological Research Design Consulting	EcologicalResearchDesign@worldnet.att.net
Vic Schaff	S&S Seeds	805-684-0436
Walt Sadinski	TNC, Central Coast Project Office	805-544-1767
Walter Earle, Margaret Graham	Mostly Native Nursery	707-878-2009
Weldon Miller	AG-Renewal	800-658-1446
William L Halvorson	US Geological Survey	bill_halvorson@usgs.gov
Zach Principe	TNC, Santa Rosa Plateau Ecological Reserve	909-677-6951

Appendix B-- Methods for Meta-Analysis of Grassland Fire and Grazing Effects

Compiling the data matrices. We compiled a data matrix with response variables reported by life form and origin groups: native perennial grass, native forb, exotic annual grass and exotic forb. Unfortunately, data was insufficient for native annual grasses or exotic perennial grasses to use in a meta-analysis. In addition, the native and exotic forb categories had to include both annual and perennial species because not all studies reported data on forbs by annual versus perennial. We also compiled a data matrix of native perennial grasses by species.

For the fire meta-analysis, we used studies that compared burned to unburned conditions one to several years following the burn date. We would have preferred to compare control and burn pre- and post-fire differences in abundance but many studies did not include pre-burn data. Studies using a single large burn adjacent to an unburned control area, although pseudoreplicated (Hulbert 1984), were included so that they could be compared to studies that applied fire on a smaller scale. All these studies included several large plots or transects throughout the control and burn areas. Although these studies represent results from a single application of fire and not the range of burn conditions that several individually ignited fires may generate, they represent the effects of a large management burn.

For the grazing meta-analysis, we used studies that compared grazed to ungrazed conditions and all of these were actively grazed rather than observations on long-term release. Data from the most immediate year following establishment of grazing treatment was used for experimental studies (Dyer unpublished, Marty unpublished, Jackson unpublished, Dyer and Rice 1997, TNC 2000). The one observational study used was for a single year of observations in a long-term grazed site (Keeley unpublished).

Fire studies with controls in different pastures, with potentially different grazing regimes, were not included. Means (X), sample sizes (*n*) and standard deviations (s) for treated (burned) and control (unburned) samples had to be reported, or were available from the authors, in order to include the study in our analysis. If variance or standard error values were reported, they were converted to standard deviation using methods described in Guervitch et al. (1992).

Response variables we looked for or put together were abundance of life-form groups, and native perennial grass taxa. Acceptable response variables in order of importance were biomass, cover, frequency and density. If more than one response variable, for a given taxon or group, from a given study was reported, only one was used. Likewise, if a given taxa was reported both as an individual species and lumped in a life form group, then only the one of these values were used per matrix. When response variables were reported by micro-habitat within a given site (mound versus intermound, slope position, etc.), or initial density, each comparison was included so that response in variety of conditions are represented.

The matrices included data for the following treatment types: ungrazed/single burn, grazed/single burn, ungrazed/annual burn 2-3 times, and grazed/ annual burn 2-3 times. A separate entry was made for each treatment type and post-fire year that data was collected. The year data was collected relative to the latest burn is recorded as post-burn year, and 1 refers to the first year after the fire. We had enough data to determine effect for most comparisons up to the third post-burn year. In studies that crossed grazing with fire, the grazed burn data where entered as separate records from the burn only data and noted as grazed. Data from sites that had been previously burned (within 2 years) were added as first post-burn year data, and noted as having been previously once or twice burned. Most of the studies shared the same control for each treatment comparison resulting in non-independence of effect sizes within these studies. We had insufficient fire and grazing interaction studies to conduct a factorial meta-analysis.

Attribute coding. Each record (data reported for a given year for a given treatment) was classified by origin of the taxa (native to California or not, using Hickman 1993), and in the main data set life form and origin group (native perennial grass, etc.). For the fire meta-analysis, we also used number of previous burns, and grazing regime as class variables with potential for influencing burn outcome. Previous burns were noted as 0 if not burned in the last three years, 1 if burned the previous year, and 2 if burned the previous two years, etc. We also wanted to test Jepson Ecoregion, soil texture and elevation as predictor variables but had insufficient study replicates.

We used fire season, post-burn precipitation, length of longest post-burn year winter drought period, abundance of native species in unburned condition as potential predictor variables. Fire season or day of year burn occurred was transformed to a numerical value such that January 1 = 1, and December 31= 365 to use as continuous data, and as month to use as categorical data. Post-burn precipitation and post-burn percentage of average precipitation were given numerical values based on the total precipitation the next growing season following the burn, and percentage of long-term rainfall average in that season. The length of the longest winter drought period was determined as the longest period of consecutive dry days before March 30 (broken by >0.09 inches precipitation in one day) following the first winter deluge (> 0.75 inches over three days). We used the nearest weather station in a comparable elevation to the study site using the CIMIS and the Western Regional Climate Center web sites.

For the grazing meta-analysis we used grazing regime as the only record attribute other than life form and origin. We standardized grazing regime into one of the following types: wet-season (winter to spring), dry season (summer through fall), or continuous.

Numerical methods. The meta-analysis database consisted of citation information (author, date), the mean for the control (X_c) and treated (X_e), standard deviation or standard error for the control (S_c) and the treated (S_e), sample size for the control (N_c) and the treated (N_e), and attribute as described above. Calculations were completed in MetaWin (Rosenberg et al. 2000). The mixed-effects model (Gurevitch and Hedges 1993) was used in the analysis because we assumed variation in the burn conditions, in addition to the variation in conditions at the study sites, but a fixed effect between classes or plant functional groups.

We used log response ratio (lnR) as the index of effect size because it quantifies proportionate changes (Hedges et al. 1999), thereby eliminating any differences due to differences in site productivity and initial abundance. The effect size for each record is calculated as (Rosenberg et al. 2000):

$$\ln R = \ln\left[X_{ij}^{e} / X_{ij}^{c}\right] = \ln(X_{ij}^{e}) - \ln(X_{ij}^{c})$$

and the variance is the following:

$$v_{\ln R} = S_e^2/N_e X_e^2 + S_c^2/N_c X_c^2$$

and the mean or cumulative effect size in the meta-analysis (lnRR) is weighted using w_{ij} which is estimated by $1/v$ and calculated as (Rosenberg et al 2000):

$$\ln RR = \sum_{i}^{m} \sum_{j}^{k} w_{ij} (\ln R)_{ij} \; / (\sum_{i}^{m} \sum_{j}^{k} w_{ij})$$

and the standard error for the cumulative effect size is calculated as:

$$s(\ln RR) = (1/ \sum_{i}^{m} \sum_{j}^{k} w_{ij})^{1/2}$$

Bias-corrected bootstrap 95% confidence intervals (95%CI) were generated from a series of randomly chosen set of studies in order to generate a distribution of possible values. This method was used because meta-analysis data generally do not conform to normal distribution criteria (Rosenthal et al. 2000). The CI were corrected if more than 50% of the values are above or below the original value. The CI for each set of studies is calculated using the following:

$$95\%CI = \ln RR \underline{+} 1.96 \, (1/ \Sigma_{i}^{n} w_i)^{1/2} (\ln RR).$$

We conducted meta-analysis by fire treatments, for each post-burn year, using the following plant group comparisons 1) general vegetation (all life forms and origins), as a means of assessing fire treatment effects on overall grassland productivity, 2) origin (native, exotic), 3) life form and origin groups (native perennial grasses, native forbs, exotic annual grasses, exotic forbs), and 4) perennial grasses by species.

Finally we used Rosenthal's fail-safe number (N_R ; Rosenthal 1979) to determine if the number of studies or records used was large enough to generate a reliable result. The fail safe number is the number of additional studies required to change the significance of the result from significant to non-significant. It is calculated by the following equation:

$$N_R = \Sigma_{i}^{n} Z(p_i)]^2 / Z_{\alpha}^2 - n$$

where $Z(p_i)$ is the Z value for individual significance values; Z_α is the one-tailed z-score associated with the α value used; and n is the number of studies used.

Statistical methods. We tested whether all studies within a life form and origin group had a common true effect size for a given treatment, that is whether the groups were homogenous or relatively consistent with respect to response to fire, and observed differences were due to variation in burn conditions and site factors. We considered the cumulative effect size a true estimate of the overall magnitude of fire effect on a given group if the bias-corrected bootstrapped 95% CI of the calculated mean effect size (lnRR) did not overlap zero ($P < 0.05$). The homogeneity of effect sizes within a given cumulative effect size for a group was determined using the weighted sum of squares statistic, Q_T (Hedges and Olkin 1985 in Rosenberg et al. 2000), which represents the total heterogeneity of a sample. A significant Q_T (using a chi-square table) indicates that there is greater variation among effect sizes than expected by sampling error and that other variables should be considered (Rosenberg et al. 2000). This statistic is similar to the sum of squares in ANOVA. We used between group measures of heterogeneity (Q_B) to determine whether fire effects are significantly different between treatment and plant groups.

Climatic variables, and burn date were used as independent variables with effect size as the dependent variable in regression. One problem with meta-analysis and combining studies for regression is that multiple effect sizes from the same study are not independent and are representative of a single landscape and climate variable. Hence, single studies with multiple effect sizes used in regression can bias the fit of regression equations in the meta-analysis (Bender et al . 1998).

We calculated the number of studies needed to calculate a meaningful value for mean effect size (Rosenthal 1979 as cited in Rosenberg et al. 2000). The equation estimates the number of studies that would be required to bring the level of probability of a Type I error to the desired significance.

Interpretation of Results. A negative response ratio (lnR) value represents a lesser abundance of that group in the burn treatment than the control, and a positive value represents greater abundance in the burn treatment than the control. If the ratio (Xe/Xc) of a given group in the burned and unburned samples is 1 [$\ln R=\ln(1)=0$], then there is no burn effect. An effect size is generally interpreted as "small" if it is 0.2; "medium" if it is 0.5; "large" if it is 0.8, and greater than 1.0 is "very large" (Cohen 1969). Effects are significant at $P<0.05$ when the 95% confidence limits for the effect sizes do not overlap zero (Gurevitch and Hedges 1993). In addition, the variation between classes in mean effect size (measured as Q_B) is calculated by MetaWin and a chi square table was used to determine critical values using one less than the number of classes as the degrees of freedom. If the fail-safe number (N_R) was much greater than the actual number of records used than the results were considered a reliable estimate of the true effect. If the number was near or less than the number of records used than the result was not considered reliable.

It is important to keep in mind that meta-analysis is useful for determining general relationships influenced by predictor variables. Monitoring of grazing effects or prescribed burn should occur to determine specific site and community prescriptions.