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THE EFFECTS OF FALL BURNING ON TWO NORTHERN
CALIFORNIA PERENNIAL BUNCHGRASS COMMUNITIES

presented by

Charles C. Hughes IV

has been accepted towards fulfillment
of the requirements for

M.S. degree in Plant Biology

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THE EFFECTS OF FALL BURNING ON TWO NORTHERN CALIFORNIA PERENNIAL BUNCHGRASS COMMUNITIES

By

Charles C. Hughes IV

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Plant Biology

2003

ABSTRACT

THE EFFECTS OF FALL BURNING ON TWO NORTHERN CALIFORNIA PERENNIAL BUNCHGRASS COMMUNITIES

By

Charles C. Hughes IV

California native perennial grasslands are declining due to pressure from exotic species, changes in disturbance regimes and loss of habitat. Prescribed burning has been used by land managers to promote native species, control invasive weeds, and increase growth and reproductive output of perennial grasses in California grasslands. This study examines the effect of fire on native species, exotic species, and perennial grasses in the northern Sacramento valley. Communities containing two native perennial bunchgrasses, *Nassella pulchra* and *Aristida ternipes* var. *hamulosa*, were selected for burning. Data on bunchgrass vegetative and reproductive growth, botanical composition, Shannon-Weiner diversity, and seed bank composition was collected in late spring of 2001 and 2002; burns were conducted in October of 2001. For *N. pulchra*, fire increased both basal area and number of inflorescences, as well as seed weight. No effect on basal area or inflorescences was found for *A. ternipes*, but fire sharply increased the mortality rate of this species. Fire increased the Shannon-Weiner diversity index in the *Nassella* community, but the heightened diversity was due to increases in exotic species. Annual grasses decreased while annual forbs increased due to fire. *Taeniatherum caput-medusae* and several other species, both native and exotic, experienced significant changes in cover with burning. Annual grasses in the seed bank were reduced by burning. Fire was helpful in restoring the *Nassella* community but not the *Aristida* community.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Carolyn Malmstrom, for all her advice and guidance throughout this project. I would also like to thank Dr. Peter Murphy, Dr. David Rothstein, and the National Science Foundation for support (DEB 9983373). I am grateful to Peter Hujik and The Nature Conservancy for the use of land and facilities at the Dye Creek Ranch and Vina Plains Preserve. Scott Butterfield and Jessica Cook provided assistance in the field and the greenhouse.

PREFACE

The composition of California grasslands has changed dramatically over the last 200 years (Clements 1934, Heady 1988, Hamilton 1997, Schiffman 2000, Holstein 2001), in part because natural disturbance regimes have been disrupted by human activities. In the past, California grassland ecosystems experienced fires, floods, and grazing by migratory elk and pronghorn antelope (Heady 1988). Now these grasslands rarely experience fires or floods, and instead are subjected to grazing by cattle and sheep, pressure from exotic species, and a general loss of habitat due to urbanization and agriculture. Perennial grasslands currently exist as widely scattered patches, sometimes no larger than a tenth of a hectare. These remaining patches of bunchgrasses usually exist within a matrix of invasive exotic species. Established bunchgrass individuals under such pressure decline in size, and populations may not recruit well (Dyer and Rice 1997, Hamilton et al. 1999, Brown and Rice 2000). Researchers have tried to mimic natural disturbance regimes in order to restore bunchgrass populations, and have met with mixed success (Dyer et al. 1996). Prescribed burning has become more common as land managers try to simulate natural fire regimes. The Nature Conservancy alone burns 3,000-10,000 acres annually in California (P. Hujik pers. comm.). The effects of prescribed burning on natural communities may be quite variable due to variables such as season of burn and annual and monthly patterns of precipitation. However, some trends are apparent and are addressed here.

Most prescribed burning in California is conducted during the spring, even though natural burns are more likely to occur during the fall when the vegetation is drier and there is more lightning as a source of ignition. Furthermore, most prescribed burning is done solely for the purpose of invasive weed control. This project examines the effects of a fall prescribed burn on several ecological attributes within two native perennial grassland communities, one containing *Nassella pulchra* (Purple Needlegrass), and one containing *Aristida ternipes* var. *hamulosa* (Prairie Three-Awn).

Chapter 1 reviews what is known about the historical extent of bunchgrasses in California and the original fire regime; the effects of fire on the seed bank, the botanical composition, and on *N. pulchra* and *A. ternipes*; and the effects of fire on soil properties. Chapter 2 describes a manipulative experiment which subjected two grasslands communities to prescribed burning. A seedling key to some common California grasses was developed as a result of work with the seed bank, and is presented in Chapter 3 as an aid to anyone concerned with identifying grasses at an early stage.

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I. California grasslands

Most of the California grasslands are located in the Central Valley, which lies between the Coastal mountain ranges and the Sierra Nevada, and in the adjacent coastal valleys. The Central Valley is completely surrounded by a ring of foothills, except for the Sacramento and San Joaquin River deltas. The foothill areas are largely comprised of an oak savannah habitat containing the California endemic *Quercus douglasii* (Blue Oak). *Q. douglasii* usually forms an open canopy forest, leaving numerous large and small patches available for grassland. The California oak savannah habitat fades into a more pure grassland habitat in the lower foothills and the valley floor. The two study sites in this project are located in the northeastern Central Valley (Figure 1).

Most of the California grasslands experience a Mediterranean climate (Figure 2)[1], which is characterized by cool, wet winters, and hot, dry summers. The rainy season in California usually begins in October or November and extends through the winter, with the last significant rainfall occurring in April or May. Precipitation is almost non-existent from June through August. The temperatures of the low elevation grasslands usually do not dip far below freezing in the winter. In the summer, highs exceeding 37° C are common. In a Mediterranean climate, the annual precipitation and the annual potential evapotranspiration are perfectly out of phase with each other. Most California grassland vegetation grows during the winter and spring. In the summer and fall, annual species are senescent while perennials have become dormant until the next growing season.

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[1] Data obtained from National Climatic Data Center, http://lwf.ncdc.noaa.gov. Potential evapotranspiration calculated according to (Thornthwaite 1948).

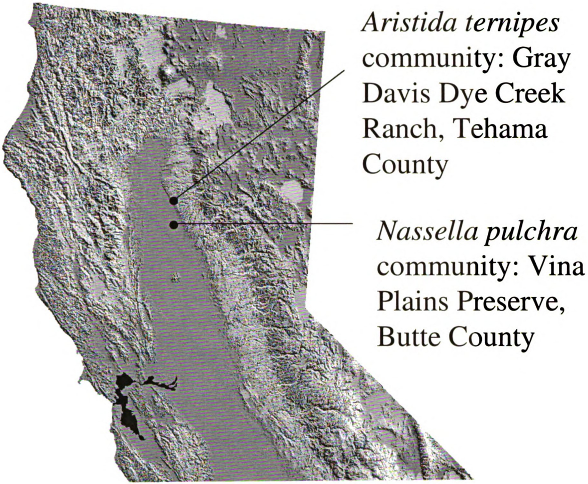

Figure 1. Map of northern California, indicating the two study sites in this project. Map obtained from U.S. Geological Service, Flagstaff Field Center, *http://wwwflag.wr.usgs.gov/USGSFlag/Data/maps/shadedRel.html*

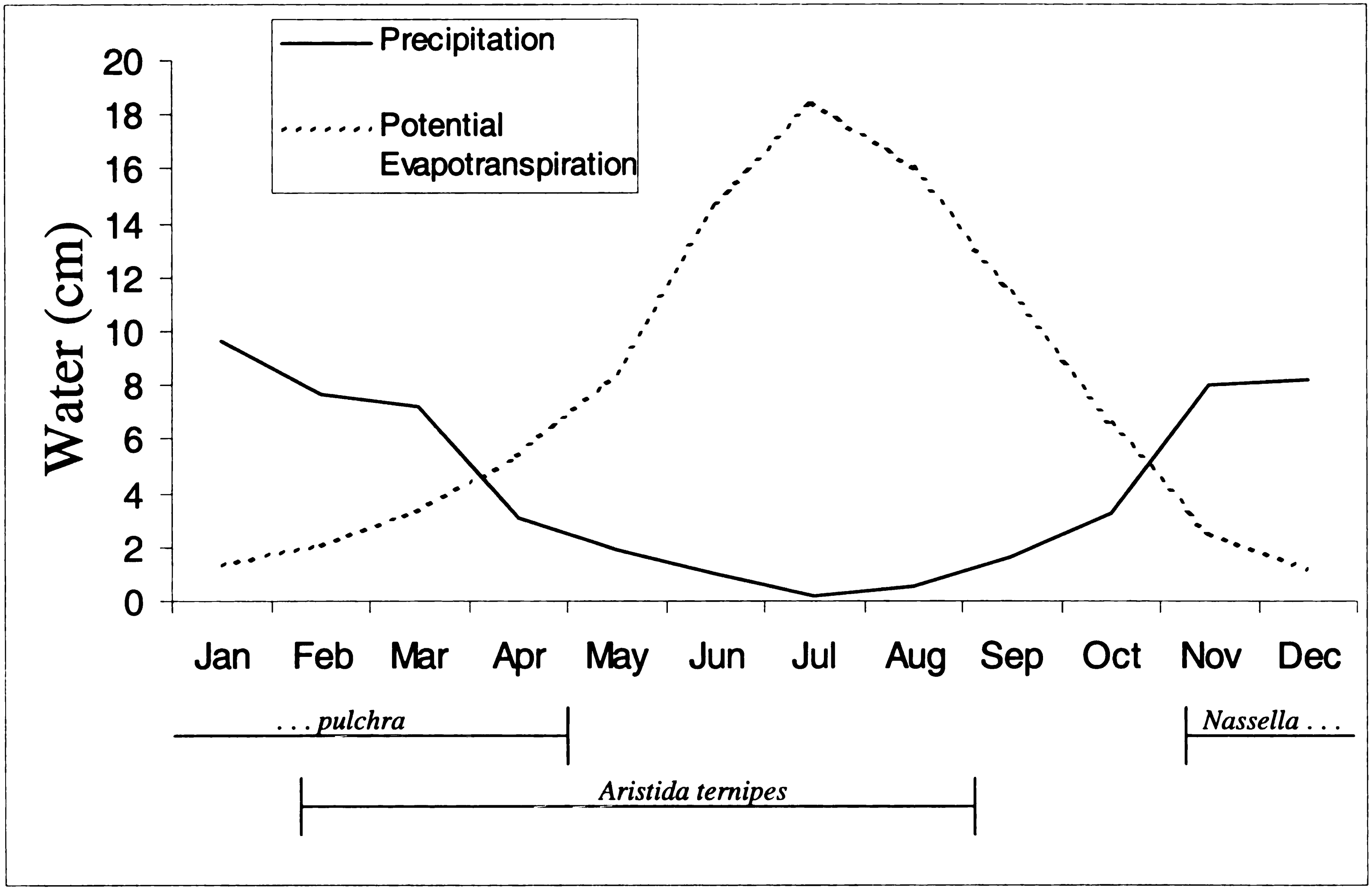

Figure 2. The average annual pattern of precipitation and PET at Red Bluff, CA. Data was obtained from the National Climatic Data Center, Red Bluff Municipal Airport station (http://lwf.ncdc.noaa.gov). PET was calculated according to Thornthwaite (1948). The approximate monthly growing periods of *N. pulchra* and *A. ternipes* are shown.

Most California grasslands are comprised almost entirely of exotic species. The most successful invaders are annual grass species from the Old World Mediterranean regions of southern Europe and Asia Minor. Particularly successful annual grass genera such as *Avena* and *Bromus* have come to be dominant species in much of the California grassland. The invasion of California grasslands by exotics may have begun even before the first permanent European settlements, the Spanish missions, were established (Mensing and Byrne 1998). The present preponderance of exotic species in California obscures the original grassland composition, but even still researchers have drawn conclusions about the composition of the grasslands before European contact.

Clements (1934) postulated that a vast perennial grassland once covered the entire valley, but his evidence was limited to observations made in often-disturbed railroad rights of way. Heady (1988) offers the opinion that perennial bunchgrasses were the climax community on most well-drained upland areas within the valley. Others suggest that a variety of habitat types may have occurred within the valley, including perennial grassland, annual grassland, chaparral, and even desert in the South (Hamilton 1997, Schiffman 2000). Holstein (2001) gives evidence that lowland areas within the valley were dominated by rhizomatous grasses and sedges. One study has demonstrated the contraction of a perennial bunchgrass population on a small spatial scale (Bartolome et al. 1986), but experimental evidence of changes in cover of perennial grassland at the landscape level is lacking. It is reasonable to assume on the basis of competition experiments between native perennials and exotic annuals that more of the California grassland was once occupied by perennial bunchgrasses (Bartolome and Gemmill 1981, Dyer and Rice 1997, Clausnitzer et al. 1999, Dyer and Rice 1999, Hamilton et al. 1999).

Current opinion holds that native rhizomatous graminoids prevailed in the lower, flood-prone areas of the valley (Holstein 2001), and that native annual grasses and forbs were common and possibly dominant in well-drained areas and the surrounding foothills (Hamilton 1997, Schiffman 2000). Patches of native perennial bunchgrasses were likely common in the surrounding foothills and some upland sites within the central valley (Heady 1988, Holstein 2001).

Since European contact, some of the ecological forces shaping California grasslands have changed. The state has experienced invasion by numerous exotic species, leading to large changes in botanical composition. Patterns of grazing have also changed in the last several hundred years (Heady 1988). Migratory herds of elk and pronghorn antelope used to move freely through the grasslands. Today, much of the range is fenced and used for cattle and sheep grazing. Grazing by domestic livestock may be much more intense if the stocking rates are high. The pattern of another disturbance agent, fire, has been altered with the development of the state (D'Antonio and Vitousek 1992). In the prehistoric grasslands, fire in the summer and fall would have been able to spread through the dry grasslands unimpeded by modern developments such as roads and irrigated pastures. Currently, active fire suppression has largely removed fire from the grasslands.

This project examines two of the many species of perennial bunchgrasses native to California. *Nassella pulchra* (Purple Needlegrass), a C3 perennial bunchgrass, is one of the more common perennial bunchgrasses in California. This species begins growth after the first significant precipitation, usually in the late fall or early winter. Vegetative growth continues through the winter and early spring. In late spring, inflorescences are produced, and the plant senesces in early summer. This seasonal growth pattern is common among perennial bunchgrasses of the state. *Aristida ternipes* var. *hamulosa* (Hook Three-Awn), a C4 perennial bunchgrass, is less common and usually grows in drier conditions than *N. pulchra*. Growth begins in the spring and the plant remains green throughout much of the summer. Inflorescences are produced continually, and may be found from late spring through the end of the summer. By fall, *A. ternipes* has senesced, and remains dormant until the next growing season. The seasonal growth pattern of *A. ternipes* is less common among California perennial bunchgrasses and provides a contrast to *N. pulchra*.

II. The history of fire in California grasslands

Fires were likely common in the grasslands of the Central Valley prior to the settlement of the region by Europeans (Biswell 1989, D'Antonio and Vitousek 1992). The grasslands are dry for several months of the year and ignition sources could have started fires that may have spread for several square kilometers. Ignition of fire in most natural cases is attributable to lightning (Barbour et al. 1999), which is more common at higher altitudes, but still occurs with sufficient frequency to potentially cause hundreds of wildfires annually in the valley and surrounding foothills (Biswell 1989). Biswell (1989) presents evidence that in some years, when climatic conditions are favorable, there may have been many more fires in the lower elevations. In addition, Native Americans are believed to have deliberately burned parts of valley grasslands for several possible reasons (Biswell 1989). The fires may have been lit to improve hunting prospects by creating a flush of new grass growth to attract grazers. Alternatively, the fires may have been lit to promote the abundance of acorns, another food source. A short fire return interval is known to promote the dominance of oaks under some conditions in other parts of North America (Abrams 1992, Van Lear and Watt 1992). Since the purpose is unclear, the season of Native American fires is not known. Natural fires may have been more common in the fall when there is a greater likelihood of lightning (Biswell 1989), but the true pre-historic fire regime is not known with accuracy.

The fire regime in the Central Valley was likely altered as settlers arrived. Not only was fire actively suppressed, but the native natural communities were also disappearing as land was plowed for agricultural use. An official government policy of fire suppression began with the creation of the Forest Service in 1905 (Biswell 1989), and it has not been until recent decades that the contributions of fire to natural ecosystem functioning have been widely recognized. Increasingly, prescribed burning has been used to simulate a natural fire regime and to restore and maintain natural ecosystem conditions and functioning in California grasslands (Menke 1992, DiTomaso et al. 1999, Meyer and Schiffman 1999). However, these goals are usually secondary to the main goal of noxious weed control.

The best times for prescribed burning in California are during the late spring and early fall, when vegetation is relatively dry and temperatures are lower than their summer extremes. Fall burns are often hotter and more complete than spring burns, since the fuels have cured throughout the summer drought. Natural burns are more likely to occur in the fall, since lightning strikes are more frequent at that time of year. Today, prescribed burning in the fall is often prohibited due to air quality constraints.

III. The effects of burning during different seasons

The season in which a burn occurs may have large effects on grassland botanical composition the year following fire. In Mediterranean climates efforts have focused on examining differences between cool-season (winter and spring) and warm-season (summer and fall) burns (Meyer and Schiffman 1999). There are two primary explanations offered to explain the different results of warm and cool-season burns. The first explanation is that target species differ in phenologies and may show differential vulnerability to burns in different seasons. For instance, some species mature and drop seed early in the spring, while others may not drop seed until mid-summer or later. Differences in phenologies have been exploited to control late maturing invasive weeds such as *Taeniatherum caput-medusae* (Medusa Head) and *Centaurea solstitialis* (Yellow Star-Thistle) in stands of earlier maturing natives (DiTomaso et al. 1999).

The second explanation is that fire intensities can differ between the two seasons due to weather conditions and fuel availability. Meyer and Schiffman (1999) found differences in the relative proportions of plant functional groups, notably increased forbs and decreased grasses, as a result of both cool and warm season burns. They also found that both late spring and fall burns had a larger impact on functional groups than winter burning. They concluded that both hypotheses were supported. Parsons and Stohlgren (1989) observed similar results from spring and fall burns but had no winter burns for comparison.

Species response to fire depends upon the point at which the fire occurs within its annual growth cycle. In the case of annual plants, a fire that occurs after a species has begun growth during the wet season but before the species has dropped seed may reduce the cover of that species the following year by reducing that species' annual contribution to the seed bank. A fire that occurs during the period an annual species is present only as seed may have little effect on that species' population if the seeds are protected from the burn. Similarly, perennial species are most likely to be affected by burns during periods of active growth, not when the species is dormant. For example, *N. pulchra* begins growing early in the wet season and has completed growth by late spring, when little moisture is left in the soil (Figure 2). The perennial bunchgrass *A. ternipes* begins growth in the spring and continues through the dry summer months, finally senescing in late summer or fall. A late spring burn may have very different effects on these two species, since it would occur just as *N. pulchra* is senescing but just as *A. ternipes* is beginning its annual growth, possibly resulting in a greatly reduced annual biomass output for *A. ternipes*. A late fall burn is less likely to have different effects on the two species since both would have senesced by that time.

Much of the prescribed burning currently performed in California is spring burning aimed at controlling late-maturing exotic weeds. Three species noted as major rangeland weeds by DiTomaso (2000) occur within the two communities I have chosen to study: *Centaurea melitensis* (Malta Star-Thistle), *C. solstitialis*, and *T. caput-medusae*. *C. melitensis* has not become an especially pernicious pest in the Central valley and is a minor component of the *Aristida* community. *C. solstitialis* is a major pest in California and has been controlled with repeated annual burning (DiTomaso et al. 1999) but only occurs in the two communities examined here in low concentrations. *T. caput-medusae* is a major weed occurring throughout much of the west and accounts for approximately a third of the cover in the *Nassella* community.

IV. *Taeniatherum caput-medusae* and the effects of thatch

T. caput-medusae is an annual grass that is unpalatable to livestock in the later stages of growth and decomposes slowly, due to the high silica content of its tissues (Young 1992). Due to the slow decomposition rate, grasslands with large amounts of *T. caput-medusae* build up a layer of senesced thatch on the soil surface. The seedlings of *T. caput-medusae* have higher germination and survival rates in a high thatch environment due to their ability to germinate above the ground and grow roots down into the soil (Evans and Young 1970, Young 1992). A deep thatch layer inhibits the seedlings of most other grassland species. This effectively creates a positive feedback loop in which the presence of *T. caput-medusae* produces thatch which promotes even more *T. caput medusae*.

The accumulation of thatch leads to moist, cool, and dark conditions near the soil surface, as well as the reduction of environmental extremes (Evans and Young 1970, Reynolds et al. 2001). Precipitation promotes thatch accumulation by stimulating plant growth, but also inhibits thatch accumulation by increasing decomposition rates. In California, the highest thatch accumulation occurs in grasslands with about 635 mm of annual rainfall (Janes 1967). 635 mm is a medium amount of precipitation for California grasslands, and close to the average received by both communities in this study. The removal of thatch opens up the surface to sunlight, creating a drier, warmer microclimate. The differing soil surface conditions created by thatch or the lack of it can control which species germinate and survive.

The seed of *T. caput-medusae* matures 2-4 weeks later than other common annual grasses, both native and exotic, and so control efforts have focused on burning in that window of time. McKell et al. (1962) found excellent control using this method in the Central valley, and even a late summer burn after most *T. caput-medusae* seed had dropped resulted in a large decrease in *T. caput-medusae* cover the following year. In contrast, fire on the Modoc Plateau in the Great Basin floristic province, slightly increased the cover of *T. caput-medusae*, even after 3 consecutive annual burns (Young et al. 1972). Differences in the seed bank may account for the varied results. The first study started with a 23% cover of forbs, while the second started with only 1%. It may be that the second study failed to control *T. caput-medusae* because there were virtually no other species present in the seed bank.

V. The seed bank

The seed bank of Mediterranean grasslands exhibits a predictable annual cycle, reaching a peak in late spring and summer following seed maturation by most species, and reaching a low point in the following early spring when most species have germinated (Russi et al. 1992). Legumes are the only prominent group with substantial seed carryover from year-to-year, and annual grasses show nearly nonexistent carryover, since nearly all grass seedlings germinate during the winter rains (Young et al. 1981, Russi et al. 1992). Perennial grasses comprise little if any of the seed bank, even in areas where they are a significant part of aboveground vegetation (Major and Pyott 1966, Kotanen 1996). The composition of the seed bank often does not wholly correspond with the composition aboveground, with species appearing aboveground absent from the seed bank and vice versa (Major and Pyott 1966). Most seeds in grasslands are in litter on the soil surface or top 2 cm of the soil (Kotanen 1996). Viable seeds are unlikely to be found in large numbers at greater depths due to the small year-to-year carryover.

Fire destroys most of the seeds on the soil surface, but even a 1-cm layer of soil will protect most seeds from the heat of the burn (Morgan 1999). Any seeds entangled in thatch will almost certainly be destroyed by fire. Burning is likely to shift the balance of the seed bank in the direction of long-term dormant seeds buried deeper in the soil. I propose that the seeds of forb species are more likely to fall through thatch to the soil because of their often smaller size relative to grass seed and because the seeds of many forb species do not posses awns. Thus, fire may destroy more grass seed than forb seed and alter the seed bank in favor of forbs. The seed bank may display significant annual variation, depending on which species are the most successful depositors in a given year (Russi et al. 1992). Fire thus indirectly alters the seed bank by affecting aboveground botanical composition.

VI. The effects of burning on botanical composition

Fire may affect the cover of different plant functional groups the following growing season, but the results have been found to vary depending on the season of the burn. This project breaks down vegetation into five commonly used functional groups; annual grasses, perennial grasses, annual forbs, perennial forbs, and legumes. Burning has been shown to decrease annual grass cover in some cases, especially when done during the spring when seeds have not all fallen to the ground (Meyer and Schiffman 1999). DiTomaso et al. (1999) observed no cover change in this group with a spring burn, but that may be because the study was done at a site heavily infested with *C.*

solstitialis. Larson and Duncan (1982) and Parsons and Stohlgren (1989) both saw little change in annual grasses the year after a fall burn. Detecting changes in the relative abundance of native and exotic annual grasses is more difficult because native annual grasses are relatively uncommon in California valley grasslands.

The cover of perennial grasses, including *N. pulchra*, has not changed significantly due to fire (DiTomaso et al. 1999, Hatch et al. 1999). Ahmed (1983) observed a significant increase in the basal area of burned *N. pulchra* individuals, but this would not necessarily have resulted in a measurable increase in vegetative cover for the species, and Langstroth (1991) observed the exact opposite effect. Vegetative cover is a broad measurement, and is unlikely to detect finer scale changes in perennial grasses.

The cover of forbs generally increases following prescribed burning (Parsons and Stohlgren 1989, Fossum 1990), particularly native species (DiTomaso et al. 1999). In particular, perennial forbs from bulbs appear to increase in cover following fire (York 1997). DiTomaso et al. (1999) and McKell et al. (1962) have reported an increase in legumes, but other studies have not always treated them as a separate functional group, although some have shown significant increases in individual legume species (Parsons and Stohlgren 1989, York 1997). Overall, native species generally increase relative to exotics following burning, but the effect is less pronounced for fall burns (York 1997, Meyer and Schiffman 1999).

The studies from California grasslands show strong agreement that species richness and diversity tend to increase following fire, with the Shannon-Weiner Diversity Index increasing 25-45% (Parsons and Stohlgren 1989, York 1997, DiTomaso et al. 1999, Meyer and Schiffman 1999). The cover of species that dominate in the absence of fire tends to be reduced, opening up space for other species, and thus increasing diversity. However, this effect may be partially offset by increases in species that compete better in soils with increased nutrients (Huenneke et al. 1990, Janssens et al. 1998). Most studies use both native and exotic species when calculating a diversity index. However, Meyer and Schiffman (1999) used a native-only Shannon-Weiner Diversity Index and found that it increased significantly from .04 to .34 with fall burning.

The vegetative cover of individual species may change greatly following fire, and again the response of a particular species may depend on the season of the burn and also the weather during the following growing season. In some cases, species that were completely undetected in the plots before burning appear afterward (Meyer and Schiffman 1999), indicating either the presence of the species in the seed bank or colonization following the fire. The general trend in the literature shows that native species occurring within the study sites of this project are more likely to increase in cover following fire than exotics (Table 1).

VII. The effects of burning on *Nassella* and *Aristida*

Fire has the potential to stimulate perennial bunchgrass growth as well as to decrease survivorship. Burning may stimulate growth by reducing competition, removing thatch, or increasing soil nutrient availability. Burning may kill or reduce the size of bunchgrasses by destroying shoot meristems, thus removing the plant's ability to

		DiTomaso et. al., 1999	York, 1999	Parsons & Stohlgren, 1989	Larson & Duncan, 1982	Meyer & Schiffman, 1999
Time of Burn		Spring	Fall	Spring & Fall	Fall	Spring & Fall
Native Species	**Func. Group**					
Brodiaea sp.	PF		+			
Castilleja attenuata	AF			+		
Crassula connata	AF		+			
Lasthenia californica	AF		+			
Lotus wranglianus	L	+		+		
Lupinus nanus	L	+				
Navarretia tagetina	AF		+			
Orthocarpus attenuatus	AF			+		
Plagiobothrys nothofulvus	AF	+				
Trifolium gracilentum	L	+				
Triphysaria eriantha spp. eriantha	AF		+			
Exotic Species						
Avena fatua	AG	+		-		
Bromus diandrus	AG	-		-		
Bromus hordeaceus	AG	-			+	
Bromus madritensis	AG					-
Centaurea melitensis	AF			+		
Gallium parisiense	AF			+		
Hypochaeris glabra	AF		-	+		
Lactuca sp.	AF					-
Silene gallica	AF	+		+		
Vulpia myuros	AG	-			-	

Table 1. The responses of individual species and functional groups to burning. Only species encountered during the experiment were listed. A "+" or "-" indicate species cover increased or decreased in cover one year after burning.

Table 1 (cont'd).

Functional Groups		DiTomaso et. al., 1999	York, 1999	Parsons & Stohlgren, 1989	Larson & Duncan, 1982	Meyer & Schiffman, 1999
Annual Grasses	AG					-
Annual Forbs	AF	+		+		
Perennial Grasses	PG					
Perennial Forbs	PF		+			
Legumes	L	+				

re-sprout. Most of what is known about the response of California perennial bunchgrasses to burning comes from the study of a single species, *Nassella pulchra*.

There exists a general belief among managers that burning is good for *N. pulchra*. In fact, the reported effects of fire on the vegetative growth of *N. pulchra* are mixed, and may depend in part on variation in local conditions and genetic ecotypes, which may be considerable (Knapp and Rice 1998). Ahmed (1983) found that both summer and fall burning dramatically increased tiller length and tillers per plant for the next two growing seasons, and caused a smaller but significant increase in basal area. In contrast, the basal areas of plants burned in late summer have been found to be as much as 40% smaller than unburned plants in the following growing season (Langstroth 1991). Spring but not summer grazing reduced the observed differences. The same study found that burned plants were 71% shorter.

One explanation for the variety of burn responses is soil differences. The Langstroth (1991) study took place on poor soil with a shallow hardpan horizon. Dyer and Rice (1997) observed the effects of burning on *N. pulchra* basal area on the same poor soil and found no difference between burned and unburned plants. Huntsinger et al. (1996) applied clipping treatments to *N. pulchra* plants in three different regimes: winter, winter and early spring, and late spring. *N. pulchra* seeds were collected from two populations but were grown in a common garden. The soil of one population was a typical grassland soil but the soil of the other was a serpentine soil, which has nutrient levels unsuitable for the growth of many plants. The winter clipping had no effect on tillers or inflorescences in either population, but winter and early spring clipping reduced tillers and inflorescences only in the serpentine population. Late spring clipping severely reduced tillers for both populations. Huntsinger et al. (1996) suggests the differing responses from the two ecotypes may be due to adaptations to different overall plant densities in the communities where they originate. These studies suggest that soil fertility and ecotype may help predict the response of *N. pulchra* vegetative growth to defoliation. *N. pulchra* ecotypes adapted to poor soils may not recover from defoliation as readily as ecotypes from more fertile soils.

The effects of defoliation on reproductive output are also mixed, and may depend in part on soil fertility. Huntsinger et al. (1996) report varied reductions in inflorescences between serpentine and non-serpentine populations with spring and winter clipping, but not with winter clipping alone. In fall-burned *N. pulchra*, Langstroth (1991) observed a reduction in both inflorescences and seeds per inflorescence, resulting in a 45% reduction in seed per plant. However, average seed weight increased by 14%. Among seeds from the same population stored for 10 years, those from burned plants were 20% larger and had a 72% higher germination rate (Dyer 2002). Ahmed (1983) found that mowing increased inflorescence and seed number per plant only sometimes, but that summer or fall burning always increased those numbers. The soil in the Langstroth (1991) study had a shallow, impermeable hardpan layer which would have prevented the plants from utilizing deep water in the late spring. This may have interfered with reproductive output and thus contributed to the different findings of the studies.

Fire may increase the germination and early survival of *N. pulchra* seedlings. Dyer et al. (1996) found that fall burning increased germination the following spring, but that mortality was high and virtually no individuals had survived four years after the start of the experiment. The authors hypothesized that a year of heavy rainfall may also be necessary for recruitment. In a greenhouse experiment, Ahmed (1983) found that *N. pulchra* seedlings had a higher survival rate in bare pots than in pots covered with a mulch layer, suggesting that the removal of thatch by fire creates conditions more favorable for seedlings. But perhaps more importantly, the same study found that burning reduced the amount of exotic annual grass seed, thus reducing the interspecific competition experienced by the seedlings. The deepest soils in the Langstroth (1991) study were observed to have more *N. pulchra* seedlings when burned and grazed than control plots.

There are many bunchgrass species other than *N. pulchra* native to California. The perennial bunchgrass group represents a range of life history strategies including both cool and warm season species, and species adapted to a range of habitats. These species may respond to burning differently than *N. pulchra*. In addition to *N. pulchra*, this study examined *Aristida ternipes*, a warm season bunchgrass whose response to fire is unknown. The effects of fire on other *Aristida* species are mixed. In some cases, burning has no effect, as Brockway et al. (2002) found for *A. purpurea* cover in a shortgrass prairie. In *A. stricta*, fire has been found to increase both vegetative and reproductive growth in established plants, as well as to increase tissue concentrations of nitrogen and phosphorous (Parrott 1967, Anderson and Menges 1997), perhaps because of increased nutrient uptake immediately following the burn. In *A. beyrichiana*, fire produces a pulse of recruitment, but can also increase mortality of young plants (Mulligan and Kirkman 2002). Winter burns also increased mortality in seedlings in annual *A. oligantha* populations in the Midwest (Owensby and Launchbaugh 1977), but did not reduce the total annual biomass of the species (Engle et al. 1990). Competition experiments with *A. stricta* in Florida show that removing surrounding vegetation also increases seedling mortality (Kindell et al. 1996), but this effect has not been seen in *A. longiseta* (Fowler 1990). On the other hand, removal of thatch by burning may promote *Aristida* populations, as thatch has been shown to inhibit *A. longiseta* seedlings (Fowler 1988), as well as preventing the seeds from contacting the soil (Fowler 1986).

VIII. The effects of burning on soil properties

Changes in the soil environment induced by fire are likely to affect the growth of both species in the following growing season. The charring effect of fire creates a darkened soil surface that may result in temperature changes both above and below the soil. A month after burning, Ewing and Engle (1988) found significantly lower temperatures 10 cm above the soil, and higher temperatures 1 cm below the soil surface. DiTomaso et al. (1999) found that increased belowground temperatures due to burning may persist for at least 3 years and extend to 10 cm. Thatch acts as an insulator, and its removal increases temperature extremes in both directions, but the effects are greater above than belowground (Evans and Young 1970). Higher temperatures in burned sites may in turn lead to lower soil moisture due to increased evaporation (Smith and Owensby 1973). Significant differences in soil water content were not found by Ewing and Engle (1988) or Larson and Duncan (1982), but the former did find lower leaf water potentials in burned perennial bunchgrasses in the Midwest. In some cases, fire may decrease soil moisture by creating a hydrophobic layer that resists absorption of rain, but this effect is most pronounced in high-intensity fires or habitats containing vegetation with large amounts of waxes and oils, such as chaparral (Biswell 1989).

Grassland fires generally have a small positive effect on the amount of soil nutrients available to plants (Smith and Owensby 1973, Vogl 1974), as long as the heat generated is not intense (Biswell 1989). Nitrogen can be volatilized and lost to the atmosphere due to the heat of the fire (Seastedt and Ramundo 1990), but this loss is often offset by nitrogen released in the conversion of litter to ash, or by the conversion of nitrogen in the soil to a usable form from the heat of the fire (White and Loftin 2000). Romanya et al. (2001) suggest that the heating of soils by fire converts organic nitrogen to ammonia, a form readily used by plants. Grasslands that have not burned recently build up a layer of thatch containing minerals in an unusable form (Harrison 1985) that are released by fire (Vogl 1974). The nutrients released by burning the thatch may be quickly utilized by vegetation re-growing after the fire from root or seed (Brockway et al. 2002). The lingering effects of burning may also increase nitrogen mineralization rates in the soil due to warmer soil temperatures from a darkened surface (Vogl 1974, Biswell 1989), but this phenomenon has not been corroborated in every study (Blair 1997). The difference in findings may be because mineralizing microorganisms require water as well as heat. Romanya et al. (2001) suggest that the effects of burning on nitrogen mineralization may be seasonal in Mediterranean grasslands, with fire increasing the rate in late winter and spring.

IX. Conclusions

N. pulchra has been observed to respond positively to fire in several cases in terms of both basal area and inflorescences. In instances where fire inhibited the growth of *N. pulchra*, poor soil may be a contributing factor. I know of no burn studies on *A.*

ternipes, but other bunchgrasses in the *Aristida* genus do well with burning in the southeastern United States. *T. caput-medusae* and other annual grasses are usually reduced by burning, while annual forbs usually increase. The effects of fire on soil properties may contribute to changes in perennial bunchgrass growth and the cover of different plant functional groups.

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Chapter 2

The Effects of Fall Burning on Two Northern California Perennial Bunchgrass Communities

I. Introduction

Grasslands are a focus of restoration in California due to declining habitat and reduced abundance of native species, including perennial bunchgrasses. Threats to native grasslands include invasive species, altered disturbance regimes, and urban encroachment. Since most researchers agree that native perennial grasslands in the state have contracted over the last 200 years and continue to decline (Bartolome et al. 1986, Heady 1988), communities of native bunchgrasses that have been invaded by large numbers of exotics have become prime targets for restoration. In California grasslands, fire is a component of the historical disturbance regime (Biswell 1989), and so prescribed burning has been increasingly used in restoration programs that aim to simulate natural conditions. Several studies have used fire in an attempt to decrease cover of noxious weeds (McKell et al. 1962, Young et al. 1972, DiTomaso et al. 1999), increase cover of native species (Meyer and Schiffman 1999), or encourage the growth of perennial grasses (Ahmed 1983, Fossum 1990, Langstroth 1991). All three of those attributes are examined in this study within two native perennial bunchgrass communities.

Most research concerning California bunchgrasses has focused on one species, *Nassella pulchra* (Purple Needlegrass). Although currently *N. pulchra* is one of the most common, many species of bunchgrasses are native to California, and they may not all respond similarly to burning. This study compares the effects of a fall burn on *N. pulchra* and *Aristida ternipes* var. *hamulosa* (Hook Three-Awn), a warm season bunchgrass. In addition to aboveground vegetation, the seed bank is also examined, since it provides the propagules for much of the re-vegetation following burning.

California grasslands have been successfully invaded by a wide variety of exotic plants, most notably annual grasses, that compete with native species for resources (Heady 1988). Biological invasions are a global problem and California is no exception (Vitousek et al. 1996), as many areas are nearly completely dominated by exotics. Prior to European settlement, fires may have burned significant areas in these grasslands, which are dry from late spring through fall (Biswell 1989). The general exclusion of fire since that time may have inhibited native species adapted to a short fire return interval. Thus, an increase in native species following prescribed burning is expected, and has been observed in California grasslands (York 1997, Meyer and Schiffman 1999). Fire has also been shown to increase Shannon-Weiner diversity 25-45% (York 1997, DiTomaso et al. 1999) and alter the relative cover of different plant functional groups within one year of burning.

Here, I have divided vegetation into five commonly used functional groups: annual grasses, perennial grasses, annual forbs, perennial forbs, and legumes. Spring burning has been found to decrease the cover of annual grasses (Meyer and Schiffman 1999), but fall burns have shown little effect on this functional group (Larson and Duncan 1982, Parsons and Stohlgren 1989). Perennial grass percent cover has generally not been observed to change following fire (DiTomaso et al. 1999, Hatch et al. 1999). However, cover is usually measured with broad classes, and so may not identify small yet significant changes. Indeed, perennial grass basal area has been found to change significantly with burning (Ahmed 1983, Langstroth 1991). Forbs and legumes have been shown to increase after fires in both spring and fall (McKell et al. 1962, Parsons and Stohlgren 1989, Fossum 1990, York 1997, DiTomaso et al. 1999). Most prescribed burning has been done in the spring to destroy late-maturing target weed species, such as *Centaurea solstitialis* (Yellow Star-Thistle), before their seeds mature. However, fall burns are a more likely time for natural fires since fuels are drier and lightning is more common (Biswell 1989). Thus prescribed burning in the fall may be a better mimic of the natural fire regime. Mechanisms for the change observed in the relative covers of functional groups include removal of the thatch layer and alteration of the seed bank.

Thatch alters surface microclimate conditions, reducing temperature extremes and light levels, and increasing moisture (Evans and Young 1970, Reynolds et al. 2001). Thatch accumulates in California grasslands quickly if fire and grazing are excluded. The presence of the exotic grass *Taeniatherum caput-medusae* (Medusa Head), increases thatch accumulation rates substantially because its high silica content renders it slow to decompose (Figure 3) (Young 1992). The thatch produces conditions favorable for *T. caput-medusae* seedlings, thus creating a positive feedback loop that enhances *T. caput-medusae* pressure on communities (Young 1992).

The *Nassella* community in this study has been heavily infested with the exotic and has a thick thatch layer, but fire removes thatch so that other species may compete more effectively with *T. caput-medusae*. McKell et al. (1962) found that burning *T. caput-medusae* even after it had dropped seed resulted in a greatly reduced cover of the exotic the next year, but Young et al. (1972) observed exactly the opposite phenomenon. The explanation of these differing results may be in the seed bank. The first study had a significant forb cover before the burn while the second study had almost none. Thus, the

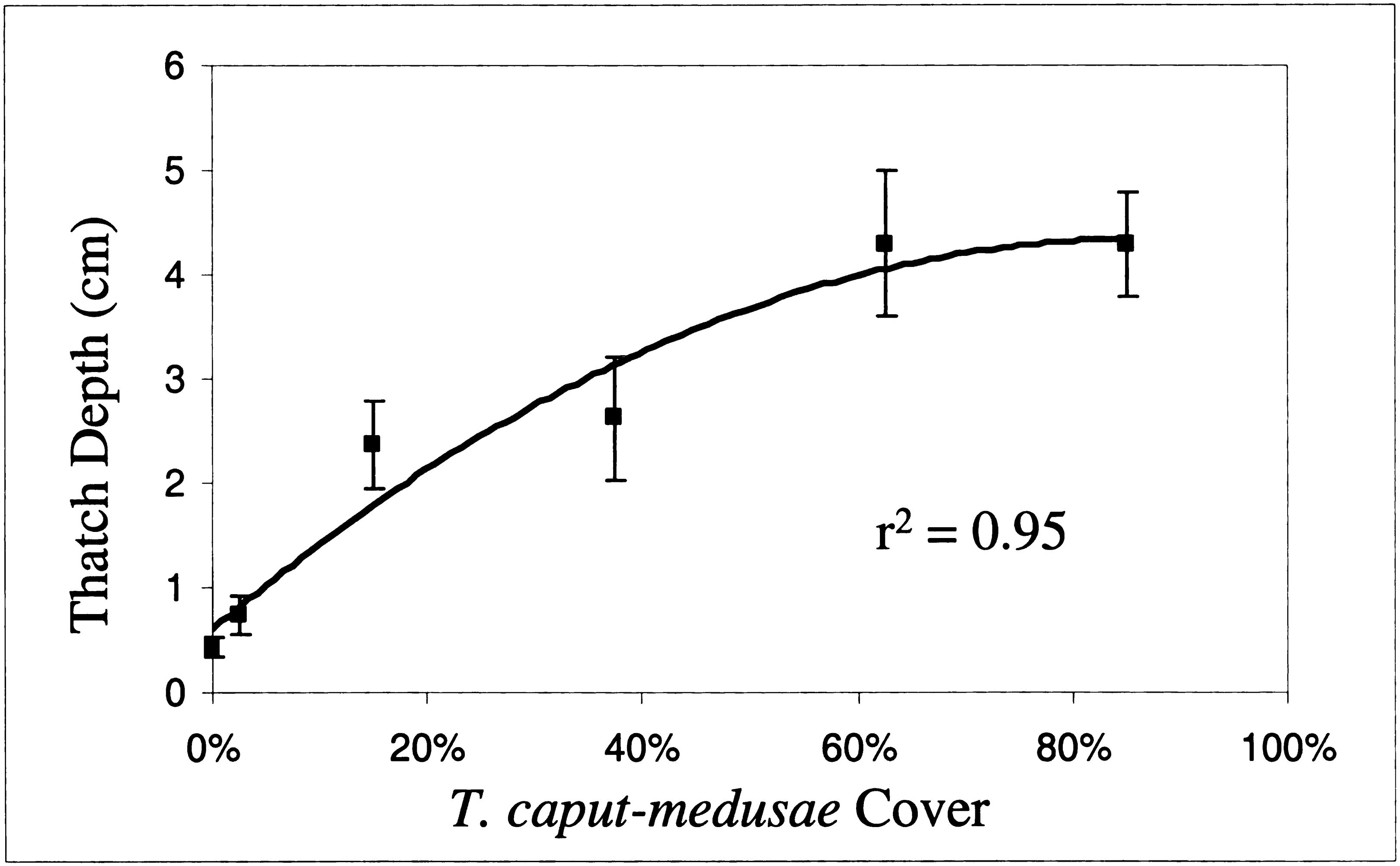


Figure 3. The relationship between *Taeniatherum caput-medusae* cover and thatch depth in plots from the Nassella community in 2001. The line is given by the equation $y = -5x^2+8.65x+0.61$

second study may have failed to control *T. caput-medusae* because there was nothing in the seed bank to take its place.

Burning reduces the seed bank by destroying seeds. Grassland fires are rarely hot enough to destroy seeds below the surface (Vogl 1974), but seeds at or above the surface may be killed. Grasses with papery glumes are especially likely to burn and this may be why annual grass cover is often reduced following fire. By fall, the seeds of most species have dispersed and lie on the surface or are suspended in the thatch layer (Young et al. 1981). Consequently, fall burning is likely to destroy the seeds of many species, but especially those seeds that are suspended in thatch. Soil is a good insulator, and so seeds that are covered by even a thin layer of soil may escape destruction by fire (DeBano et al. 1998). Thus, species with seeds that persist for years underground or exhibit hygroscopic boring may increase in cover the year following burning due to reduced competition. Legumes have a high year-to-year seed bank carryover in Mediterranean grasslands (Young et al. 1981, Russi et al. 1992) and *Erodium* sp. (filaree) are hygroscopic borers (Stamp 1989), so these vegetation types would be likely to increase following a fall burn. A seed possessing a long awn such as *T. caput-medusae*, but no hygroscopic boring capabilities, may be more likely to become ensnared in the thatch and be destroyed by fire.

Warm season burning has been reported to both increase (Ahmed 1983) and decrease (Langstroth 1991) the basal area and inflorescences of *N. pulchra*. The soil in the latter study had a shallow hardpan layer that decreased soil fertility and may have contributed to the different results. Burned plants have produced seeds that are 14-20% heavier (Langstroth 1991, Dyer 2002). Investigators have demonstrated that burning promotes *N. pulchra* germination (Dyer et al. 1996) and also early seedling growth by removing thatch (Ahmed 1983). However, the pulse of seedlings documented by Dyer et al. (1996) experienced high mortality and virtually no seedlings were still alive 4 years after the beginning of the experiment. *N. pulchra* is a species that can thrive with a short fire return interval (Hamilton 1997).

I know of no studies that have examined the effects of fire on *A. ternipes*, but *A. stricta* and *A. longiseta* in longleaf pine communities in the southeast benefit from fire (Parrott 1967, Anderson and Menges 1997) and thatch removal (Fowler 1986, 1988). In California, *A. ternipes* is a C4 grass that continues to grow during the dry summer months after *N. pulchra* has senesced. However, both species have senesced by autumn when burning occurred in this study.

The deep thatch in the *Nassella* community of this project traps numerous *T. caput-medusae* seed, which is likely to be consumed by the fire. As a result, I expect *T. caput-medusae* to be reduced in the seed bank and in the following seasons botanical cover. Most previous studies agree that annual grasses decrease and annual forbs increase as a result of fire, and there is no reason not to expect those results in this case as well. Likewise, Shannon-Weiner diversity is likely to increase, and native species are expected to increase as percent of botanical cover.

The *N. pulchra* population in this project occurs on soil underlain by a hard duripan similar to the Langstroth (1991) study, which found that fire decreased bunchgrass basal area and inflorescence output the following year. Thus, I expect a decrease in *N. pulchra* basal area and inflorescences. Although other bunchgrasses in the *Aristida* genus do well with frequent burning, the *A. ternipes* population in this project may not experience the same results. The soil under the population is underlain by a shallow layer of cemented cobble and gravel, which may inhibit the bunchgrasses similarly to *N. pulchra* under the same conditions.

II. Methods

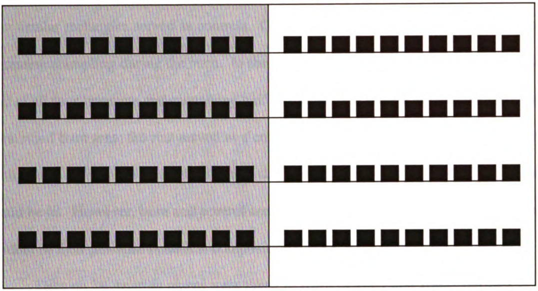
1. Study Sites

Both study sites are in the northeastern Central Valley (Figure 1). The *Nassella* community is situated on Anita Clay Loam at 39° 18' N and 121° 59' W, 20 km northwest of Chico, where mean annual precipitation is 670 mm. Precipitation in the period from July to June was 82% and 83% of average for the periods ending in 2001 and 2002, respectively (Chico University Farm, National Climatic Data Center, http://lwf.ncdc.noaa.gov). The *Nassella* community has not been grazed by livestock since 1986 or earlier, but is open to grazing by wild animals. The *Aristida* community is on a 26% grade of Tuscan cobbly loam at 40° 06' N and 122° 02' W, 19 km southeast of Red Bluff, where mean annual precipitation is 566 mm. Precipitation in the aforementioned periods was 94% and 80% of average (Red Bluff Municipal Airport, National Climatic Data Center). The *Aristida* community was grazed by cattle during the experiment and for many years previously, but the stocking rate during the experiment was low, just 0.07 head per acre. Cattle were put on the range around mid-December, and removed in late April.

2. Design

In March of 2001, 1-m^2 plots were established in both communities on four parallel transects within populations of the two bunchgrass species (Figure 4). In the

Nassella community plot layout



Aristida community plot layout

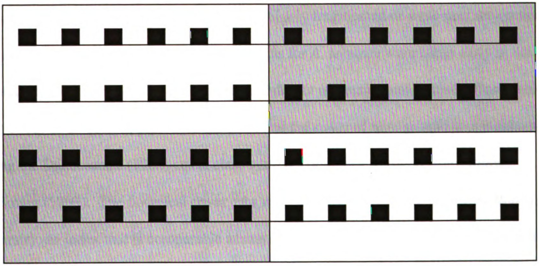


Figure 4. Plot layouts in both communities. White areas are control, grey areas were burned in October, 2001. Black squares represent 1 m^2 plots.

Aristida community, two rectangles covering the ends of two transects and each containing a quarter of the 48 total plots were designated as the prescribed burn area and two similar rectangles served as controls. One control plot was later discarded due to excessive trampling during the burn. In the *Nassella* community, a square covering one end of all four transects and containing half of the 80 total plots was designated as the prescribed burn area; the rest served as a control. Randomization of the burn treatment with regard to the plots was not an option due to constraints on the number of fires that could be lit. However, burn and control areas were chosen for their similarity, which is evident in their pre-burn botanical composition (Table 2).

Data on 39 *Aristida* plants were taken in April of 2001 and 2002, and 210 *Nassella* plants were measured in May of 2001 and 2002. In each plot the basal circumference and number of inflorescences for individuals of the two bunchgrass species was recorded. Individuals that were highly fragmented or were near the corners of the plot were not used. Inflorescence counts for *A. ternipes* were taken early in the annual reproductive cycle of the species, and do not represent total annual inflorescences. The cover of all species present in the plots and the cover of bare ground was measured using the Daubenmire (1968) cover class system. Botanical nomenclature follows Hickman (1993). The botanical cover data were used to calculate the Shannon-Weiner diversity, an index that is comparable across different spatial scales due to the fact that the area sampled is not used in the equation. The depth of senesced thatch was measured 4 times in each plot, 20 cm from each corner with a ruler.

In both communities, cover of different plant functional groups can vary annually, as is the case with all California grasslands. Variability may be driven by differences in

		Initial Cover (%)		Cover Change (%)	
		No Burn	Before Burn	No Burn	After Burn
***Nassella* Community**					
Native Species		31.33 (2.08)	31.63 (1.97)	-5.50 (2.04)	-7.00 (1.88)
Exotic Species		65.19 (3.12)	57.25 (3.71)	-11.25 (3.74)	-1.75 (3.87)
Annual Forbs	(AF)	22.19 (2.07)	22.19 (2.13)	**-12.38 (2.16)**	**6.69 (2.71)**
Annual Grasses	(AG)	41.13 (3.82)	36.63 (4.65)	3.25 (4.92)	-9.31 (5.31)
Perennial Forbs	(PF)	3.81 (0.61)	2.75 (0.22)	-0.69 (0.49)	0.25 (0.37)
Perennial Grasses	(PG)	23.56 (2.36)	25.69 (2.19)	-4.56 (1.77)	-7.38 (1.80)
Legumes	(L)	**5.81 (1.17)**	**1.63 (0.23)**	-2.38 (0.95)	1.00 (0.61)
Bare Ground		4.19 (0.88)	5.31 (0.97)	**-3.38 (0.85)**	**18.91 (1.97)**
***Aristida* Community**					
Native Species		49.79 (3.45)	53.44 (4.33)	4.78 (3.94)	2.81 (6.41)
Exotic Species		30.94 (3.02)	34.90 (4.27)	7.17 (2.25)	13.75 (4.57)
Annual Forbs	(AF)	54.24 (4.23)	51.77 (4.28)	**-5.87 (3.44)**	**19.90 (6.40)**
Annual Grasses	(AG)	12.72 (1.64)	17.08 (3.00)	**12.72 (2.20)**	**-0.83 (2.80)**
Perennial Forbs	(PF)	8.70 (3.04)	12.29 (3.09)	1.85 (0.82)	-5.73 (3.48)
Perennial Grasses	(PG)	1.30 (0.66)	1.88 (0.63)	0.00 (0.00)	-0.94 (0.54)
Legumes	(L)	4.13 (0.62)	5.31 (0.63)	3.26 (1.00)	4.17 (1.18)
Bare Ground		5.94 (1.69)	5.52 (1.15)	**-0.98 (1.48)**	**17.92 (2.87)**

Table 2. Response of functional group cover for both communities. Data is Mean(SE). Significant ($p < 0.05$) differences for a given year are in bold.

both total annual precipitation and its monthly distribution. In order to quantify this natural annual variation, botanical monitoring data were obtained from the Dye Creek Ranch from 1997 to 2002. The author collected the Dye Creek data for the two most recent years.

To measure the seed bank in the *Nassella* community, 8 soil samples were taken pre-burn in both treatment and control areas an hour before the prescribed fire was lit. In the treatment area, 8 additional samples were taken 30 min after the fire was extinguished within 30 cm of the spots that had been sampled pre-burn. Soil samples were taken outside of the quadrats used for botanical composition data. The top 5 cm of soil, as well as any over-lying thatch, was removed with a 7.14 cm diameter soil auger. The samples were weighed with the largest rocks removed, and the data are expressed as seeds per gram of soil. The seed bank was estimated by a direct germination method similar to Gross (1990). Soil samples were stored at room temperature for not more than three months following collection. The samples were spread on top of potting soil to a depth of 0.5-1.0 cm and kept moist in a greenhouse set to 70° F at night and 80° F during the day. As seedlings emerged they were identified, recorded, and removed. Seedlings that were not identifiable were allowed to grow until flowering and were then identified. After 48 d very few new seeds were germinating and the seed bank experiment was terminated. Seed bank data from the *Aristida* community were compromised by approximately 1.3 cm of fall rain that caused seeds to germinate before samples were taken. Thus, seed bank data for the *Aristida* community are not presented.

The *Nassella* community was burned on 10 October 2001 when temperature was 83° F, relative humidity was 21%, and the wind was 5.5 km per h. The *Aristida* community was burned on 22 October 2001 when temperature was 62° F, relative humidity was 53%, and the wind was calm. Peak fire temperature was measured at the soil surface with temperature pellets (Omega Engineering Inc., Stamford, CT), and ranged between 200-300° C for both burns.

In the spring of 2002, seeds were collected from *Nassella* plants for a weight and germination experiment. Seeds were individually weighed and then kept moist in potting soil in a greenhouse set to 70° F at night and 80° during the day. Germinated seeds were recorded and removed. After 3 weeks no new seeds were germinating and the experiment was terminated. Seed weights and germination rates per plant were calculated before statistical analysis. Seed data are not presented for *Aristida* plants, since their seeds matured too late for collection.

3. Analysis

All statistical analyses were performed with SYSTAT Version 10 (SPSS Inc. 2000). Inflorescence counts, species and functional group cover data, seed bank data, and germination rates were not normally distributed, and could not be successfully transformed, so Mann-Whitney U-tests were used to evaluate the changes in these variables. Seed weights and Shannon-Weiner diversity were analyzed with t-tests. Chi-square tests were used for bunchgrass mortality. Preliminary data analysis showed that average *N. pulchra* basal area in the treatment area was somewhat larger than in the control area prior to burning. To remedy this, individuals of similar size in control and burned areas were paired, and a paired t-test was used on the change in basal area. A t-test was used for analysis of *A. ternipes* change in basal area. A modified Bonferroni correction was used to adjust p-values in the species and functional groups sets of comparisons in both communities.

III. Results

The two bunchgrass species responded differently to fire. Burned *N. pulchra* increased in basal area by an average of 7.7 cm^2, while unburned plants increased by only 1.5 cm^2 (Figure 5). In contrast, both burned and unburned *A. ternipes* experienced a decrease in basal area. Burning also increased the number of inflorescences on *N. pulchra* plants, while it had no effect on the inflorescences of *A. ternipes* (Figure 6). Mortality was much higher among *A. ternipes*, even for unburned controls. 38% of burned *A. ternipes* died, compared to only 4.5% of unburned controls ($p < 0.01$) (Figure 7). There was no significant difference in mortality among *N. pulchra*, where 0.6% of burned plants died, while mortality of unburned controls was 2.4%. Seed from burned *N. pulchra* plants was found to be significantly heavier. Seed from unburned controls had a mean weight of 0.01 g per seed, while seed from burned plants was 8% heavier ($p < 0.01$). Figure 8 shows that although seed weight affects germination rate, the effect above ≈0.009 g per seed is minimal and the germination rate levels off at about 95%. As a result, there was no significant difference in germination rate between burned and control *N. pulchra* plants.

Significant cover changes were detected in several functional groups (Table 2), but burning did not significantly affect the total cover of native and exotic species in either community. The cover of annual forbs increased in burn plots from 19.1-25.8% relative to controls. The largest variation in annual forbs in the Dye Creek monitoring

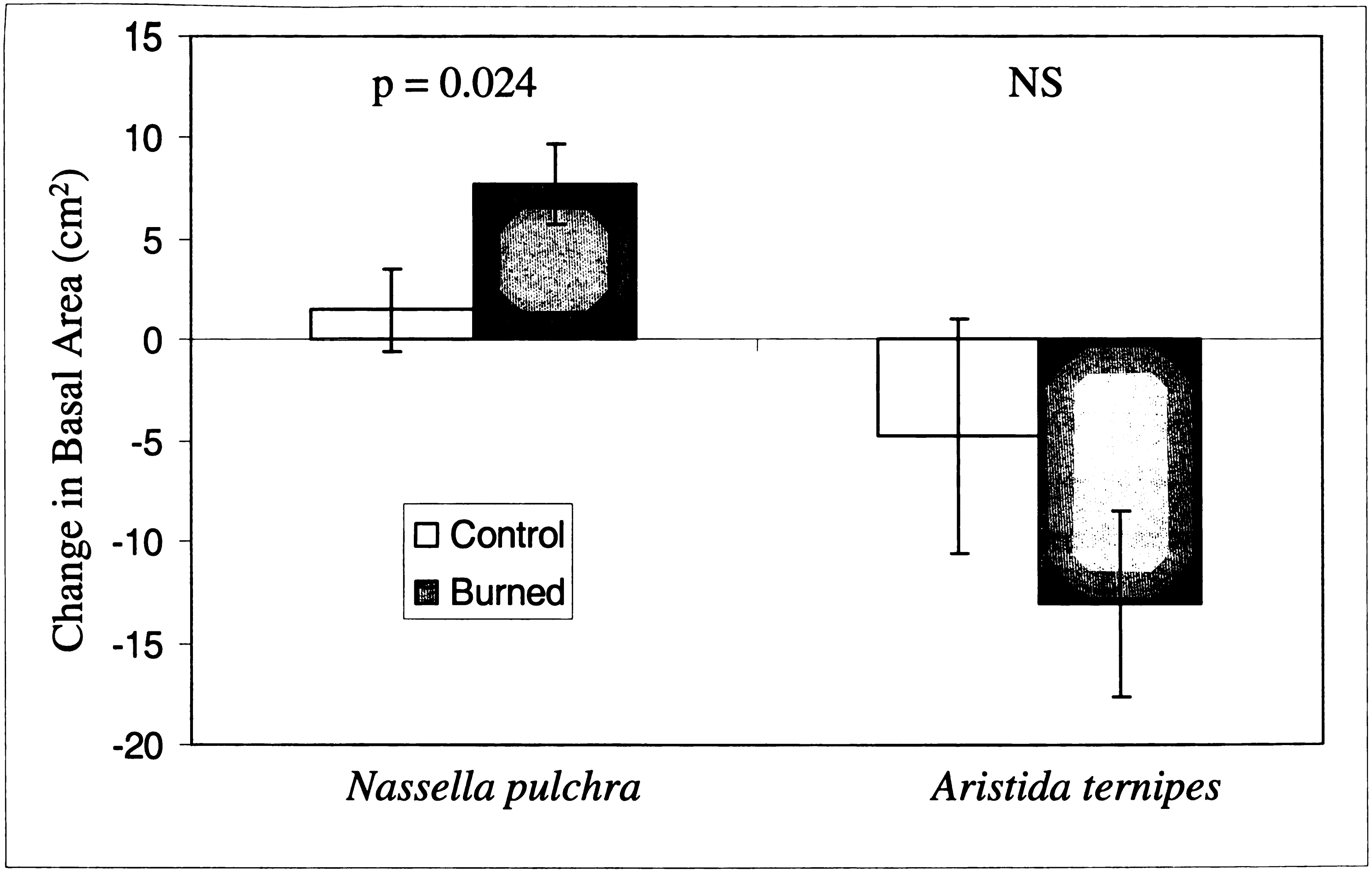


Figure 5. Mean change in basal area per plant from Spring 2001 to Spring 2002. The burn treatment was applied in October 2001. Standard error is shown. Individuals that died were not included.

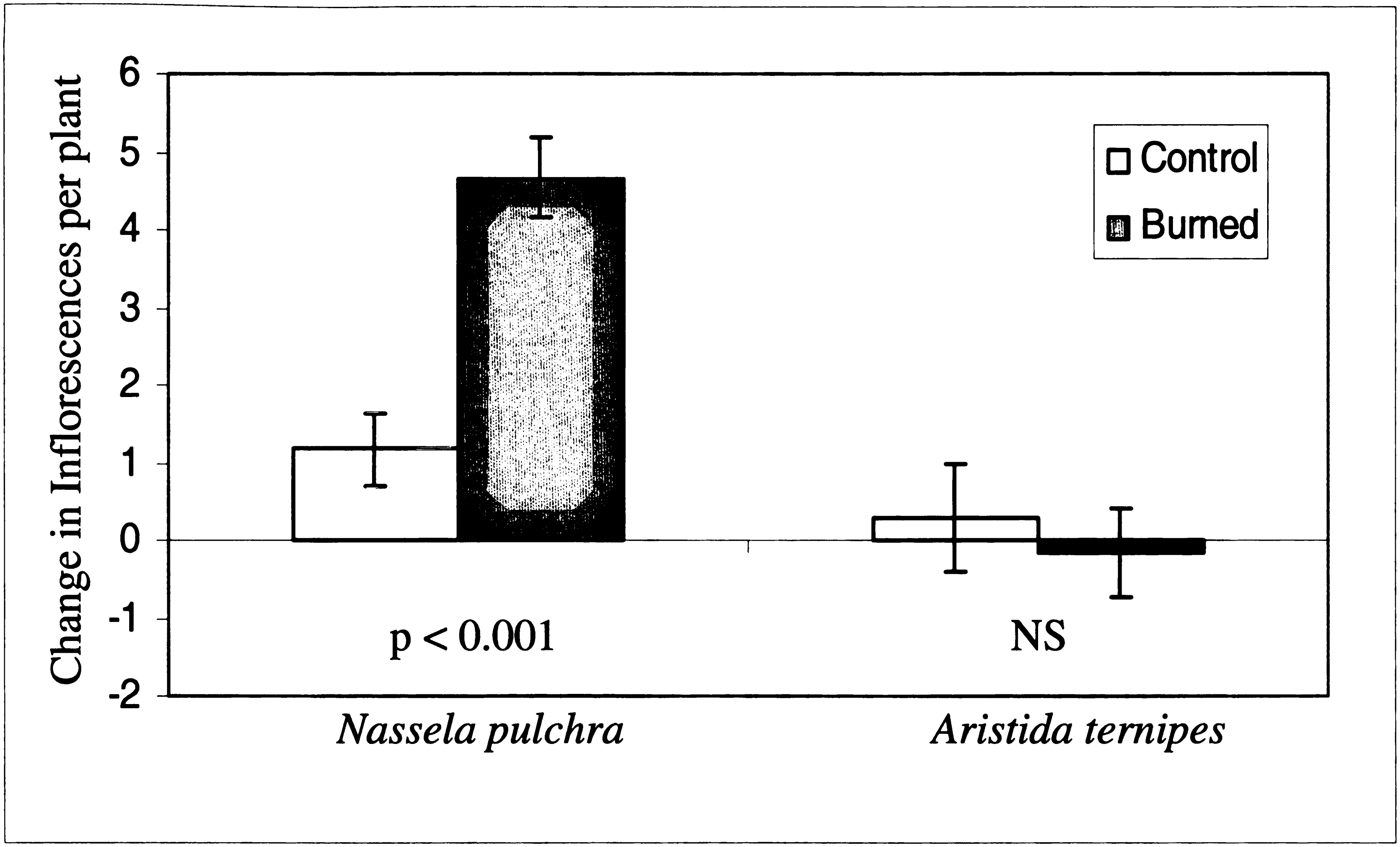


Figure 6. Mean change in number of inflorescences per plant from spring 2001 to spring 2002. The burn treatment was applied in October 2001. Standard error is shown.

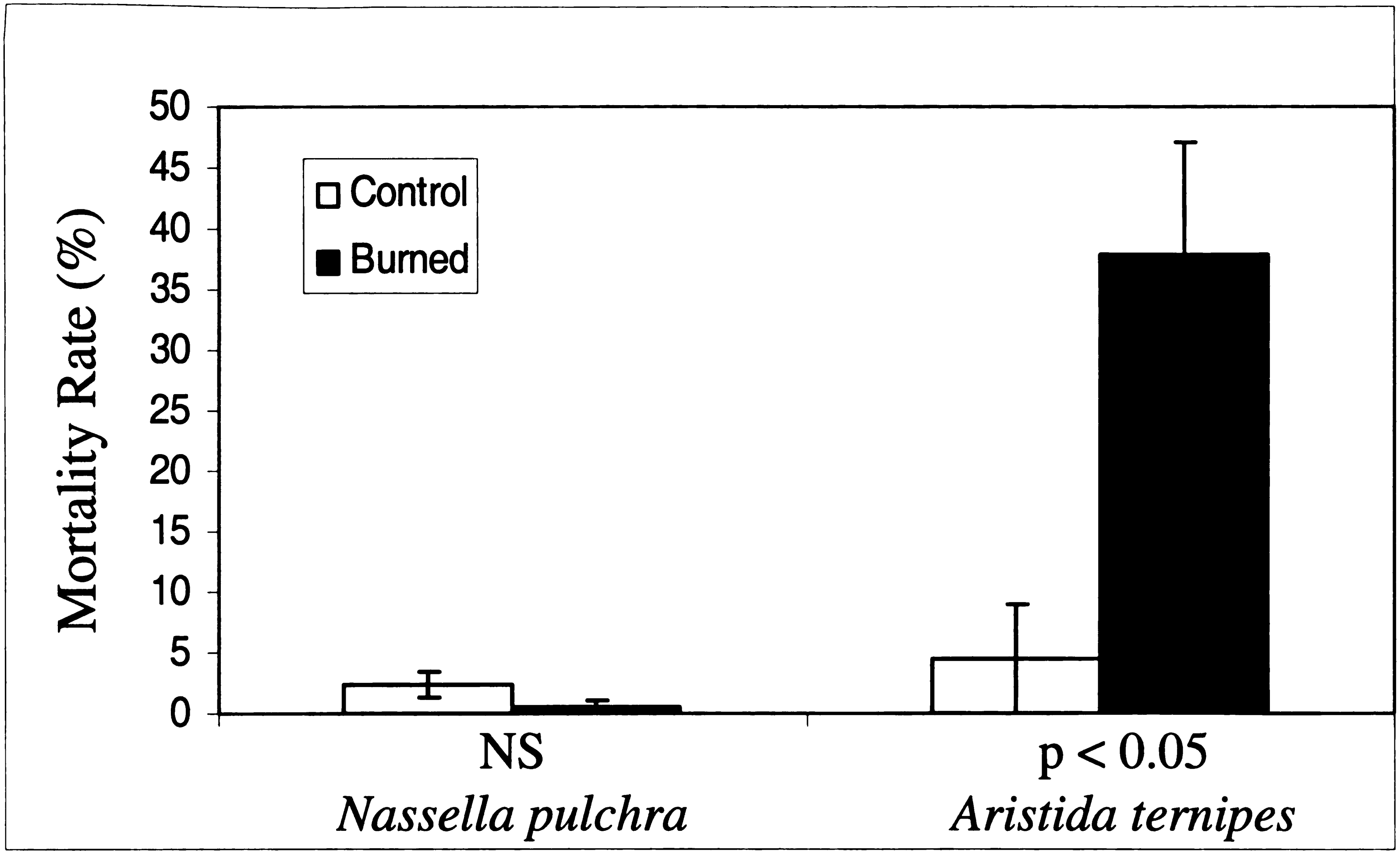


Figure 7. The mortality rate for individual bunchgrasses in 2002. Standard error is shown. Significance was calculated with a Chi-square test.

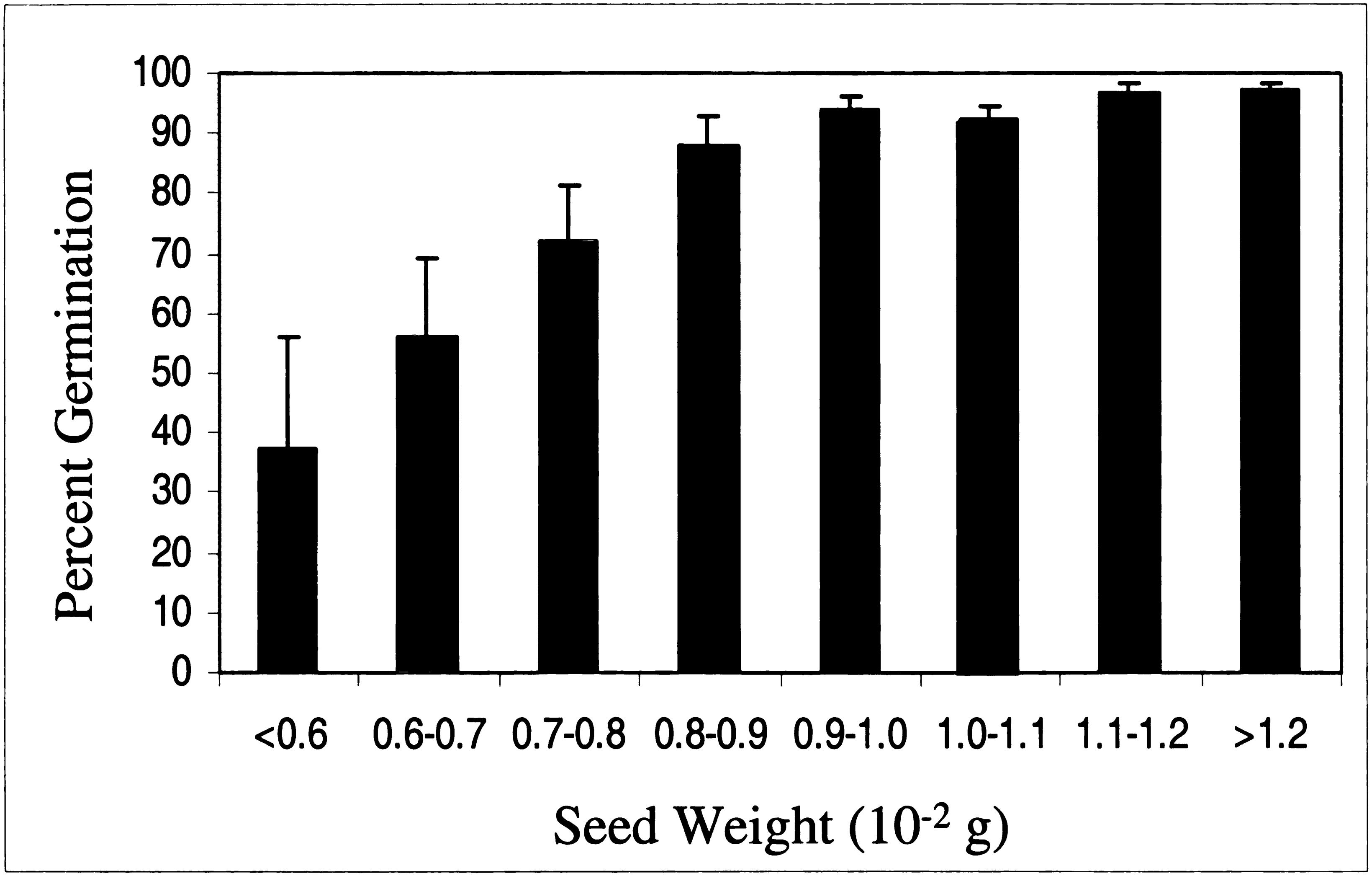


Figure 8. Effect of seed weight on *Nassella pulchra* germination rate. Standard error is shown. Although burned plants produced heavier seeds, seed from both burned and control plants fell within the outlined size class.

data was about 14% (Figure 9). Burning significantly decreased annual grasses in the *Aristida* community by 13.6%. The largest variation in the Dye Creek monitoring data was about 21%. The cover of annual grasses in burned plots also dropped sharply relative to controls in the *Nassella* community, but large variability resulted in non-significance. Burning also tended to increase the cover of legumes and decrease the cover of perennial grasses in both communities, but neither result was statistically significant. The reason that cover of perennial grasses in the burned *Nassella* community decreased, while the average basal area of burned individuals increased is that the burned plants had shorter leaves. Cover was higher in the unburned plots where the longer leaves of the plants covered more area but did not contribute to basal area any more than short leaves.

Several species from both communities experienced significant changes in cover following the burn (Table 3, Table 4). *Erodium brachycarpum* and *E. cicutarium* increased due to burning in both sites, but the result was only significant in the *Nassella* community. Some other exotic annual forbs also increased significantly in the *Nassella* community, leading to the overall increase in the annual forb functional group. Two species declined in cover significantly due to burning, *Selaginella hansenii* and *T. caput-medusae*. Fire had a positive effect on overall Shannon-Weiner diversity in the *Nassella* community, but it had no effect on the native component of diversity alone (Figure 10). Thus, the Shannon-Weiner index was increased by greater diversity among exotic species, not natives. The *Aristida* community exhibited the same pattern, except burning had only a near-significant (p = 0.07) effect on overall diversity. In both communities,

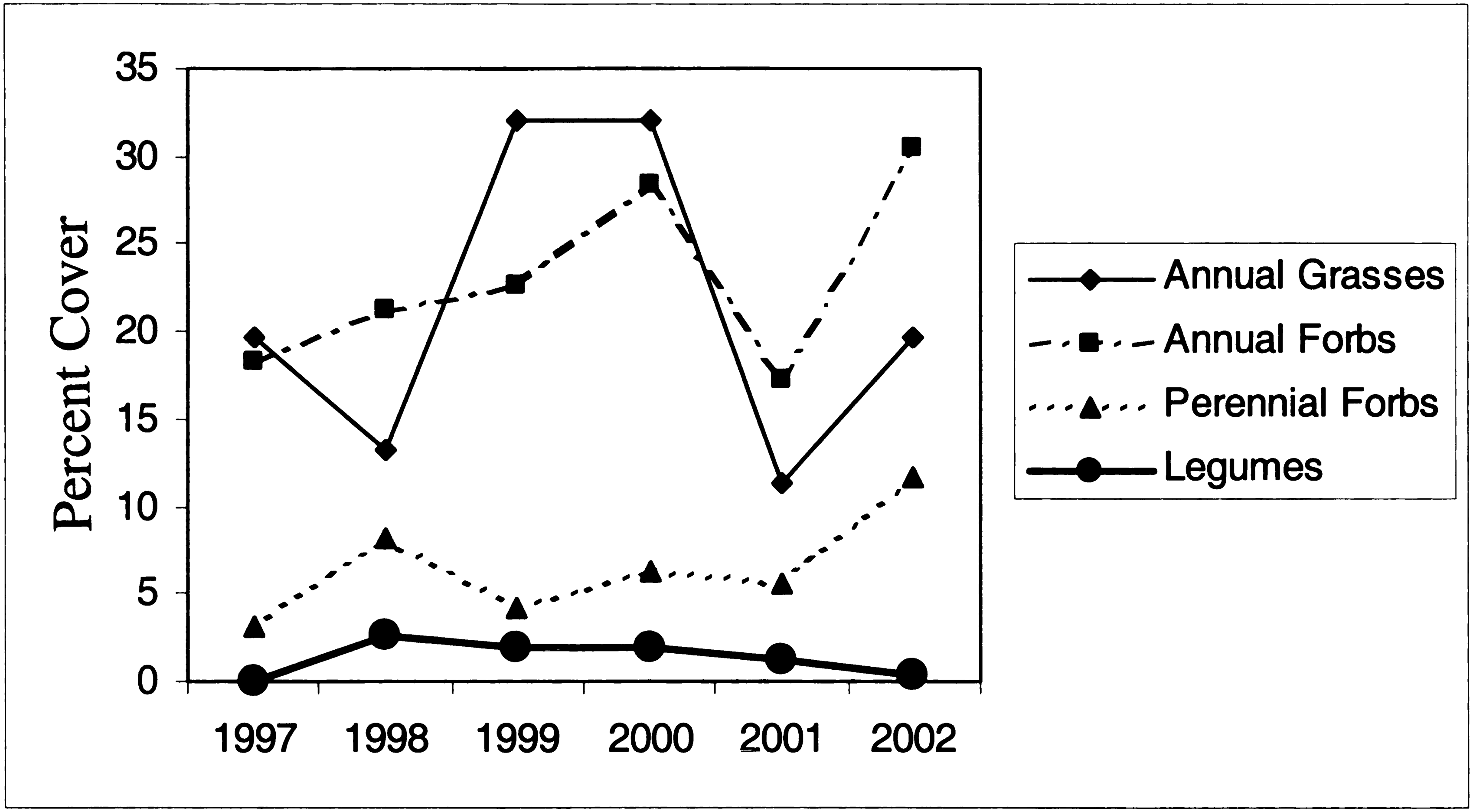


Figure 9. The cover of four plant functional groups at the Gray Davis Dye Creek Preserve from 1997 – 2002. Cover data were Collected between 15 April and 15 May. There were no perennial grasses observed. Data were obtained from the Nature Conservancies Dye Creek botanical monitoring program; data for 2001 and 2002 were collected by the author. Data used by permission of Peter Hujik, Dye Creek Preserve manager.

Native Species	Func. Group	Initial Cover (%) No Burn	Initial Cover (%) Before Burn	Cover Change (%) No Burn	Cover Change (%) After Burn
Neutral Response					
Achyrachaena mollis	AF	0.94 (0.19)	0.25 (0.12)	0.75 (0.47)	-0.06 (0.14)
Allium/Triteleia/Dichelostemma	PF	2.75 (0.47)	2.25 (0.12)	-0.13 (0.37)	0.13 (0.13)
Calycadenia fremontii	AF	0.56 (0.17)	0.19 (0.11)	0.19 (0.14)	0.19 (0.17)
Cardamine oligosperma	AF	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	-0.06 (0.06)
Clarkia purpurea ssp. quadrivulnera	AF	0.06 (0.06)	0.81 (0.39)	0.00 (0.09)	-0.31 (0.13)
Delphinium variegatum ssp. variegatum	PF	0.25 (0.12)	0.25 (0.12)	-0.19 (0.11)	-0.13 (0.09)
Dodecatheon clevelandii	PF	0.44 (0.38)	0.00 (0.00)	-0.31 (0.00)	0.00 (0.00)
Epilobium foliosum	AF	0.00 (0.00)	0.00 (0.00)	0.44 (0.15)	0.13 (0.09)
Eremocarpus setigerus	AF	0.56 (0.17)	0.88 (0.19)	-0.50 (0.18)	-0.19 (0.19)
Eryngium castrense	PF	0.38 (0.14)	0.25 (0.12)	-0.06 (0.06)	0.25 (0.33)
Hemizonia fitchii	AF	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.50 (0.16)
Layia fremontii	AF	0.06 (0.06)	0.00 (0.00)	-0.06 (0.06)	0.00 (0.00)
Lupinus nanus	L	0.44 (0.15)	0.06 (0.06)	0.00 (0.16)	0.06 (0.06)
Nassella pulchra	PG	23.56 (2.35)	25.69 (2.19)	-4.56 (1.77)	-7.38 (1.80)
Plagiobothrys nothofulvus	AF	0.06 (0.06)	0.13 (0.09)	0.00 (0.00)	-0.06 (0.06)
Plantago erecta	AF	0.56 (0.38)	0.06 (0.06)	-0.38 (0.32)	0.06 (0.06)
Sagina apetala	AF	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)
Sidalcea diploscypha	AG	0.50 (0.38)	0.56 (0.17)	-0.31 (0.33)	-0.13 (0.13)
Trifolium depauperatum var. amplectens	L	0.13 (0.09)	0.13 (0.09)	0.06 (0.11)	0.00 (0.13)
Trifolium gracilentum	L	0.00 (0.00)	0.00 (0.00)	0.13 (0.09)	0.00 (0.00)
Triphysaria eriantha ssp. eriantha	AF	0.06 (0.06)	0.06 (0.06)	-0.06 (0.06)	0.00 (0.00)

Table 3. Response of species cover in the *Nassella* community. Data is Mean(SE). Significant ($p < 0.05$) differences for a given year are in bold. Functional group abbreviations are defined in Table 1. Members of the genera *Allium*, *Triteleia*, and *Dichelostemma* were grouped together because they are difficult to separate without flowers and they are all bulbaceous members of Liliaceae.

Table 3 (cont'd)

Exotic Species					
Positive Response					
Erodium brachycarpum	AF	14.81 (1.77)	14.63 (1.77)	**-13.00 (1.76)**	**-1.00 (1.87)**
Erodium cicutarium	AF	1.00 (0.20)	1.56 (0.19)	**-0.19 (0.40)**	**0.94 (0.19)**
Filago gallica	AF	0.00 (0.00)	0.00 (0.00)	**0.25 (0.12)**	**2.06 (0.38)**
Petrorhagia dubia	AF	0.06 (0.06)	0.19 (0.11)	**0.13 (0.13)**	**1.25 (0.22)**
Vulpia myuros var. hirsuta	AG	2.06 (1.05)	3.06 (0.82)	**-0.44 (0.79)**	**6.56 (1.58)**
Neutral Response					
Avena fatua	AG	0.56 (0.38)	0.19 (0.11)	-0.06 (0.06)	-0.19 (0.11)
Bromus hordeaceus	AG	8.44 (1.31)	5.44 (0.96)	-1.94 (1.09)	0.75 (1.07)
Bromus madritensis ssp. Rubens	AG	0.00 (0.00)	0.38 (0.38)	0.00 (0.00)	-0.31 (0.31)
Centaurea solstitialis	AF	0.13 (0.09)	0.63 (0.39)	0.75 (0.46)	-0.44 (0.31)
Cerastium glomeratum	AF	0.00 (0.00)	0.00 (0.00)	0.69 (0.18)	0.13 (0.09)
Hypochaeris glabra	AF	0.56 (0.17)	0.63 (0.17)	0.13 (0.20)	0.44 (0.25)
Koeleria phleoides	AG	0.00 (0.00)	0.00 (0.00)	0.31 (0.13)	0.06 (0.06)
Lolium multiflorum	AG	0.81 (0.39)	1.00 (0.40)	0.38 (0.38)	0.38 (0.17)
Medicago polymorpha	L	0.25 (0.12)	0.06 (0.06)	-0.13 (0.09)	0.00 (0.00)
Senecio vulgaris	AF	0.31 (0.13)	0.06 (0.06)	0.19 (0.17)	0.44 (0.15)
Trifolium dubium	L	0.00 (0.00)	0.00 (0.00)	0.13 (0.09)	0.00 (0.00)
Trifolium hirtum	L	**5.69 (1.16)**	**1.50 (0.20)**	-2.56 (0.95)	0.75 (0.61)
Trifolium microcephalum	L	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)	0.06 (0.06)
Sonchus asper	AF	1.25 (0.20)	1.38 (0.20)	0.50 (0.20)	0.88 (0.41)
Negative Response					
Taeniatherum caput-medusae	AG	29.25 (4.70)	26.56 (5.09)	**5.31 (5.26)**	**-16.88 (4.87)**

	Func.	Initial Cover (%)		Cover Change (%)	
Native Species	**Group**	**No Burn**	**Before Burn**	**No Burn**	**After Burn**
Positive Response					
Crassula connata	AF	0.52 (0.21)	0.21 (0.14)	**-0.11 (0.33)**	**6.67 (1.27)**
Neutral Response					
Achyrachaena mollis	AF	0.00 (0.00)	0.21 (0.14)	0.00 (0.00)	-0.21 (0.14)
Allium/Triteliea/Dichelostemma	PF	1.77 (0.24)	1.98 (0.21)	0.65 (0.23)	3.54 (1.16)
Aristida ternipes	PG	1.25 (0.64)	1.88 (0.63)	0.00 (0.00)	-0.94 (0.54)
Astragalus gambelianus	L	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)
Calycadenia fremontii	AF	0.00 (0.00)	1.25 (0.86)	0.00 (0.00)	0.00 (0.00)
Calycadenia truncata	AF	1.98 (0.85)	2.29 (0.84)	-1.20 (0.77)	-1.25 (0.74)
Castillija attenuata/T. eriantha	AF	0.83 (0.25)	0.83 (0.25)	0.76 (0.25)	1.35 (0.56)
Chorizanthe polygonoides	AF	0.00 (0.00)	0.10 (0.10)	0.00 (0.00)	0.21 (0.14)
Clarkia purpurea ssp. quadrivulnera	AF	0.52 (0.21)	0.63 (0.23)	-0.11 (0.19)	0.00 (0.26)
Eremocarpus setigerus	AF	1.56 (0.25)	1.04 (0.26)	-0.54 (0.31)	0.21 (0.21)
Eriogonum nudum	PF	0.00 (0.00)	0.10 (0.10)	0.00 (0.00)	0.00 (0.00)
Gilia tricolor	AF	4.27 (1.17)	2.19 (0.84)	-1.96 (1.04)	0.21 (0.78)
Hemizonia fitchii	AF	0.73 (0.24)	0.21 (0.14)	0.33 (0.18)	1.46 (0.54)
Juncus bufonius	AF	0.00 (0.00)	0.00 (0.00)	0.11 (0.11)	0.94 (0.64)
Lasthenia californica	AF	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)
Layia fremontii	AF	0.31 (0.17)	0.31 (0.17)	0.00 (0.00)	0.63 (0.53)
Lepidium nitidum	AF	0.21 (0.14)	0.42 (0.19)	1.20 (0.27)	0.52 (0.21)
Lessingia nemaclada	AF	1.67 (0.25)	2.08 (0.61)	-0.43 (0.26)	-1.35 (0.58)
Lotus wrangelianus	L	0.83 (0.25)	1.67 (0.25)	0.87 (0.25)	0.31 (0.17)
Micropus californicus	AF	0.00 (0.00)	0.10 (0.10)	0.76 (0.25)	0.73 (0.24)
Microseris acuminata	AF	0.10 (0.10)	0.10 (0.10)	2.61 (1.68)	0.73 (0.65)
Microseris douglasii	AF	0.00 (0.00)	0.00 (0.00)	0.22 (0.15)	0.00 (0.00)
Navarretia heterandra	AF	0.00 (0.00)	0.31 (0.17)	0.22 (0.15)	0.00 (0.00)

Table 4. Response of species cover in the *Aristida* community. Data is Mean(SE). Significant ($p<0.05$) differences for a given year are in bold. California Native Plant Society list 4 Species are in bold. *Castillija attenuata* and *Triphysaria eriantha* ssp. *eriantha* were grouped together because they are difficult to separate after senescence, and they are both root hemiparasites.

Table 4 (cont'd)

Navarretia pubescens	AF	4.48 (0.99)	3.44 (0.73)	-1.63 (0.90)	2.50 (1.09)
Navarretia tagetina	AF	4.17 (2.19)	2.19 (1.55)	-1.30 (1.50)	-0.31 (1.10)
Plagiobothrys austinae	AF	0.00 (0.00)	0.21 (0.14)	0.00 (0.00)	0.10 (0.10)
Plantago elongata	AF	0.00 (0.00)	0.21 (0.14)	0.00 (0.00)	-0.10 (0.10)
Plantago erecta	AF	11.35 (1.18)	11.98 (2.06)	-2.17 (1.01)	-4.48 (1.65)
Polygonum bidwelliae	AF	0.42 (0.19)	0.52 (0.21)	-0.22 (0.15)	-0.10 (0.10)
Rigiopappus leptocladus	AF	0.00 (0.00)	0.00 (0.00)	0.33 (0.18)	0.00 (0.00)
Sagina apetala	AF	0.00 (0.00)	0.00 (0.00)	0.11 (0.11)	0.10 (0.10)
Trifolium albopurpureum	L	0.63 (0.23)	0.42 (0.19)	0.22 (0.15)	0.21 (0.21)
Trifolium depauperatum	L	0.42 (0.19)	0.31 (0.17)	0.00 (0.22)	0.52 (0.21)
Trifolium microcephalum	L	0.31 (0.17)	0.83 (0.25)	-0.11 (0.19)	-0.10 (0.28)
Vulpia microstachys	AG	4.27 (1.01)	5.21 (1.19)	5.00 (1.30)	-0.21 (1.14)
Negative Response					
Selaginella hansenii	PF	7.19 (3.01)	10.21 (3.08)	**1.20 (0.83)**	**-9.27 (2.93)**
Exotic Species					
Neutral Response					
Aira caryophyllea	AG	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.21 (0.14)
Anagallis arvensis	AF	0.10 (0.10)	0.42 (0.19)	-0.11 (0.11)	-0.42 (0.19)
Avena barbata	AG	1.35 (0.26)	1.25 (0.26)	0.00 (0.22)	-0.52 (0.26)
Bromus hordeaceous	AG	4.27 (1.01)	3.65 (0.92)	7.17 (1.65)	-0.31 (1.20)
Bromus madritensis ssp. r.	AG	1.04 (0.26)	0.63 (0.23)	1.52 (0.56)	0.83 (0.29)
Centaurea melitensis	AF	0.21 (0.14)	0.73 (0.63)	-0.11 (0.11)	0.00 (0.00)
Centaurea solstitialis	AF	0.32 (0.17)	0.00 (0.00)	-0.32 (0.17)	0.00 (0.00)
Erodium brachycarpum	AF	4.69 (1.12)	4.79 (1.61)	1.96 (1.19)	10.73 (3.14)
Erodium cicutarium	AF	0.83 (0.25)	0.83 (0.25)	0.43 (0.34)	1.35 (0.56)
Filago gallica	AF	0.83 (0.25)	1.15 (0.26)	0.65 (0.28)	1.77 (0.79)
Galium parisiense	AF	0.42 (0.19)	0.73 (0.24)	0.11 (0.19)	0.21 (0.21)
Hordeum marinum ssp. g.	AG	0.00 (0.00)	0.63 (0.63)	0.00 (0.00)	-0.63 (0.63)

Table 4 (cont'd)

Hypochaeris glabra	AF	2.40 (0.59)	1.98 (0.21)	0.65 (0.57)	0.52 (0.21)
Koeleria phleiodes	AG	0.00 (0.00)	0.63 (0.63)	0.33 (0.18)	0.63 (0.23)
Lolium multiflorum	AG	1.77 (0.86)	5.10 (2.56)	-1.30 (0.75)	-2.92 (1.55)
Medicago praecox	L	1.88 (0.63)	1.98 (0.62)	2.28 (1.02)	3.23 (1.19)
Petrorhagia dubia	AF	10.63 (1.74)	10.00 (1.79)	-6.41 (1.50)	-2.81 (2.11)
Senecio vulgaris	AF	0.00 (0.00)	0.00 (0.00)	0.22 (0.15)	0.00 (0.00)
Silene gallica	AF	0.00 (0.00)	0.21 (0.14)	0.11 (0.11)	-0.21 (0.14)
Torilis nodosa	AF	0.10 (0.10)	0.10 (0.10)	0.00 (0.00)	0.00 (0.15)
Trifolium dubium	L	0.00 (0.00)	0.10 (0.10)	0.00 (0.00)	-0.10 (0.10)
Trifolium hirtum	L	0.10 (0.10)	0.00 (0.00)	0.00 (0.16)	0.00 (0.00)
Vulpia myuros	AG	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	2.08 (1.55)

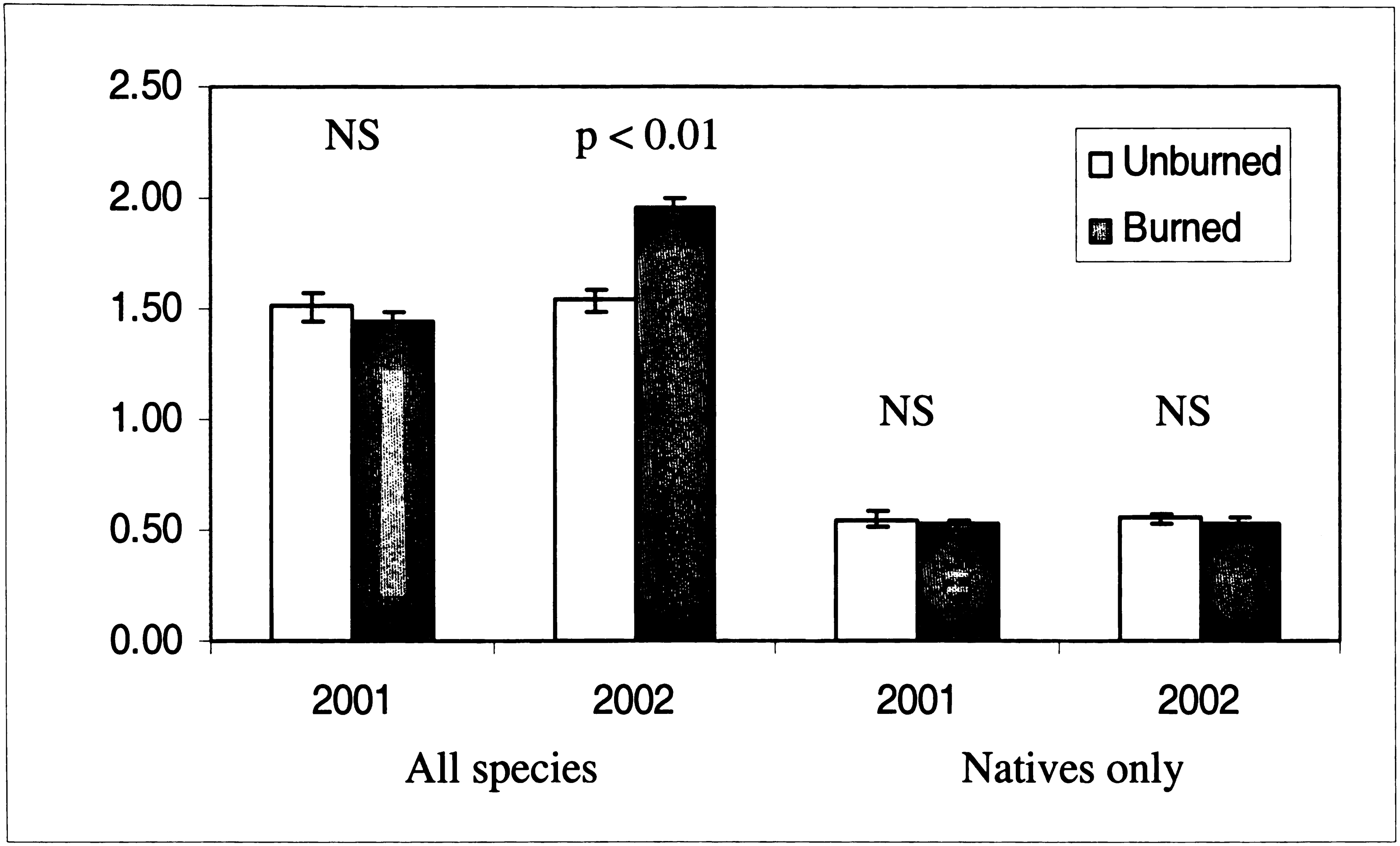


Figure 10. Shannon-Weiner diversity in the *Nassella* community. Standard error is shown. Burns were conducted in October, 2001.

increases in the Shannon-Weiner diversity were mainly attributable to an increase in the evenness of species, rather than an increase in species richness.

Estimates of the seed bank are presented in Table 5. The annual grass functional group was reduced significantly by burning. This was due to combined reductions in the seed bank of three exotic annual grasses, *T. caput-medusae*, *Vulpia myuros* (Zorro Fescue), and *Bromus hordeaceus* (Soft Chess). Thus, burning was more likely to reduce the seed bank of annual grasses than any other functional group. Other intriguing but non-significant changes due to burning in the seed bank were a reduction in exotic species, and an increase in the native annual forb *Crassula connata* (Pygmyweed).

IV. Discussion

Most research done on fire and *N. pulchra* has found that burning is beneficial for that species. The greatest restoration benefit to burning the *N. pulchra* populations is likely increased reproduction potential. Increased inflorescence numbers were found in this study and others (Ahmed 1983), although in one case inflorescences were found to produce fewer seeds (Langstroth 1991). It was surprising that *N. pulchra* plants growing in a soil with a shallow hardpan responded positively to burning, as that result was not the case for Langstroth (1991). Other studies have found heavier seeds (Dyer 2002), although not a higher germination rate. However, Fossum (1990) found that heavier seeds grew more quickly as seedlings and were more likely to survive their first year. Fire may also increase the probability of *N. pulchra* seedling survival by removing the thatch layer (Ahmed 1983). In this study basal area increased and mortality was flat at

Species	Func. Group	Control	Before Burn	After Burn
Bromus hordeaceus	AG	0.104 (0.049)	0.068 (0.022)	0.018 (0.011)
Calycadenia fremontii	AF	0.000 (0.000)	0.000 (0.000)	0.002 0.001
Cardamine oligosperma	AF	0.000 (0.000)	0.004 (0.002)	<0.001 (0.000)
Cerastium glomeratum	AF	0.021 (0.010)	0.044 (0.032)	0.061 (0.036)
Delphinium variegatum	PF	<0.001 (0.000)	0.000 (0.000)	<0.001 (0.000)
Filago gallica	AF	0.025 (0.001)	0.043 (0.024)	0.006 (0.003)
Crassula connata	AF	0.006 (0.002)	0.018 (0.005)	0.036 (0.019)
Erodium brachycarpum	AF	0.033 (0.012)	0.051 (0.016)	0.063 (0.023)
Hemizonia fitchii	AF	<0.001 (0.000)	0.000 (0.000)	0.000 (0.000)
Hypochaeris glabra	AF	0.002 (0.001)	0.001 (0.001)	0.000 (0.000)
Lolium multiflorum	AG	0.011 (0.010)	0.001 (0.001)	0.001 (0.001)
Nassella pulchra	PG	0.003 (0.001)	0.000 (0.000)	0.002 (0.001)
Petrorhagia dubia	AF	0.009 (0.005)	0.009 (0.008)	0.003 (0.001)
Juncus bufonius	AF	0.034 (0.022)	0.019 (0.006)	0.020 (0.007)
Sagina apetala	AF	0.061 (0.041)	0.034 (0.032)	0.026 (0.016)
Senecio vulgaris	AF	0.000 (0.000)	0.001 (0.001)	0.000 (0.000)
Taeniatherum caput-medusae	AG	0.084 (0.021)	0.074 (0.014)	0.045 (0.027)
Trifolium hirtum	L	0.039 (0.021)	0.000 (0.000)	0.000 (0.000)
Vulpia myuros	AG	0.040 (0.021)	0.110 (0.037)	0.031 (0.011)
Functional Groups				
Native Species		0.109 (0.046)	0.081 (0.035)	0.089 (0.022)
Exotic Species		0.346 (0.095)	0.404 (0.077)	0.229 (0.048)
Annual Forbs		0.191 (0.047)	0.227 (0.073)	0.217 (0.063)
Annual Grasses		**0.239 (0.082)**	**0.255 (0.040)**	**0.096 (0.025)**
Perennial Forbs		<0.001 (0.000)	0.000 (0.000)	<0.001 (0.000)
Perennial Grasses		0.003 (0.001)	0.000 (0.000)	0.002 (0.001)
Legumes		0.039 (0.021)	0.000 (0.000)	0.000 (0.000)

Table 5. Number of seeds per gram of soil in the *Nassella* community. Data is Mean(SE). Significant ($p<0.05$) differences are in bold. n = 8 for each treatment.

the same time that these reproductive benefits were realized. Thus, I conclude that burning is helpful for sustaining the *N. pulchra* population.

I found the *A. ternipes* population to be in decline, and burning only appeared to hasten the process. Both burned and control *A. ternipes* decreased in basal area, but their number of inflorescences were unchanged. Control plants had a mortality rate of 4.5%, but the rate for burned plants was more than eight times greater. No new seedlings were observed in either control or burn plots. The plants were grazed, although not heavily, and this may be contributing to their decline. The crowns of the *Aristida* plants appear more exposed and less embedded in the soil than *Nassella*, perhaps due to the rocky soil in the *Aristida* community. The greater exposure may have added to the heat experienced by the plants during the fire, thus increasing mortality. Overall, burning was detrimental to the *A. ternipes* population. Since so much of the research on perennial bunchgrasses in California has focused on *N. pulchra*, special care should be taken when extrapolating those results to other bunchgrass species.

In neither case did burning increase the percentage of native species cover or decrease the exotic species cover. In the *Nassella* community, however, fire decreased cover of the noxious weed *T. caput-medusae*. Most efforts at controlling *T. caput-medusae* with fire have utilized spring burns. Although we were able to significantly reduce *T. caput-medusae* with a fall burn, the species still had a cover of about 10%, and so is likely to quickly return to pre-burn levels within 1-2 years (Young 1992). Controlling *T. caput-medusae* with fall burning may require burning in at least 2 consecutive years. The space created by the reduction of this weed was exploited more by exotic species, particularly *Erodium* and *Vulpia myuros*, than by natives. This result was to be expected considering exotic species dominate the seed bank. Meyer and Schiffman (1999) found an increase in native species cover with fall burning, but they used plots that had much less native cover to begin with. The failure to increase the cover of native species was reflected in the native component of the Shannon-Weiner diversity index, which was unchanged in both communities. Although reducing specific weeds is possible with burning, decreasing the overall cover of exotics is unlikely in grasslands with such a large number of naturalized exotic species. In grasslands that have few native species in the seed bank, managers should consider adding native species seed post-burn.

As expected, annual forbs were increased in both communities. Annual grasses decreased in both, although the effect was significant only in the *Aristida* community. Annual grasses were also reduced in the seed bank, while annual forb seeds were not affected by the burn. The changes observed in both these groups were similar to natural annual fluctuations driven by weather variation (Figure 9), indicating that fire is at least as important as annual weather in determining the botanical composition of these communities. If an objective is to increase native species, however, management practices that produce trade-offs between annual grasses and annual forbs are unlikely to achieve that goal, since both groups include many exotic species. Even the legumes are comprised of several exotic species in the *Trifolium* and *Medicago* genera. However, in most California grasslands the other two functional groups, perennial grasses and perennial forbs, are almost entirely composed of native species. Management practices that benefit these two groups are more likely to result in an increase in native species. Perennial grasses, with the exception of *N. pulchra*, have been little studied. Grassland studies rarely focus on perennial forbs, even though they are often a significant component of cover.

Holstein (2001) has recently suggested that tarweeds may have originally dominated the part of the Central Valley where the study sites are located. In the *Nassella* community, it is interesting to note that *Hemizonia fitchii*, a tarweed, was found only in burned plots. *H. fitchii* also tended to increase with burning in the *Aristida* community, although not to significant levels. It may be that a lack of fire, or an accumulation of thatch, has prevented this and similar species from being as prevalent as they may once have been. Tarweeds are deep-rooted warm season annuals, just like the invasive *Centaurea solstitialis*, which is present in the *Nassella* community. Tarweeds and *C. solstitialis* are more likely to experience competition from each other than from cool season species. Promoting tarweeds, or other late season native annuals, may decrease the odds of a *C. solstitialis* invasion (Dukes 2001).

The reduction of *Selaginella hansenii* in the *Aristida* community due to burning may have consequences that are of concern to restoration ecologists. This spike-moss species grows as a tightly packed groundcover and excludes most other plants from the area it occupies. In the spring following the burn the areas that had been covered by *S. hansenii* were readily apparent because they had very few seedlings and were mostly bare soil. This pattern is evidence that *S. hansenii* largely prevents seeds from penetrating the thick vegetation mat it forms. The bare soil that persists after its removal, even through the wet season, may experience higher erosion rates (Heady 1956), especially in steep areas such as the *Aristida* community. Consideration of this effect should be given before administering prescribed burning on land with significant slope and *S. hansenii* cover. The same effect is likely to be observed in other areas that contain groundcovers, especially ones that reproduce primarily by vegetative means.

The physical characteristics of a seed may determine whether it survives a burn in an area with a deep thatch layer. Seeds with long awns are more likely to become trapped in the thatch, where they are sure to be destroyed in a burn. *T. caput-medusae* has long awns and is adapted to germinating while suspended in its own thatch (Young 1992). This explains the observed drop in *T. caput-medusae* in the seed bank and in cover due to burning. *N. pulchra* seed also has long awns, and although it is a weak hygroscopic borer, is likely to be caught in the thatch layer and destroyed in a fire. However, unlike *T. caput-medusae*, there was very little *N. pulchra* seed in the seed bank to begin with. The bare ground created by fire may benefit *N. pulchra* recruitment more the second year after burning, when mature plants have had time to disperse more seed.

Fall would have been the most likely time for natural fires in California grasslands since that is when they are driest. However, fall burns do not appear to have any more beneficial effects than late spring burns when the literature is examined. The cover of native species and the performance of native bunchgrasses are sometimes increased with burns in either season, but neither season appears to be particularly advantageous. A spring burn is preferred when a late-maturing invasive species is present, because it will offer better control than a fall burn. Other than that scenario, there does not appear to be an obvious advantage to either late-spring or fall burning. In the *Nassella* community, two common management goals were achieved with our fall burn: a decrease in noxious weeds and an increase in native bunchgrass population viability. No management goals were achieved in the *Aristida* community with fall burning. I would not suggest a spring burn either in that community because *A. ternipes* is still green and growing at that time.

N. pulchra is possibly the most widespread and common of California's native bunchgrasses, and certainly the most studied. Researchers dating back to (Clements 1934) have noted its ability to persist and thrive in areas that experience frequent fire. This study found that fall burning can enhance the vigor of *N. pulchra* plants, an outcome that largely agrees with previous work. However, there are dozens of native bunchgrass species in California, most of which are potential targets for conservation or restoration, and which may respond differently to fire. Some of those species have significantly different life histories than *N. pulchra.* The negative effect of burning on *A. ternipes* in this study should serve as a warning that other species of bunchgrasses may have different responses to fire than *N. pulchra.* That possibility should be taken into account when designing management plans in California grasslands.

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Chapter 3
A Seedling Key to Some Common California Grasses

I. Introduction

The ability to reliably identify plant species at the seedling stage has challenged botanists around the world. In some cases, waiting until the plant flowers to allow for easier identification is an option, but in others reliable identification is needed earlier. Dicots, even those within the same family, display an astounding variety of leaf shapes and characteristics. Even though leaves are known for large environmental plasticity, many defining characteristics can be found on the first leaves to develop after the cotyledons. If the investigator knows the geographic area from which the seed came, the species can often be narrowed down to a few dozen possible candidates based on the primary leaves alone. Grasses present an especially difficult problem in this case because of the similarity of their leaves. Grass keys rely on floral characteristics even more than keys to dicot families.

Land management decisions sometimes require a botanical survey early in the growing season. For example, burning permits must be obtained well in advance, so the decision of which areas to burn must be made long before plants in those areas have matured and become easily identifiable. Few plants, and possibly no grasses, flower early in the season. However, invasive, late-maturing grasses such as *Taeniatherum caput-medusae* (Medusahead) are often the targets of management decisions. The Poaceae in California is treated exhaustively by Munz and Keck (1959) and Hickman (1993), and partially by Crampton (1974). However, these keys rely primarily on floral characteristics. Having a grass seedling key will increase the information available to land managers and thus increase the value of their decisions. This key includes some of the most common California grass species, including some species that are often specific targets of management plans, such as *T. caput-medusae* and *Nassella pulchra* (purple needlegrass).

Focusing on seedlings greatly limits the number of useful characteristics available for writing a key. There are relatively few morphological traits with significant interspecific variation among grass seedlings. I found the ligule to be one of the most useful. The length of the ligule may be used to differentiate between species in several places throughout the key. In the case of *Aristida ternipes* var. *hamulosa*, bristly hairs in place of a ligule provide a unique trait for identification.

The overall hairiness, or in some cases the positions or relative lengths of hairs, is sometimes useful. Some seedlings have hairs easily seen with the naked eye, such as *Bromus carinatus* (California Brome), while others such as *Lolium multiflorum* (Italian ryegrass) are completely glabrous even under magnification. In some cases, species have noticeably different length hairs on blades and sheaths. In the case of sheath hairs, observations should be concentrated on the upper parts of the sheath nearest the collar.

Some traits are displayed by only a few species, and so are helpful in identification. When present, auricles are an unmistakable clue to two species in the key. Two other species have bow-tipped leaves. Their leaves are pointed in a shape reminiscent of the bow of a canoe. Leaf width is an occasionally useful trait, as some species have much wider or narrower leaves than most other species.

Since only a select set of California species are included in this key, it should be used only when something is known about the botanical composition of the area in which the specimen at hand came from. It will be most useful when species included in the key are known to comprise the bulk of the grasses found in the area from which the specimen came. This is often the case on actively managed lands. Specimens should have at least three primary leaves in order to be at a stage at which they will key reliably. The key may then be used until the grass begins to flower, at which point other keys, such as Hickman (1993), should be used. In the case of grass seedlings, the leftover seed hull can often still be found where root and shoot meet. This leftover hull can be invaluable for identification, even in cases where the seedling is too young even for this key.

II. Methods

Plants used to create this key were grown from known seed. Seed was obtained commercially as well as gathered from wild communities. Most of the seed came from plants originating in the Sacramento Valley. Seeds were germinated and grown in a greenhouse until they had produced 3-4 leaves, and then examined for useful characteristics.

The key was tested with plants grown from the same seed. Unknown seedlings were keyed out by myself, and then checked against a previously sealed list. Under these conditions the key worked greater than 90% of the time. The most common error occurred in couplet 17, where the key sometimes failed to accurately separate *Vulpia myuros* and *V. microstachys*.

III. The grass seedling key

1. Ligule composed of bristly hairs ... *Aristida ternipes var. hamulosa*
1' Ligule membranous
2. Ligules ≥ 0.8 mm
3. Auricles present ... *Hordeum vulgare*
3' Auricles absent
4. Sheath puberulent
5. Sheath hairs < 0.5 mm ... *Hordeum b.* ssp. *brachyantherum*
5' Some sheath hairs ≥ 0.8 mm ... *Bromus carinatus*
4' Sheath glabrous
6. Blade flat-tipped ... *Melica californica*
6' Blade bow-tipped[1]
7. Ligule pointed at tip, > 2 mm ... *Scribneria bolanderi*
7' Ligule rounded at tip, 1-2 mm ... *Poa s.* ssp. *secunda*
2' Ligules < 0.8 mm
8. Base of stem green/white
9. Many sheath hairs > 0.2 mm
10. Some hairs > 1.5 mm ... *Koeleria phleoides*
10' All hairs < 1.5 mm ... *Koeleria macrantha*
9' Sheath hairs < 0.2 mm
11. Blade hairs < 0.4 mm ... *Nassella lepida*
11' Blade hairs ≥ 0.4 mm
12. Ligule < 0.4 mm ... *Nassella cernua*
12' Ligule ≥ 0.4 mm ... *Nassella pulchra*
8' Base of stem with some red
13. Some sheath hairs ≥ 1 mm ... *Elymus multisetus*
13' Sheath glabrous or hairs < 1 mm
14. Sheath glabrous
15. Auricles present ... *Lolium multiflorum*
15' Auricles absent
16. Leaf width ≥ 3mm ... *Gastridium ventricosum*
16' Leaf width < 3 mm
17. Lines of scabrous protrusions[2] on sheath at 15X ... *Vulpia myuros*
17' No lines of scabrous protrusions on sheath at 15X ... *Vulpia microstachys*

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[1] In bow-tipped leaves, the halves of the leaf on either side of the midrib come together like the bow of a canoe.

[2] Small protrusions of tissue arranged vertically along the length of the sheath are the scabrous protrusions referred to in this couplet.

14’ Sheath puberulent
18. Blades puberulent
19. Lower sheath with prominent red veins on translucent background ... *Taeniatherum caput-medusae*
19’ Lower sheath evenly red ... *Hordeum brachyantheru* ssp. *californicum*

18’ Blades glabrous
20. Blade width > 2.5 mm ... *Elymus glaucus*
20’ Blade width < 2.5 mm
21. Ligule ≥ 0.3 mm ... *Festuca californica*
21’ Ligule < 0.3 mm
22. Reddish color extending up to ligule on outermost leaf ... *Festuca rubra*
22’ Reddish color not extending to ligule ... *Festuca occidentalis* or *Festuca idahoensis*

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