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Optimal prescribed burn frequency to manage foundation California native perennial species and enhance native flora

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Abstract Grasslands can be diverse assemblages of grasses and forbs but not much is known how perennial grass species management affects native plant diversity except in a few instances. We studied the use of late-spring prescribed burns over a span of eleven years where the perennial grass *Poa secunda* was the foundation species, with four additional years of measurements after the final burn. We evaluated burn effects on *P. secunda*, the rare native annual forb *Amsinckia grandiflora* and local native and exotic species. Annual burning maintained *P. secunda* number, resulted in significant expansion, the lowest thatch and exotic grass cover, the highest percentage of bare ground, but also the lowest native forb and highest exotic forb cover. Burning approximately every three years maintained a lower number of *P. secunda* plants, allowed for expansion, and resulted in the highest native forb cover with a low exotic grass cover. Burning approximately every five years and the control (burned once from a wildfire) resulted in a decline in *P. secunda* number, the highest exotic grass and thatch cover and the lowest percentage of bare ground. *P. secunda* numbers were maintained up to four years after the final burn. While local native forbs benefited from burning approximately every three years, planted *A. grandiflora* performed best in the control treatment. *A. grandiflora* did not occur naturally at the site; therefore, no seed bank was present to provide across-year protection from the effects of the burns. Thus, perennial grass species management must also consider other native species life history and phenology to enhance native flora diversity.

Key words native California forbs; native California grasses; perennial grassland restoration; enhancing native flora

Introduction

Perennial grasslands in Mediterranean climates around the globe have been transformed by annual grass invasions (Heady 1988; Lenz et al. 2003; Milton 2004). This transformation has been underway in the native perennial grasslands of California (US) since the arrival of the first Europeans on the West Coast (Baker 1989; Bartolome et al. 2007; Evett & Bartolome 2013). In contrast, annual grasses native to the Mediterranean are present only as ruderal species in their native range (Jackson 1985) and comprise a fraction of the exotic grasses introduced to South African grasslands (Milton 2004). Transformation of California grasslands were likely facilitated by changes in the disturbance regime, including the introduction of grazing by domestic species and the suppression of natural and human-initiated fire (Hatch et al. 1999; Jackson & Bartolome 2002; Barry et al. 2006). By the 1850's, non-native annual grasses and forbs had become well established (Baker 1989; Murphy & Ehrlich 1989). Increases in exotic species abundance is continuing, even more than 250 years after exotic species began to spread (Brandt & Seabloom 2012), which is common in systems with disturbances such as fire and grazing (Hobbs & Huenneke 1992).

Foundation species are dominant members of an ecological community that can mediate ecological processes (Rodhouse et al. 2014), and native perennial grasses may provide this service to Mediterranean grasslands. The loss of foundation species may result in an increase of exotic plants and a decrease in native species (Prevey et al. 2010). Positive relationships between native perennial grasses, increased native forbs and reduced exotic species may be due to a direct benefit of perennial grasses as foundation species or simply similar niches among native species that oppose those of exotic species. Although invasive annual grasses can reduce perennial grass productivity and abundance (Milton 2004), established perennial grasses may shift competitive interactions in favor of native species (Corbin & D'Antonio 2004; Carlsen et al. 2000; Gillespie & Allen 2004), and the grassland may resist annual grass invasion (Lulow 2006, 2008). Exotic annual grass abundance is associated with decreased native forb diversity (Milton 2004; Suttle et al. 2008). Thus, it may be possible to enhance the presence of native forbs and reduce the abundance and number of invasive annual grasses and other exotic species by focusing on increasing native perennial grass density, although some have suggested that focusing on a single perennial grass species could be detrimental to other important native species (Hatch et al. 1999).

Prescribed fire is one tool used to enhance native perennial grasses (Meyer & Schiffman 1999; Klinger & Messer 2001; Dyer 2002, 2003; Bartolome et al. 2004; Marty et al. 2005; Moyes et al. 2005), reduce exotic annual grasses (Musil et al. 2005; Almeida-Neto et al. 2010), and improve biodiversity (Bond & Archibald 2003; van Wilgen et al. 2007). In California, much of this research has been on *Stipa pulchra* (purple needlegrass, also known as *Nassella pulchra*), as this species may have dominated pre-invasion native perennial grasslands (Heady 1988; Bartolome et al. 2007). However, current California grasslands can be dominated by native perennial grass species such as *Poa secunda* (pine bluegrass), *Leymus triticoides* (creeping wild rye) and *Sporobolus airoides* (alkali sacaton) (Barry 1972; Holland 1986; Holstein 2001; Kimball & Schiffman 2003), and these species may also serve as foundation, or matrix species, for California's perennial grasslands. Others have challenged the idea that *S. pulchra* was the sole historic foundation species in California perennial grasslands (Hamilton 1997; Holstein 2001; Schiffman 2007).

The timing of burns is important in Mediterranean systems, as well as in tropical grasslands and savannas where there is a similar alternation of wet and dry seasons. "Early-season" burns conducted when fuel loads are just beginning to dry reduce the catastrophic hazards associated with "late-season" burns that occur when fuel loads are much higher (Andersen et al. 1998; Rossiter et al. 2003). Fire can control annual species in perennial grasslands when undispersed seeds are vulnerable to the fire (Pollak & Kan 1998). However, native annual forbs may be seed limited, with only those with a substantial seed bank and complimentary phenology benefiting from burning (Rice 1989; DiTomaso et al. 1999; Meyer & Schiffman 1999; Almeida-Neto et al. 2010; Driscoll et al. 2010; Brandt & Seabloom 2012). While fire may be used to expand rare forb habitat (e.g. Almeida-Neto et al. 2010), new plantings may be susceptible to extirpation from fire when there is no existing seed bank.

Fire can decrease thatch and increase bare ground, which has been shown to benefit native plants (Rice 1985, 1989; Bergelson 1990; Meyer & Schiffman 1999; Lenz et al. 2003). Reduced thatch and increased bare ground can influence forb seed germination through changes in the light and temperature regimes (Rice 1989; Lenz et al. 2003). Litter removal is associated with increased native plant recruitment (Brandt & Seabloom 2012). Both fire and grazing has been used to reduce thatch (Bartolome et al. 2004; Meyer & Schiffman 1999; Hatch et al. 1999; Kimball & Schiffman 2003) and increase biodiversity (Hobbs & Huenneke 1992), although it can be unclear if the benefits are from thatch reduction, increased bare ground, reduced competition, or a combination of the three.

Some have found the effects of burning perennial grasslands to be variable and transitory. Fire-prone systems are resilient to fire (Lavorel 1999; Bennett et al. 2002; Rossiter et al. 2003), thus the effects of burning may appear transient in the short-term. For example, prescribed burns can increase perennial grass recruitment that fails to translate into greater cover in the years after the burn (Hatch et al. 1991; Dyer et al.1996; Marty et al. 2005). Although burning rarely results in species extirpation in these systems (Lavorel 1999), changes in abundance may occur immediately post-burn, whereas abundance levels several years after the burn likely depends upon other ecological drivers such as climate and microhabitat (e.g. Hatch et al. 1999; Bartolome et al. 2004). Therefore, recurring fire may be required to maintain desired species abundance (Bond & Archibald 2003; Lloret et al. 2003;

van Wilgen et al. 2007). While small-scale controlled, manipulative burn studies are effective at identifying the immediate effects of the burn and interactions between burning, predation, and invasion of native species (Espeland et al. 2005; Driscoll et al. 2010), most last a single season or two, rarely going beyond four years. And although long-term observational and large scale manipulative research has yielded important information regarding the landscape effects of fire, it has not been translated into effective species management protocols (Bond & Archibald 2003; van Wilgen et al. 2007). Long-term small-scale manipulative burn studies spanning ten years or longer are likely needed to overcome strong ecological influences of climate and microhabitat and allow the effect of the prescribed burn to become apparent, particularly on forbs that respond strongly to inter-annual variation (Musil et al 2005; Alder & Levine 2007).

Previous work we have conducted at a site in California that we have studied for many years (Carlsen et al. 2000; Gregory et al. 2001; Carlsen et al. 2002; Espeland & Carlsen 2003; Espeland et al. 2005; Paterson et al. 2010; Carlsen et al. 2012) suggests prescribed burns can increase the abundance of the foundation species *P. secunda*. This site, Lawrence Livermore National Laboratory's (LLNL) Experimental Test Site, Site 300, is a 2,711-ha high explosive testing facility located in the Altamont Hills of the Diablo Range in the California Inner South Coast Ranges. It has been protected from livestock grazing and many other human activities since its establishment in the early 1950s, and less than 5% of the site consists of buildings or roads. Beginning in 1960, annual late-spring prescribed burns have been conducted on approximately half of the facility to reduce the threat of wildfire, and high densities of *P. secunda* occur in these areas. Grasslands dominated by *P. secunda* were originally described at the site in 1986 (Taylor & Davilla 1986), and this work was used by Holland (1986) in developing the original description of this grassland.

In addition to *P. secunda*, the rare native winter annual forb, *Amsinckia grandiflora* (large-flowered fiddleneck), is also found at Site 300, occurring in two small native populations in grasslands with substantial *P. secunda* cover outside of the area subjected to the annual prescribed burns. We have conducted restoration activities on this species at Site 300 since 1993, when we established an experimental population near the largest native population. Our previous work found an intermediate density of *P. secunda* resulted in higher *A. grandiflora* fecundity when compared to a similar density of exotic annual grasses (Carlsen et al. 2000). However, we also found that prescribed burns can increase seed predation (Espeland et al. 2005). As *A. grandiflora* does not occur naturally in the experimental population, a substantial seed bank is not present. While we have determined the optimal density of *P.*

secunda for the conservation of *A. grandiflora*, we do not know how maintaining this high *P. secunda* density through fire affects *A. grandiflora* populations.

We have evidence that annual prescribed burns can increase the density of *P. secunda* and it is unknown if such high frequency burning is beneficial to other native species. Therefore, we performed a long-term (fifteen year) controlled study to determine how managing *P. secunda* as a foundation species within the grasslands of Site 300 affects other native species. We wanted to define a burn strategy that maintains *P. secunda* and native species while reducing annual grasses and other exotic species. We evaluated the effect of the prescribed burns on all naturally co-occurring species (both native and exotic). We also measured the burn response of *A. grandiflora* as a focal forb that, while native to California and occurs in the grasslands of Site 300, does not occur naturally at the experimental site.

Methods

Foundation Perennial Grass

Poa secunda is a small statured, cool season bunchgrass that is very common throughout the western US. It is variously known as pine bluegrass, Nevada bluegrass, one-sided bluegrass, and curly bluegrass. Under the older name *Poa scabrella*, Holland (1986) described the distribution of grassland dominated by this species as "lower elevations in the Inner South Coast Ranges, at least from Contra Costa County south to the Carrizo Plains area of eastern San Luis Obispo County". Holland considered this community rare and worthy of further research. Sawyer et al. (2009) renamed this community the *Poa secunda* Herbaceous Alliance and updated the regional distribution to include other bioregions, including the Sierra Nevada and Great Basin. The California Department of Fish and Wildlife considers it a rare natural community (California Department of Fish and Game 2010) with a rarity ranking of G4 S3, where G4 indicates the grassland is apparently globally secure (uncommon but not rare with some cause for long-term concern due to declines or other factors) and S3 indicates the grassland is vulnerable in California due to a restricted range, relatively few stands, recent and widespread declines, or other factors making it vulnerable to extirpation. At Site 300, *P. secunda* breaks dormancy in the fall with new leaf growth apparent in the tussocks once temperatures drop and humidity rises. The species completes seed set in early spring, the tussock leaves dry and the plant becomes dormant by the end of April, prior to the annual prescribed burns.

Focal Native Forb

Amsinckia grandiflora is a winter annual forb listed as endangered in the US (US FWS 1997). It germinates in the fall with the onset of winter rain, grows vegetatively throughout the winter, and blooms in early spring, typically in full bloom by the end of March. While most blooms have faded by mid-April, seed maturation can occur through May, with seeds potentially remaining in the inflorescence through June. The numbers of *A. grandiflora* plants at Site 300 have dropped dramatically, we have observed no plants in the naturally occurring populations since 2006, and the experimental population is maintained only through periodic seeding. The naturally occurring population adjacent to Site 300 has been reasonably stable in recent years, often numbering several thousand plants.

Study Area

The study area is located at the site of the experimentally introduced population of *A. grandiflora* at Site 300 (Carlsen et al. 2000, 2002; Espeland et al. 2005). We originally established this population in 1993. It is located in the same rugged north/south trending canyon as the larger native Site 300 *A. grandiflora* population on a 45% to 75% northwest-facing slope of approximately 303 m elevation in sandy loam soil, bordered by blue oak woodland and coastal sage scrub. The community includes annual exotic grasses *Bromus hordeaceus*, *Vulpia myuros*, *Bromus diandrus*, *Bromus madritensis* ssp. *rubens*, and *Avena barbata*, as well as the exotic forb *Erodium cicutarium*. In addition to *P. secunda*, native species include various forbs and legumes, including *Clarkia* spp., *Lupinus bicolor*, and *Castilleja exserta*.

Field Design and Experimental Treatments

The study area was burned in June 1998. Twenty 2m x 2m ($4m^2$) plots with a 0.5m buffer between each plot were sited in October 1998. In January 1999, all existing *P. secunda* tussocks were cleared from the $4m^2$ plots, divided into 3cm diameter plugs, and transplanted into the center $1m^2$ of each plot. The center $1m^2$ was planted with 33 plants in a hexagonal pattern in 6 rows, with each row alternating between 5 and 6 plants, with additional *P. secunda* tussocks obtained from outside of the $4m^2$ plots as needed. We have shown this density of *P. secunda* (33 plants/m^2) to be the most favorable to *A. grandiflora* fecundity (Carlsen et al. 2000). Immediately after planting, no *P. secunda* plants occurred within the $4m^2$ plot outside of the center $1m^2$. Establishment was monitored throughout February 1999. Plugs lost to rodent herbivory were replaced. All plugs established successfully. Additional *P. secunda* tussocks lost to rodent damage were replaced in January 2000.

Ten *A. grandiflora* seedlings were transplanted into the center 1m^2 of each plot in December 1999, using methods described in Carlsen et al. (2000). Seedlings were interspersed with the central *P. secunda* plants. Seedlings lost to herbivory were replaced through the end of January 2000. Seedlings were of similar growth stage at the time of transplantation (cotyledon or first true leaf stage). The center 1m^2 of each plot was covered with bird net in January 2000 to prevent further loss to herbivory. Bird net was removed once the seedlings reached the two to three true leaf stage. All *A. grandiflora* and *P. secunda* plants were censused in the spring of 2000. To maintain the *A. grandiflora* population, each plot was periodically seeded throughout the experiment. Seeds were planted in a grid with seeds approximately 10cm apart in the center 1m^2 of the plot. Seeding was conducted in December 2000 through January 2001 (15 seeds, haphazardly located), June 2002 (60 seeds per plot, 11 rows of 5 to 6 seeds), October 2004 (64 seeds per plot, 8 rows of 8 seeds), December 2006 (64 seeds per plot, 8 rows of 8 seeds), December 2009 (100 seeds per plot, 10 rows of 10 seeds) and November 2012 (100 seeds per plot, 10 rows of 10 seeds).

Plots were assigned to burn treatments using a stratified randomized block design (Fig. 1a); no two plots of the same treatment were adjacent to each other to maintain equal-sized burn areas. Although we attempted to locate blocks in similar microhabitats, there were some differences between blocks. Block 1 is north facing and steeper, and a bit wetter, while Block 5 is higher elevation, southerly facing and a bit drier. The twenty plots were assigned to one of four planned burn frequencies (Table 1): 1) Control: no prescribed burns beyond the initial site burn in 1998; 2) Low frequency: prescribed burns approximately once every 10 years; 3) Medium frequency: prescribed burns every three to four years; and 4) High frequency: prescribed burn every year.

Burn treatments began in 2001 and were conducted through 2011 (Table 1). Firebreaks were created around each plot designated for burning. The LLNL fire department conducted all prescribed burns (Fig. 1b and 1c). One month after the June 2005 prescribed burn, a wildfire burned through the study area and nearby native *A. grandiflora* site. Thirteen of the twenty plots burned in the 2005 wildfire, twelve of which had not been burned in the 2005 prescribed burn. To ensure that all plots were comparably affected by the wildfire, the three plots that had not been burned in 2005 were burned in the 2006 prescribed burn (Table 1). The net effect of the wildfire and the 2006 prescribed burn was that the actual burn frequencies from 2001 through 2011 were: 1) control plots burned once approximately mid-way through the experiment, 2) low frequency plots burned about every five years, 3) medium frequency plots burned about every three years, and 4) high burn frequency plots burned every year.

Vegetation Sampling

We censused *A. grandiflora* and *P. secunda* in the plots each spring beginning in 2000 continuing through 2015. Most counting was conducted in late March to early April in the peak flowering period for *A. grandiflora*. We also collected data on the height and the number of flowering branches of each *A. grandiflora* plant. We counted each inflorescence that was at least 2cm long as a branch.

We collected data on *P. secunda* plant number per $4m^2$ plot except for the years 2008, 2009 and 2012 when we recorded plants from the originally planted $1m^2$ center of the plot. Beginning in the spring of 2001, cover data were collected on all co-occurring species. A 0.6m by 0.6m quadrat ($0.36m^2$) was placed in the center of the plot. Cover was visually estimated for each species (identified at least to genus), as well as the amount of bare ground and thatch cover.

Data Analysis

For *P. secunda*, the number of plants per plot was summarized. For *A. grandiflora*, the number of plants, and the mean height, mean branch number and mean robustness index (the product of the height in cm and branch number) of plants present in each plot were calculated. If no *A. grandiflora* plants were present in the plot, the plot was excluded from subsequent height, branch number and robustness index statistical analysis. The vegetation cover data were organized into four guilds: native grasses, native forbs, exotic grasses and exotic forbs. For each guild, the number of species and percent cover was summarized for each plot. Thatch and bare ground cover was also summarized for each plot.

To evaluate the effect of the prescribed burns on vegetation between treatments we used a two-way randomized block ANOVA, with burn frequency as the treatment. Each year was considered an independent experiment beginning in 2002 (the year after the first burn treatment). For each year, for each vegetation variable, only treatments with at least three plots containing data were included in the ANOVA. For *P. secunda* number, we used only years in which data were collected from the larger $4m^2$ plot. Residual histograms and standardized residual plots were examined, and did not vary significantly from normality. Although the assumption of normality was met, we conducted both the Freidman and Quade non-parametric tests for years and vegetation variables in which there were no missing data, and compared the results of these tests to the results of the ANOVA. Tukey's HSD was used for post-hoc comparison between all treatments, and the glht function in R was used for post-hoc comparisons of each burn treatment to the control treatment only.

We evaluated changes in *P. secunda* number within treatments by comparing the number of *P. secunda* plants observed each year to the number of *P. secunda* plants in the year 2000 (the first year after establishment and prior to burn treatments). As all *P. secunda* plants in the 4m^2 plot were initially removed and then planted into the center 1m^2, the number of plants in 2000 is equivalent between 1m^2 plot and 4m^2 plot sizes. To evaluate expansion from the center 1m^2 plot, we compared *P. secunda* number in year 2012 (collected from center 1m^2) to *P. secunda* number in year 2013 (collected from larger 4m^2 plot) within each treatment. Means that are not significantly different suggests no expansion (all plants remaining in the center 1m^2): all observed changes in *P. secunda* since 2000 would be due to changes within the center 1m^2 of the plot. Although it is not possible to determine if apparent expansion was due to incomplete excavation of *P. secunda* plants and resprouting facilitated by the burn treatments, we interpret a significant change as a positive effect of fire on *P. secunda*, since we expect incomplete excavation to be randomly distributed throughout the plots. For the within treatment evaluations, we used a two-way randomized block ANOVA with year as the treatment. All statistical analyses were conducted using version 3.1.1 of the statistical program R (R Core Team 2014).

Study Limitations

The large number of ANOVA analyses conducted increases the likelihood of false positives (that is, burn treatments found to be significant for a given vegetation variable solely by chance). However, we elected not to use Bonferroni-adjusted significance levels (Rice 1989), as we were interested in a weight of evidence approach that involved examining statistically significant results and variance in the data for each vegetation variable over the course of the study.

The difficulty in maintaining *A. grandiflora* in the experimental plots (requiring periodic seeding) resulted in many plots containing no or few *A. grandiflora* plants. Thus, while *A. grandiflora* density (number of plants per plot) was readily evaluated statistically, the mean branch number, mean height and mean robustness index of *A. grandiflora* plants was less amenable to such analysis, due to the low number of plants in many plots, and the number of plots with no plants.

Results

Effect of burn treatments on Poa secunda

As the experiment progressed, the number of *P. secunda* plants increased significantly in the high burn frequency treatment, and to a lesser extent in the medium burn frequency, relative to the control and low burn frequency treatments (Fig. 2). Variation in the data was low, and we observed significant differences between treatments in all years after 2007. Although *P. secunda* number in the high burn frequency treatment decreased after the final prescribed burn in 2011 (conducted after the spring census), it remained significantly greater than in the control and low burn frequency treatments over the course of the study. A strong block effect ($p<0.01$) was observed in 2015, with higher numbers of *P. secunda* plants in Block 1 compared to the remaining blocks.

Changes in mean *P. secunda* number within treatments were observed almost immediately in unburned plots (Table 2). In 2002, the low, medium and high frequency burn treatments maintained the initial number of *P. secunda* (these treatments were burned the previous spring), while the mean number of plants in the control treatment declined ($p<0.1$), and remained significantly lower than 2000 through 2015 ($p<0.001$). Mean *P. secunda* number also declined in the low burn frequency treatment ($p<0.05$ from 2005 through 2014), with numbers increasing in 2015. Even with the declines in *P. secunda* number in the low burn frequency and control treatments, there was some expansion of *P. secunda* into the larger 4m^2 plot. In 2012 (one year after the final burn), the mean number of *P. secunda* plants in the center 1m^2 of the control plots was 3.8, whereas in 2013 the mean number of plants in the larger 4m^2 plot was significantly higher at 15.6 plants (had plants not expanded into the 4m^2 plot, the two means would have been similar).

The medium and high frequency burn treatments maintained a mean number of *P. secunda* plants of 18.6 and 33.2 plants (respectively) in the center 1m^2 of the plot by 2012, compared to 30.0 and 26.2 plants (respectively) in 2000 (Table 2). Numbers typically increased immediately after the burns. Significant expansion into the larger 4m^2 plot was observed in both medium and high frequency burn treatments, being greatest in the high frequency burn treatment. In 2013, a mean of 88.3 plants were observed in the high burn frequency treatment in the larger 4m^2 plot, compared to 33.2 plants in 2012 in the center 1m^2. A mean of 41.8 plants were observed in the medium burn frequency treatment in 2013 in the 4m^2 plot, compared to 18.6 plants in the center 1m^2 in 2012. Mean *P. secunda* number was maintained (or increased) through 2015 at the level observed at the completion of the burn treatments (2011) in all treatments except the high frequency burn treatment, which saw a significant decline in mean *P. secunda* number after the completion of burn treatments.

Effect of burn treatments on Amsinckia grandiflora

Unlike *P. secunda*, the control treatment had the highest mean number of *A. grandiflora* plants in 2004 through 2006, and 2012 through 2014 (Fig. 3). The high and medium burn frequency treatments resulted in mean *A.*

grandiflora numbers lower than the control treatment during these years. This was not observed in 2007 through 2009, after all plots (including control plots) had been burned in 2006 and 2007 due to the 2005 wildfire. In the 2012 census following the final burn (in which all burn treatment plots were burned), the control plots contained more *A. grandiflora* compared to all the burn treatment plots, this continued through 2015. In the years in which a significant treatment effect (p<0.1) on *A. grandiflora* plant number was identified using ANOVA (2004 through 2006 and 2012 through 2014), stronger treatment effects were identified using the non-parametric Freidman and Quade tests (p ranging from 0.007 to 0.03).

Mean *A. grandiflora* height in the high burn frequency plots was lower than that observed in the control plots in 2003 and 2013 (Table 3). These years followed seeding of *A. grandiflora* resulting in most plots having plants, whereas in most years the low number of plants resulted in high data variability which reduced our ability to observe treatment differences. Mean *A. grandiflora* height in the low burn frequency plots was similar to that observed in the control plots except in 2002, immediately following the first burn treatment, in which it was significantly lower. When *A. grandiflora* plants in either the medium or high frequency plots were taller than control plants, there was only one plot that contained plants, and usually that plot only contained one plant. This was the case for the medium frequency burn treatment in 2011 and the high frequency burn treatment in 2015.

The number of branches per *A. grandiflora* plant was not significantly different between treatments (Table 4). We again observed high variability in the data due to the low and variable number of *A. grandiflora* plants. Robustness index was significantly lower in the high frequency treatment when compared to the control in 2003 (again, after seeding resulted in plants present in most plots). In 2015 (three years after the final burn conducted in the spring of 2011), while the medium and high frequency burn treatments continued to have few plants, those present were very tall and multi-branched.

Effect of burn treatments on vegetation cover

Burn treatments had an immediate effect on the amount of bare cover and thatch. The high burn frequency treatment had the highest bare ground cover in most years, followed by the medium burn frequency treatment (Fig. 4a). The control and low frequency burn treatments had the lowest bare ground cover in most years. The amount of bare ground within a plot was higher if the plot had been burned the previous year. After the first (2001) and final (2011) burns, in which all plots except control plots were burned, all burn treatments had significantly higher bare ground compared to the control. After the 2005 wildfire, where most plots were burned, the amount of bare ground between treatments was again similar. The amount of bare ground cover in the high and medium burn frequency treatments declined from 2013 through 2015 following the last burn treatment in the late spring of 2011. Not surprisingly, thatch cover showed the opposite pattern compared to bare ground cover (Fig. 4b). A higher percentage of bare ground and lower thatch cover in block 3 (Fig. 1a) was responsible for block effects in 2014 and 2015.

Although there were only three native grass species present in the study area, after 2003 the number of native grass species was highest in the high and medium burn frequency treatments (Fig. 5a); significantly greater than either the control or low burn frequency treatments between 2009 and 2014. The number of native grass species may be incorrect between 2001 and 2003, as it is likely that the native annual *Festuca microstachys* was misidentified as the exotic annual *Vulpia myuros* during this time. One native perennial grass, *Elymus multisetus*, was not present until after the burn treatments began, and this species was rarely observed in the control plots (one plot in 2011). Although highly variable in the early years of the study, the high burn frequency treatment maintained a high amount of native grass cover in the center 0.36m^2 of the plot, followed by the medium burn frequency treatment (Fig. 5b), while native grass cover in the control and low burn frequency treatments declined over time. The amount of native grass cover is primarily due to *P. secunda* cover and is consistent with the effects observed on mean *P. secunda* number (Fig. 2; Table 2). The amount of native grass cover in the high and medium frequency burn treatments remained significantly higher than the control and low frequency burn treatments after the completion of the burn treatments in 2011 except for in 2015.

The mean number of native forb species in the high burn frequency treatment was significantly lower than the control or medium burn frequency treatment in 2008, 2010, 2014 and 2015 (Fig. 6a). On the other hand, the medium burn frequency treatment had significantly higher numbers native forb species than the control or high burn frequency treatment in 2010 and 2014. The control and low burn frequency treatment had somewhat intermediate numbers of native forb species. This pattern is similar in the native forb cover (Fig. 6b). The number of native forb species and total native forb cover remained low in the high burn frequency treatment plots through 2015, with the medium burn frequency remaining the highest. Although there is a high amount of variation in both native forb number and cover, the positive effect of the medium burn treatment is most apparent two to three years following the burn treatment (i.e. 2004 after the initial 2001 burn; 2010 after the 2005/2006 burns and 2014 and 2015 following the final burn in 2011). Unlike *P. secunda* density in which Block 1 was responsible for the strong block effect observed at the end of the study in 2015, the native forb block effects observed throughout the study were primarily due to Block 5 (Fig. 1a). This block had significantly more numbers of native forb species and native forb cover compared to the remaining blocks.

Mean exotic species number was highly variable over the course of the study (Fig. 7a). The only significant treatment effect was observed in 2014, when the high burn frequency treatment had the lowest number of exotic species compared to the control, which had the highest number. The exotic grass cover data was less variable, with the control and low burn frequency plots having significantly higher amounts of exotic grass cover in most years, with the medium and high frequency plots having the lowest (Fig. 7b).

There was a low number of exotic forb species present in all treatments (Fig. 8a), and there does not appear to be a burn treatment effect. However, the high and medium burn frequency treatments had the highest amount of exotic forb cover through 2011 (Fig. 8b), primarily due to high *Erodium cicutarium* cover. Years with observed block effects in the exotic grass and exotic forb ANOVAs were few, with no clear pattern emerging among blocks.

Discussion

High frequency fire maintained target densities of *P. secunda* and increased native grass cover while medium burn frequencies maintained a lower density of *P. secunda* and maximized native forbs. These results are consistent with long-term simulations showing resprouting species increase with fire frequency, and seed-dependent species (such as native annual forbs) may increase under medium-frequency fire regimes (Lloret et al. 2003). Both high and medium burn frequencies reduced exotic grass cover, therefore we found that regular burning is a viable approach for conserving biodiversity, maintaining foundation species, and controlling exotic species. Our results support those of others from perennial grass communities in biomes with alternating wet and dry seasons (Meyer & Schiffman 1999; Klinger & Messer 2001; Dyer 2002, 2003; Bond & Archibald 2003; Bartolome et al. 2004; Marty et al. 2005; Moyes et al. 2005; Musil et al. 2005; van Wilgen et al. 2007; Almeida-Neto et al. 2010) and adds to them in illustrating the longevity of treatment effects when long-term (11-year) repeated burning ends.

Annual late-spring prescribed burns (the high burn frequency treatment) maintained the initial number of *P. secunda* plants and allowed for significant expansion of *P. secunda* by the final burn in 2011. Prescribed burns conducted roughly every three years (the medium burn frequency treatment) also maintained a substantial number of *P. secunda* plants and resulted in significant expansion, whereas the low burn frequency and control treatments resulted in a decline in *P. secunda* number and little expansion. Native grass cover remained high in the medium and high burn frequency treatments over the course of the study, and dropped in the low burn frequency and control treatments. *Poa secunda* was the major contributor to the native grass cover, with the native annual grass *Festuca microstacys* present in most years. One native perennial grass species, *Elymus elymoides*, appeared in burn treatment plots only after the burn treatments began. *Stipa pulchra*, a native perennial grass that also forms the foundation of California's grassland, also responds positively to burns conducted at dormancy, which for this species is late summer (Dyer 2002, 2003; Moyes et al. 2005). In one of the few studies that that evaluated late-spring burning effects on *S. pulchra*, mortality was higher in burned plots compared to unburned plots (Marty et al. 2005). Timing burns to fuel loads and plant phenology is essential to meet specific conservation objectives in grassland systems where wet and dry seasons alternate (Anderson et al. 1998; Rossiter et al. 2003). The timing of our prescribed burn (late-spring) complemented the early spring phenology of *P. secunda*, as this species is typically dormant by the time of the burns.

We report a positive response to burning by *P. secunda* that appears to be greater than that reported for other perennial grasses. However, most of these studies were conducted over shorter time periods, allowing climate and/or microhabitat to exert a stronger influence on the results (e.g. Driscoll et al. 2010). For example, drought can drive seedling recruitment (Hatch et al. 1991) and survival (Dyer et al. 1996) more than fire, and perennial grass cover can also be influenced more by slope (due to likely differences in soil type and water holding capacity) than fire (Hatch et al. 1999; Bartolome et al. 2004). After the conclusion of the burn treatments in 2011, we also observed effects we attributed to climate or microhabitat. The extreme California drought of 2012 through 2015 resulted in very low cover of annual grasses, which may have facilitated the maintenance of *P. secunda* numbers in the control, low and medium burn frequency treatment plots, and may have exacerbated intraspecific competition in the high frequency burn treatment plots. Very high numbers of *P. secunda* plants resulted in a *P. secunda* decline in these plots. In addition, significantly more *P. secunda* plants were observed in Block 1 in 2015. Block 1 is a bit more north facing (and presumably more mesic) and steeper than the other blocks, a microhabitat we have observed *P. secunda* to prefer at Site 300. Microhabitat effects may be masked by the prescribed burns, and only obvious in the absence of the burns (Klinger and Messer 2001). The length of our study and the repetition and frequency of the prescribed burns was able to largely overcome the influence of climate and microhabitat.

Because four years of data were collected after the last prescribed burn, we can determine the longevity of treatment effects when management through repeated burning ends. While the number of *P. secunda* plants in the high burn frequency treatment remained higher than controls, it began to decline after the last prescribed burn in

2011, indicating these very high *P. secunda* densities are only maintained by burning annually. Others have suggested that the effects of burning in perennial grasslands are transient (Hatch et al. 1991; Dyer et al. 1996; Lavorel 1999; Rossiter et al. 2003). However, the fact that *P. secunda* numbers did not decline in the control, low and medium burn frequency treatments after the final burn suggests that these densities are sustainable in the face of less frequent fire and possibly severe drought, particularly in suitable habitat. In addition, evidence from plots we established in February 1993 (Carlsen et al. 2000) and not actively managed further suggests that moderate densities of *P. secunda* are sustainable. The density of *P. secunda* in plots established through planting has remained significantly greater up to seventeen years after establishment than in plots of exotic annual grasses whose density was established by manual thinning and removal of all *P. secunda* (Carlsen et al. 2012, unpublished data).

Native forbs naturally occurring at our site also benefited from the medium burn frequency, with the highest cover and number of native forb species observed in this treatment, whereas the high burn frequency resulted in the lowest number of native forb species and lowest native forb cover in most years of the study. Conversely, the high and medium burn frequency treatments had the highest amount of exotic forb cover, due primarily to high cover of *Erodium cicutarium*. This species commonly increases after burns, even when these burns successfully reduce other exotic forb species (Pollak and Kan 1998; DiTomaso et al. 2006; Marty et al. 2015). Local native forbs at our site were also sensitive to microhabitat. When block effects were observed throughout the course of the study (Fig. 6a and b), the number of native forb species and native forb cover was significantly greater in Block 5 (Fig. 1a). Block 5 is higher in elevation with a more southerly aspect, and thus presumably drier and may have lower soil fertility than the remaining blocks. In California, native forbs may be more suited to low fertility or drier soils compared to exotic annuals (Seabloom et al. 2003), and thus better able to take advantage of the reduced competition provided for by these soil types in combination with fire (Harrison et al. 2003; Klinger & Messer 2001).

In contrast to *P. secunda* and resident co-occurring native forbs, the seeded population of the rare annual forb *A. grandiflora* performed poorly in the burn treatments and best in the control. The high burn frequency treatment maintained a density of *P. secunda* that we found to be beneficial to *A. grandiflora* (Carlsen et al. 2000), suggesting the burn itself was detrimental to the species. The reduction in *A. grandiflora* number in 2007 after the control plots had recently burned provides further evidence that *A. grandiflora* is very sensitive to the immediate impacts of fire. Our previous work showed *A. grandiflora* seeds are sensitive to high temperatures (unpublished data). Thus, any seeds present on the ground surface or in the inflorescence at the time of the burns were subject to direct mortality.

We have also shown prescribed burns to facilitate seed predation (Espeland et al. 2005). Thus, the presence of frequent fire likely increased the risk of predation and seed mortality, making it difficult for *A. grandiflora* to build a protective seed bank (as in Driscoll et al. 2010). The high percentage of bare ground cover in the high frequency burn treatment may have also created an unfavorable microenvironment for germination. Although bare ground has been shown to benefit native plants (Rice 1985, 1989; Bergelson 1990; Meyer & Schiffman 1999), the benefit has not typically been studied using fire to create the bare ground. Germination and emergence can be reduced by fire due to the formation of a water-repellent layer beneath the soil surface (Biswell 1989) and the resulting loss of cover can result in soil compaction, higher soil temperatures, and lower soil water content (Bennett et al. 2002; Snyman 2002, 2003). Burning can be a benefit by reducing competitive pressure on *A. grandiflora* resulting in higher fecundity. Four years post-burn, *A. grandiflora* plants that were present in the medium and high burn frequency plots were large and robust, although numbers were still low. This balancing act between low establishment after burns but increased fecundity from decreased competition has been found for other forbs (e.g. Gillespie & Allen 2004). We observed significant enhancement of native forb cover at our site two to four years after the medium burn frequency treatment, suggesting an initial detrimental impact of the burn followed by a period when the native forbs took advantage of the reduced exotic grass cover. Klinger and Messer (2001) also found fire to significantly increase native forbs the first two years after a burn in a California coastal grassland site, although Marty et al. (2015) found native plant diversity to increase the first year after a spring burn in a California interior grassland site, but was not different in subsequent years. These differing responses may be due to differences in the initial species composition between coastal and interior grasslands and their response to fire. Additional evidence that *A. grandiflora* may benefit from some burning comes from the Site 300 native site. Here, four *A. grandiflora* plants were observed in 2006, whereas no plants were observed in 2005 just prior to the 2005 wildfire (Carlsen et al. 2012). An intensive seeding program carried out over many years would likely be required to establish an *A. grandiflora* population that could take advantage of periodic burning, building a protective seed bank buried to a sufficient depth to protect the seeds from both fire and predation, allowing the species to take advantage of the more open space in the years between burns.

It is likely that in many of the grasslands of the Inner South Coast Ranges of California, *P. secunda* is the primary foundation perennial grass species. Managing *P. secunda* with annual burning would significantly increase the cover of this species and reduce the amount of exotic annual grass cover. However, such high frequency burning is likely to be detrimental to the local native annual flora. Less frequent burning (on the order of every three years) has the potential to maintain a high cover of *P. secunda* while promoting many of the local native annual forbs. This result may depend upon the lack of intensive ungulate grazing at our site. Others working in grazed systems found that regular burning every three years improves biodiversity in the short term, but in the long-term this fire interval increases desertification (Bond & Archibald 2003; van Wilgen et al. 2007). While not all native forbs will benefit equally from medium frequency late-spring burning, detailed knowledge of the life history and phenology of the local native species should allow for the creation of a beneficial prescribed fire regime. Such an active management regime could also help slow the steady increase of exotic annual grasses. Our data suggests solely focusing on foundation perennial grass species without considering other local native species life history and phenology may be detrimental to overall native flora diversity.

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Table 1 Summary of prescribed burns and wildfires at the study area.

		Year											
		2001	2002	2003	2004	2005	2005 wildfire	2006	2007	2008	2009	2010	2011
Number of Prescribed Burns Planned By Treatment													
Control	0												
Low	2	burn											burn
Med	4	burn			burn					burn			burn
High	11	burn	burn	burn	burn	burn		burn	burn	burn	burn	burn	burn
Date of Burns		July 18	June 20	June 30	June 6	June 11	July 18	June 13	June 4	June 24	June 9	June 22	June 17
Number of Burns Actually Occurring by Plot													
D (Control)	1							burn					
G (Control)	1						burn						
I (Control)	1						burn						
M (Control)	1						burn						
S (Control)	1						burn						
C (Low)	3	burn						burn					burn
H (Low)	3	burn					burn						burn
J (Low)	3	burn					burn						burn
N (Low)	3	burn					burn						burn
Q (Low)	3	burn					burn						burn
A (Medium)	5	burn			burn			burn		burn			burn
F (Medium)	5	burn			burn		burn			burn			burn
L (Medium)	5	burn			burn		burn			burn			burn
P (Medium)	5	burn			burn		burn			burn			burn
R (Medium)	5	burn			burn		burn			burn			burn
B (High)	11	burn	burn	burn	burn	burn		burn	burn	burn	burn	burn	burn
E (High)	11	burn	burn	burn	burn	burn		burn	burn	burn	burn	burn	burn
K (High)	11	burn	burn	burn	burn	burn		burn	burn	burn	burn	burn	burn
O (High)	12	burn	burn	burn	burn	burn	burn	burn	burn	burn	burn	burn	burn
T (High)	11	burn	burn	burn	burn	burn		burn	burn	burn	burn	burn	burn

Table 2 Effect of burn treatments on the mean number of *Poa secunda* plants in the center $1m^2$ and in the entire $4m^2$ plot.

Treatment	Pretreatment *P. secunda* number[a]		*P. secunda* number entire $4m^2$ plot											*P. secunda* number center $1m^2$		
	2000	2001	2002	2003	2004	2005	2006	2007	2010	2011	2013	2014	2015	2008	2009	2012
Control	31.6 ± 2.0	22.0 ± 2.6	20.6 ± 2.9 •	20.6 ± 4.2 •	8.0 ± 1.9 ***	12.0 ± 1.9 ***	9.2 ± 2.2 ***	12.6 ± 3.9 ***	4.2 ± 1.2 ***	4.6 ± 3.0 ***	15.6 ± 4.8 ***a	10.2 ± 2.5 ***	14.2 ± 5.2 ***	6.0 ± 2.3 ***	3.2 ± 1.2 ***	3.8 ± 1.5 ***b
Low Burn Frequency	29.2 ± 0.5	20.0 ± 2.3	28.0 ± 3.0	24.0 ± 3.1	19.6 ± 2.7	17.4 ± 2.2 *	13.8 ± 1.9 **	11.6 ± 2.1 ***	2.6 ± 1.3 ***	2.4 ± 1.1 ***	10.8 ± 1.9 ***a	14.0 ± 3.7 **	23.6 ± 7.0	6.4 ± 2.2 ***	1.2 ± 0.5 ***	4.2 ± 1.7 ***a
Medium Burn Frequency	30.0 ± 0.9	23.2 ± 1.5	31.8 ± 1.3	26.8 ± 2.4	21.8 ± 1.3	20.0 ± 3.0	30.6 ± 5.0	24.0 ± 3.1	21.8 ± 3.9	13.8 ± 5.0 •	41.8 ± 4.0 a	36.4 ± 4.5	52.8 ± 9.2 ***	17.8 ± 3.5	13.8 ± 2.9 •	18.6 ± 2.0 b
High Burn Frequency	26.2 ± 5.1	21.6 ± 3.2	27.6 ± 4.7	26.4 ± 5.1	27.2 ± 3.1	31.5 ± 0.6	31.2 ± 4.6	46.8 ± 8.9	60.8 ± 14.2	109.2 ± 27.4 ***	88.2 ± 24.3 **a	77.6 ± 21.8 *	70.4 ± 15.5 •	27.2 ± 6.6	23.0 ± 6.6	33.2 ± 6.3 b

[a] Number of *P. secunda* plants that had established in the center $1m^2$ of the plot by the spring census of 2000 and 2001 from the 33 plants originally planted in 1999, representing both the number of *P. secunda* plants in the center $1m^2$ and in the larger $4m^2$ plot. The first prescribed burn was July 18, 2001, when all treatments except the control were burned.

Treatments shaded in gray were burned the previous spring.

Error is one standard error, n=5 except 2005 high burn frequency treatment, where n=4.

Mean *P. secunda* numbers in years 2012 and 2013 with different letters are significantly different at $p<0.05$.

• Significantly different from *P. secunda* pretreatment number in year 2000 at $p < 0.1$.

* Significantly different from *P. secunda* pretreatment number in year 2000 at $p < 0.05$.

** Significantly different from *P. secunda* pretreatment number in year 2000 at $p < 0.01$.

*** Significantly different from *P. secunda* pretreatment number in year 2000 at $p < 0.001$.

Table 3 Mean height of *Amsinckia grandiflora* plants present per plot by burn treatment.

	Control			Low Burn Frequency			Medium Burn Frequency			High Burn Frequency		
Year	Height cm	Plot n[d]	Range of plant n/plot[e]	Height cm	Plot n[d]	Range of plant n/plot[e]	Height cm	Plot n[d]	Range of plant n/plot[e]	Height cm	Plot n[d]	Range of plant n/plot[e]
2000	17.2 ± 0.9	5	6–8	18.2 ± 0.9	5	7–9	14.5 ± 1.5	5	5–8	16.4 ± 1.7	5	6–10
2001	17.2 ± 1.2	5	2–26	13.8 ± 2.2	4	1–19	14.4 ± 1.0	4	3–10	15.5 ± 0.9	5	6–24
First Burn June 2001: Low, Medium and High Burn Treatment Plots												
2002	17.8 ± 2.8	5	2–14	9.7 ± 0.6•	3	1–5	3.0·	1	1	13.3 ± 1.3	3	2–10
2003[c]	19.2 ± 0.2	2	2–8	14.5 ± 2.5	2	2–8	13.1 ± 0.7	4	3–7	10.5 ± 0.8•	4	1–3
2004	19.5 ± 1.7	3	3–4	13.3 ± 3.3	2	1	12.0 ± 0.5	2	1	NA	0	0
2005[c]	23.3 ± 3.2	5	2–18	19.4 ± 3.2	4	1–25	16.1 ± 2.9	5	1–5	13.0 ± 4.0	2	1
July 2005 Wildfire												
2006	19.2 ± 1.2	3	4–15	13.2 ± 2.9	3	1–10	10.6 ± 0.6	2	1–2	NA	0	0
2007[b,c]	16.2 ± 2.2	5	1–16	17.1 ± 2.7	5	5–21	14.7 ± 1.5	5	2–22	13.3 ± 0.9	5	3–25
2008	17.4 ± 2.9	4	2–12	21.4 ± 5.5	3	4–6	20.4 ± 1.9	3	2–6	10.0 ± 0.0	1	4
2009	27.5 ± 1.0	2	1	21.0 ± 5.0	2	1–2	13.3 ± 1.3	4	2–3	15.5 ± 4.0	2	1–6
2010[a,c]	15.7 ± 0.8	5	2–32	15.1 ± 2.0	5	4–31	12.3 ± 0.6	5	4–22	12.1 ± 2.1·	4	1–6
2011	30.0 ± 1.0	4	1–32	30.0 ± 2.5	3	2–32	42.0	1	1	21.5·	1	1
Final Burn June 2011: Low, Medium and High Burn Treatment Plots												
2012	16.7 ± 0.6	4	2–57	12.9 ± 1.7	2	5–20	NA	0	0	10.3	1	1
2013[a,c]	17.2 ± 1.1	5	11–150	16.9 ± 0.6	5	3–46	14.4 ± 1.2	5	4–18	13.6 ± 1.7*, •L	5	6–25
2014	16.5 ± 2.9	5	1–26	19.2	1	7	17.5 ± 1.7	2	2–2	14.6	1	3
2015	29.6 ± 2.8	2	9–10	NA	0	0	32.1	1	3	64.5	1	1

Significance Levels: • = p<0.1, * = p<0.05. Significance levels with no letter indicate compared to control treatment. Significance levels with letters indicate compared to: L = Low burn frequency, M = Medium burn frequency, and H = High burn frequency treatments.

[a] Block effects detected at p<0.05

[b] Block effects detected at p<0.1

[c] Plots were seeded the previous fall.

[d] Number of plots that contained *A. grandiflora* plants.

[e] Range of the number of *A. grandiflora* plants in each plot.

Error is one standard error.

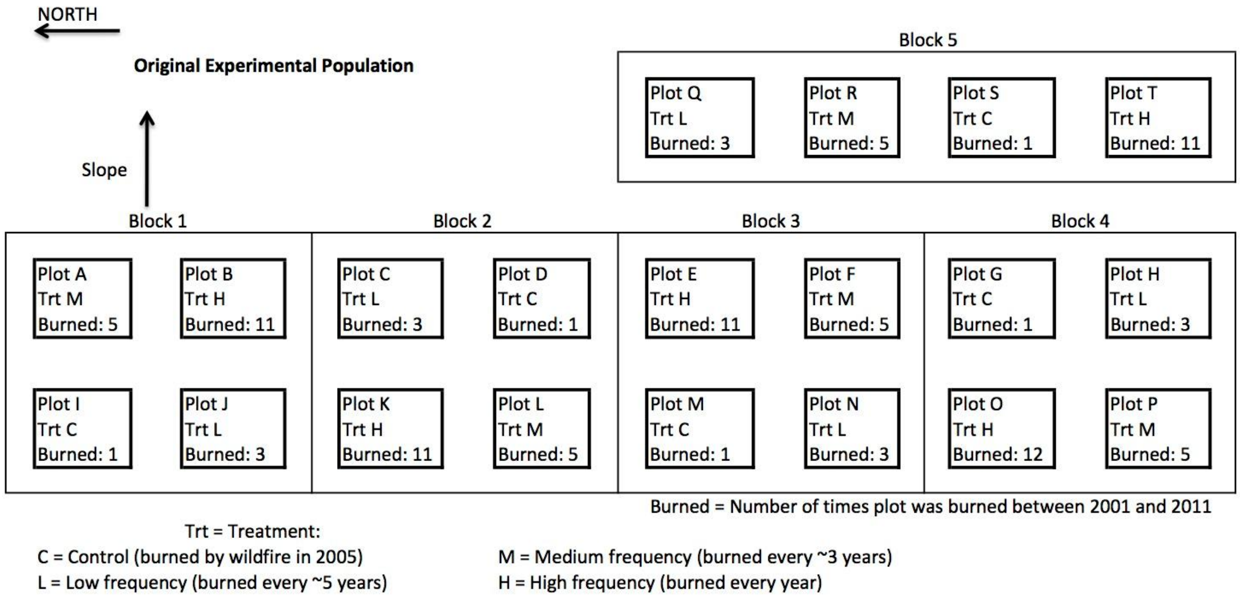
NA = Not applicable. No plants were present in any treatment plots.

Table 4 Mean branch number and robustness index of *Amsinckia grandiflora* plants present per plot by burn treatment.

	Control		Low Burn Frequency		Medium Burn Frequency		High Burn Frequency	
Year	Branch number	Robustness Index	Branch number	Robustness Index	Branch number	Robustness Index	Branch number	Robustness Index
2000	2.1 ± 0.28	39.9 ± 6.47	2.5 ± 0.37	51.0 ± 8.48	1.7 ± 0.29	26.9 ± 6.52	2.5 ± 0.19	46.1 ± 6.76
2001	1.0 ± 0.00	18.1 ± 1.69	1.0 ± 0.04	14.9 ± 2.58	1.0 ± 0.00	14.4 ± 1.00	1.0 ± 0.00	15.5 ± 0.94
First Burn June 2001: Low, Medium and High Burn Treatment Plots								
2002	1.1 ± 0.05	16.8 ± 2.39	1.0 ± 0.00	9.7 ± 0.60	1.0	3.0	1.1 ± 0.07	14.2 ± 2.19
2003[c]	1.0 ± 0.00	19.2 ± 0.15	1.0 ± 0.00	13.5 ± 2.15	1.0 ± 0.00	13.1 ± 0.71	1.0 ± 0.00	10.5 ± 0.84*
2004	1.3 ± 0.20	26.0 ± 4.52	1.0 ± 0.00	13.3 ± 3.25	1.0 ± 0.00	12.0 ± 0.50	NA	NA
2005[c]	1.3 ± 0.16	32.1 ± 8.07	1.2 ± 0.08	24.0 ± 5.77	1.1 ± 0.05	17.4 ± 5.61	1.0 ± 0.00	13.0 ± 4.00
July 2005 Wildfire								
2006	1.3 ± 0.33	26.3 ± 6.77	1.1 ± 0.07	14.8 ± 3.88	1.3 ± 0.25	14.4 ± 4.38	NA	NA
2007[c]	1.3 ± 0.20	23.0 ± 6.48	1.2 ± 0.09	21.3 ± 5.42	1.1 ± 0.03	16.7 ± 2.25	1.1 ± 0.07	15.3 ± 1.26
2008	1.3 ± 0.19	26.8 ± 7.99	1.9 ± 0.59	47.2 ± 23.87	1.4 ± 0.29	31.4 ± 7.46	2.0	23.0
2009	2.0 ± 1.00	56.0 ± 29.50	1.0 ± 0.00	21.0 ± 5.00	1.0 ± 0.00	13.3 ± 1.27	1.0 ± 0.00	15.5 ± 4.02
2010[c]	1.1 ± 0.09[a]	18.6 ± 2.38[a]	1.2 ± 0.19[a]	21.1 ± 7.21[a]	1.0 ± 0.00[a]	12.3 ± 0.63[a]	1.3 ± 0.25[a]	17.4 ± 7.24[a]
2011	1.4 ± 0.26	46.0 ± 12.39	2.3 ± 0.65	83.3 ± 28.98	3.0 ± 0.00	126	1.0	21.5
Final Burn June 2011: Low, Medium and High Burn Treatment Plots								
2012	2.4 ± 0.44	41.9 ± 7.28	2.6 ± 0.77	37.5 ± 17.68	NA	NA	1.0	10.3
2013[c]	1.1 ± 0.04[b]	20.2 ± 2.40[a]	1.1 ± 0.04[b]	19.5 ± 1.61[a]	1.1 ± 0.04[b]	16.3 ± 1.73[a]	1.2 ± 0.10[b]	16.7 ± 3.66[a]
2014	1.0 ± 0.00	16.5 ± 2.87	1.0	19.2	1.0 ± 0.00	17.5 ± 1.65	1.0	14.6
2015	2.7 ± 0.70	92.0 ± 30.05	NA	NA	2.7	97.8	3.0	193.5

See Table 4 for number of plots with plants present for each treatment, and range of the number of plants per plot.
Robustness Index = height (cm) * branch number.
Significance Levels: * = Different from control treatment at $p<0.05$.
[a] Block effects detected at $p<0.05$
[b] Block effects detected at $p<0.1$
[c] Plots were seeded the previous fall
Error is one standard error. Values with no standard error indicate plants were present in a single treatment plot.
NA = Not applicable. No plants were present in any treatment plots.

a)



b)

c)

Fig. 1 Study site: a) layout of experimental plots; b) burning of high frequency plots; and c) high frequency plots at the completion of burning. The original *Amsinckia grandiflora* experimental population is located in the upper left of Figure 1c, enclosed in metal flashing.

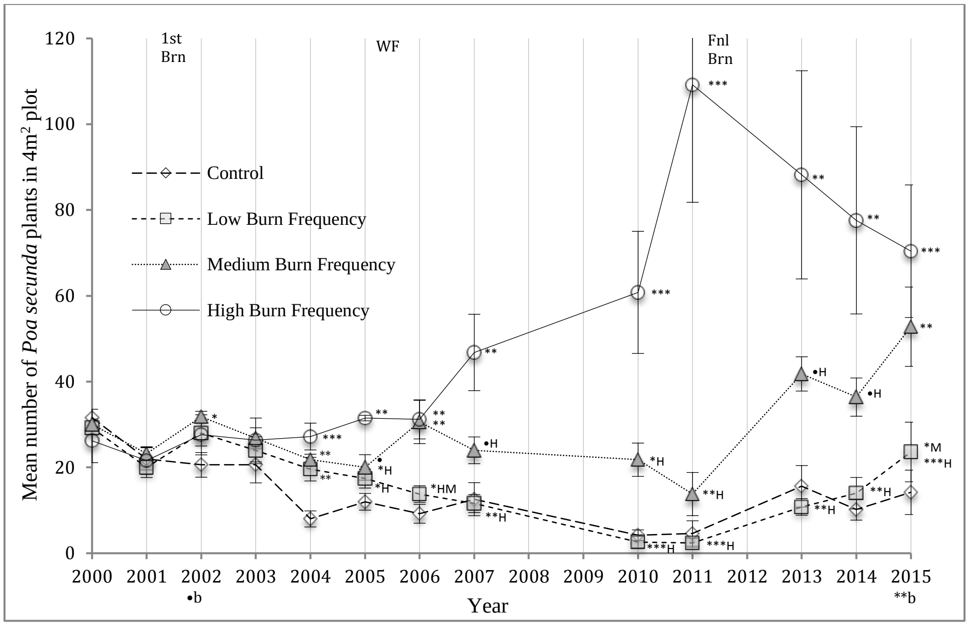


Fig. 2 Burn frequency effect on the mean number of *Poa secunda* plants in the $4m^2$ plot. Error bars are one standard error, n=5 except for the 2005 high burn frequency treatment, where n=4. Significance levels: • = p<0.1, * = p<0.05, ** = p<0.01, *** = p < 0.001. Significance levels without letters indicate the particular burn treatment compared to control treatment. Significance levels with letters indicate burn treatment compared to: L = low burn frequency, M = medium burn frequency, and H = high burn frequency treatment. Years with significant block effects are indicated by the letter b under the given year. Notes: 1st Brn = first burn treatments on low, medium and high burn frequency plots. WF = July 2005 wildfire. Fnl Brn = final burn treatments on low, medium and high burn frequency plots.

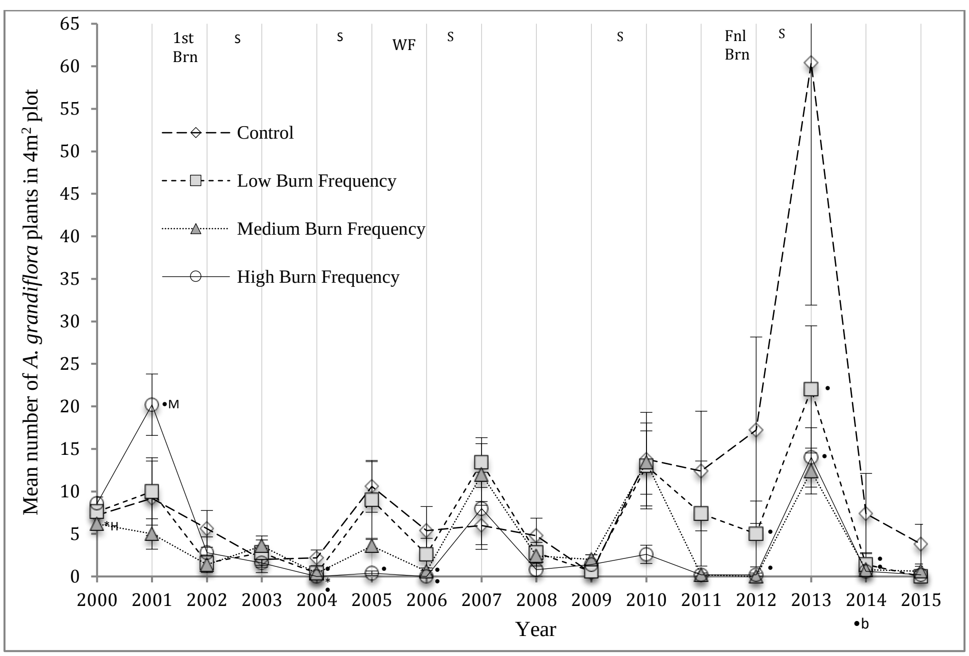


Fig. 3 Burn frequency effect on the mean number of *Amsinckia grandiflora* plants in the $4m^2$ plot. S = fall seeding of *A. grandiflora*. Error bars are one standard error, n=5. See Fig. 2 for significance levels and notes.

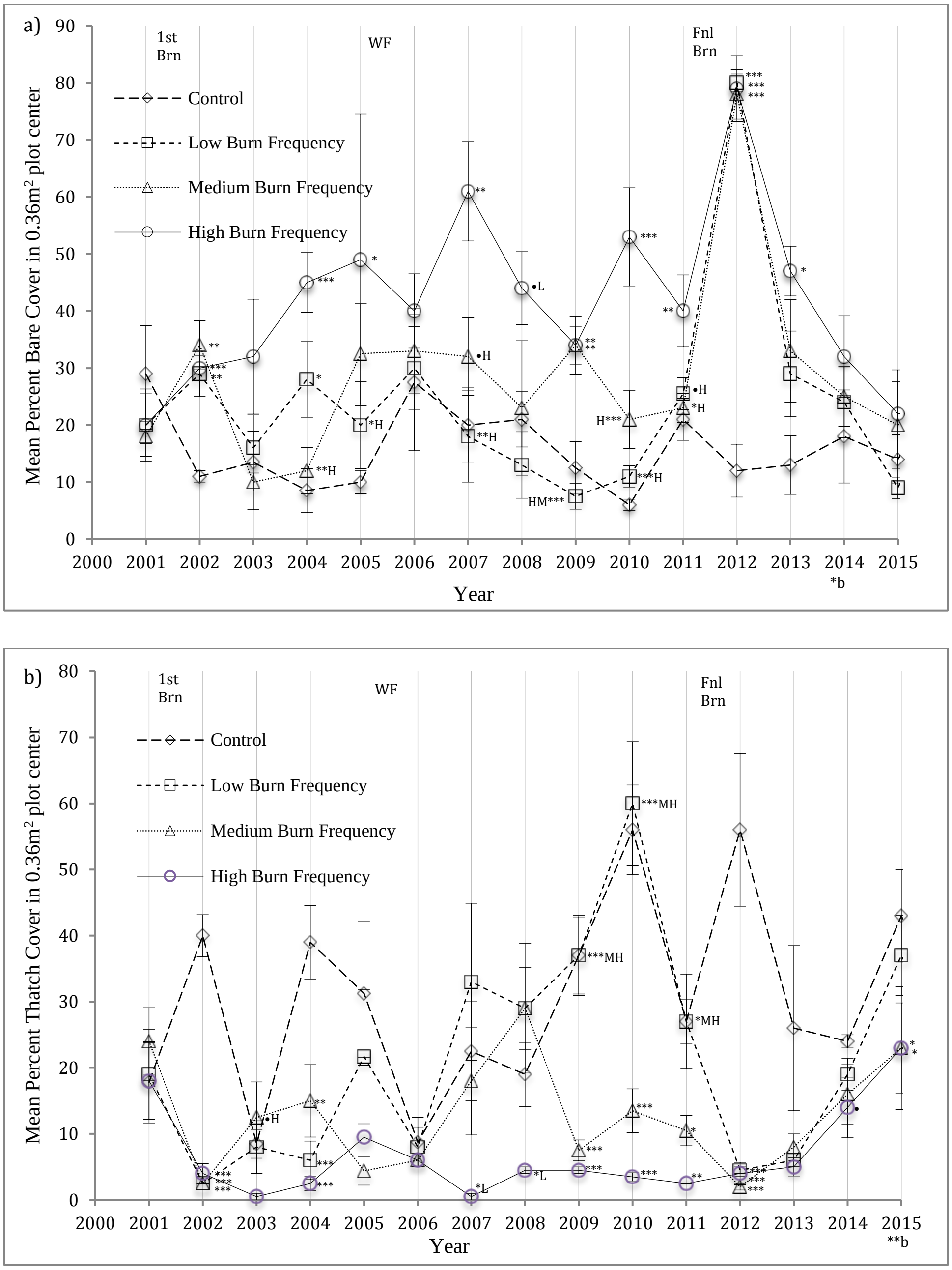
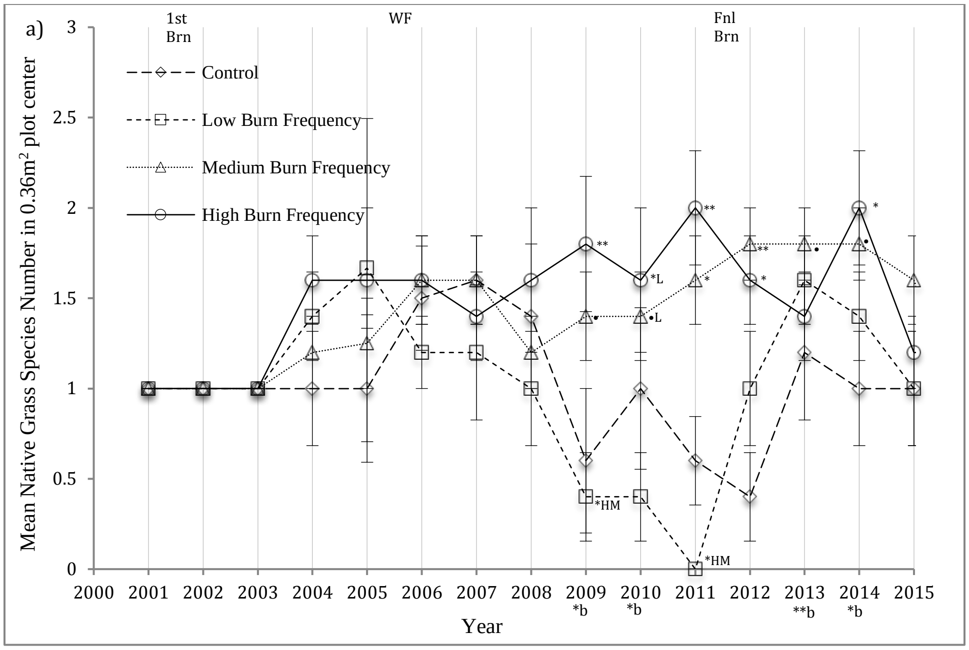


Fig. 4 Burn frequency effect on a) mean percent bare ground cover and b) mean percent thatch cover in the 0.36m^2 plot center. Error bars are one standard error, n=5 except for control treatment in 2006, where n=4. See Fig. 2 for significance levels and notes.



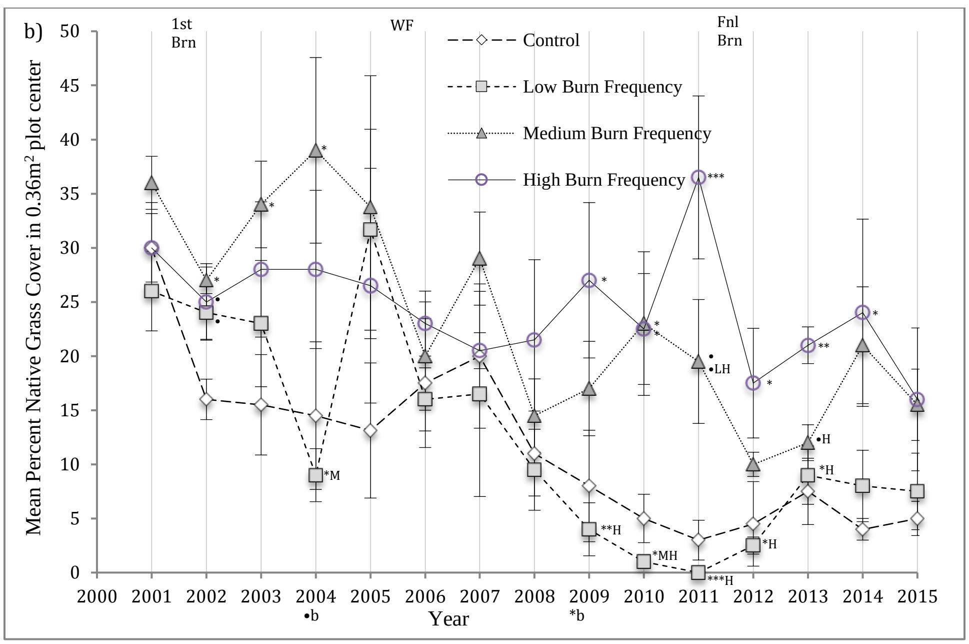
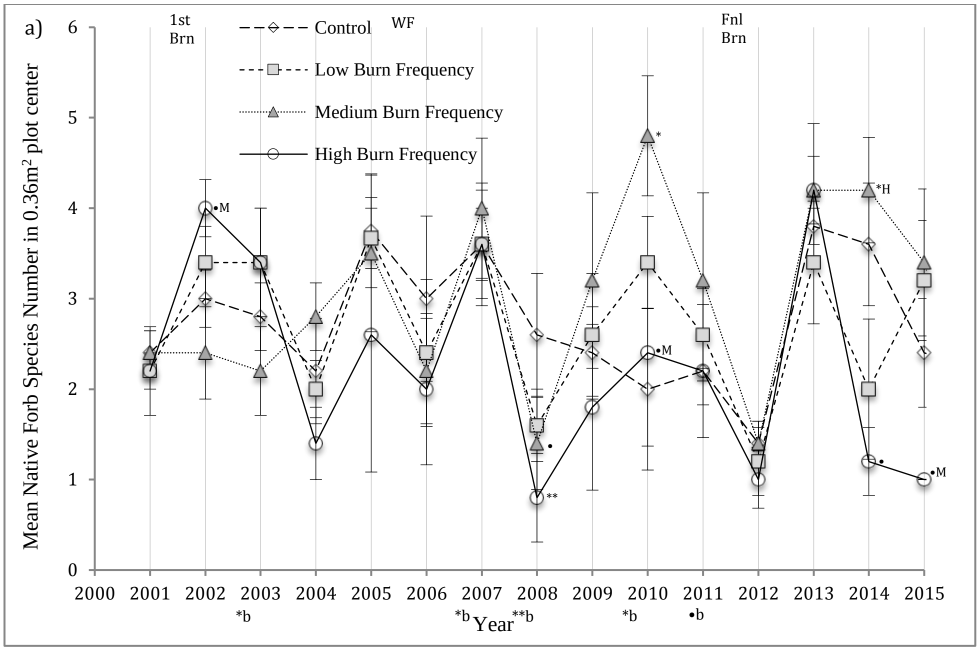


Fig. 5 Burn frequency effect on a) mean native grass species number and b) mean percent native grass cover in the 0.36m² plot center. Error bars are one standard error, n=5 except for control treatment in 2006, where n=4. See Fig. 2 for significance levels and notes.



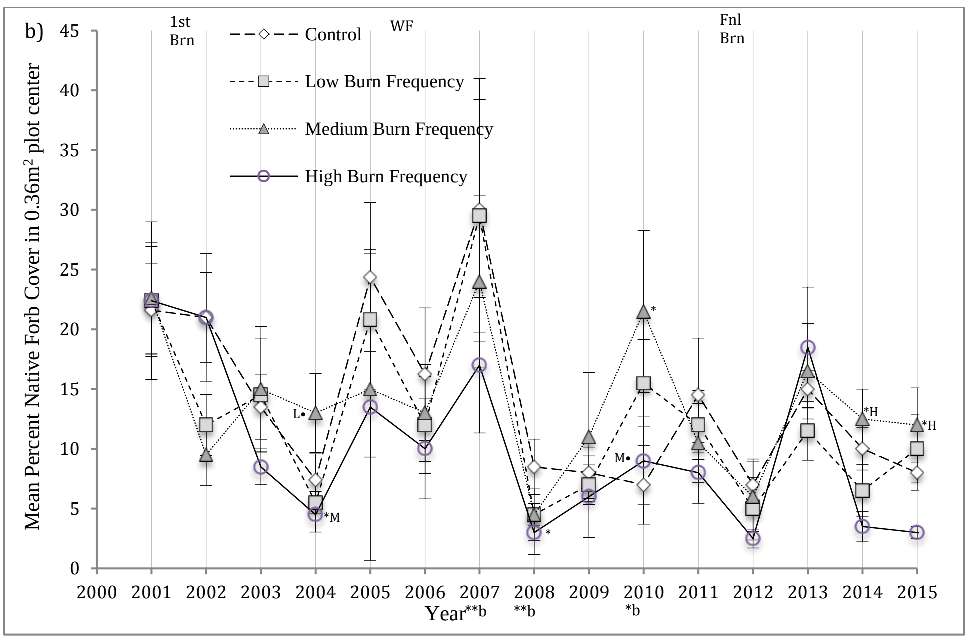


Fig. 6 Burn frequency effect on a) mean native forb species number and b) mean percent native forb species cover in the $0.36m^2$ plot center. Error bars are one standard error, n=5 except for control treatment in 2006, where n=4. See Fig. 2 for significance levels and notes.

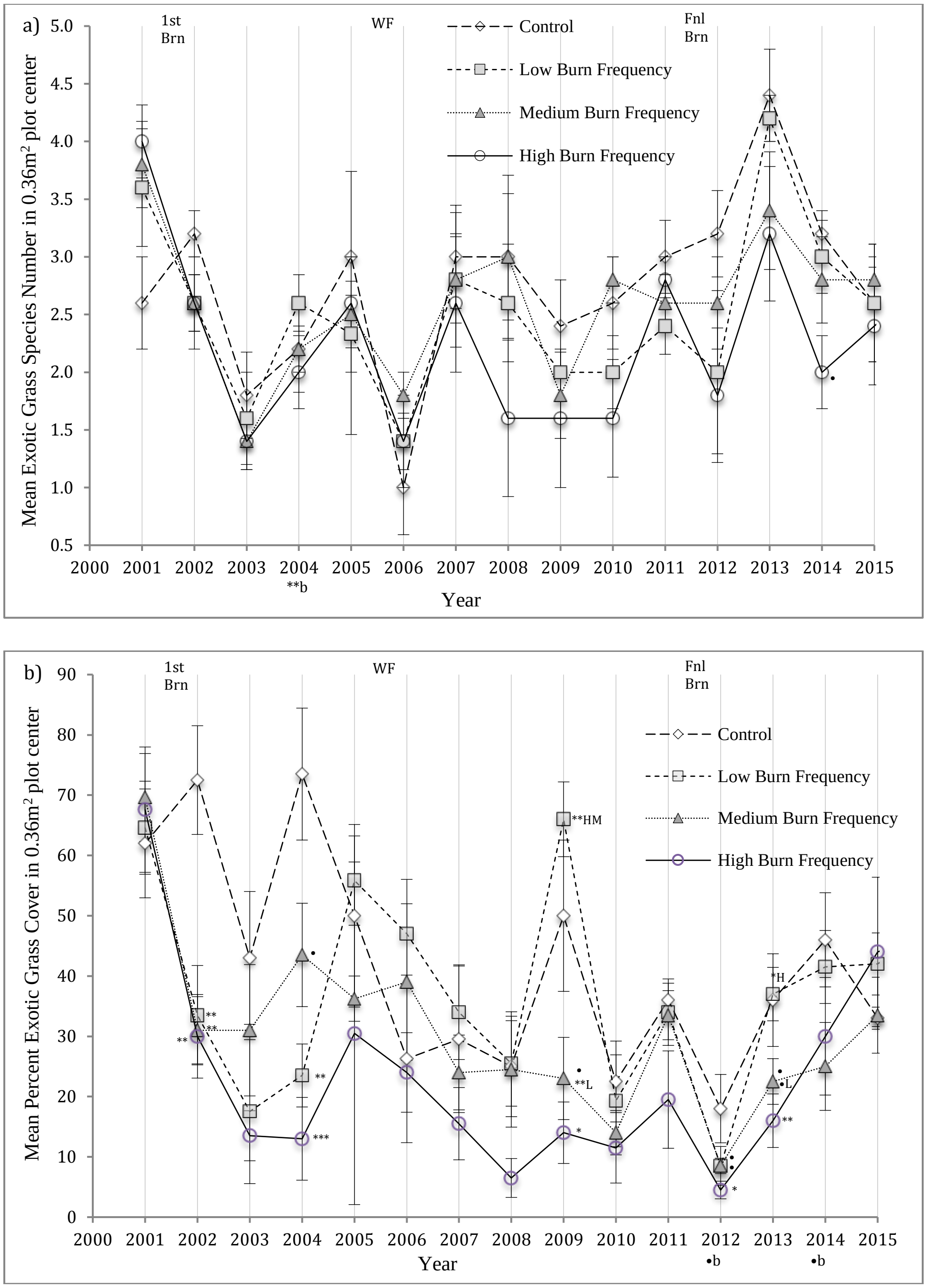
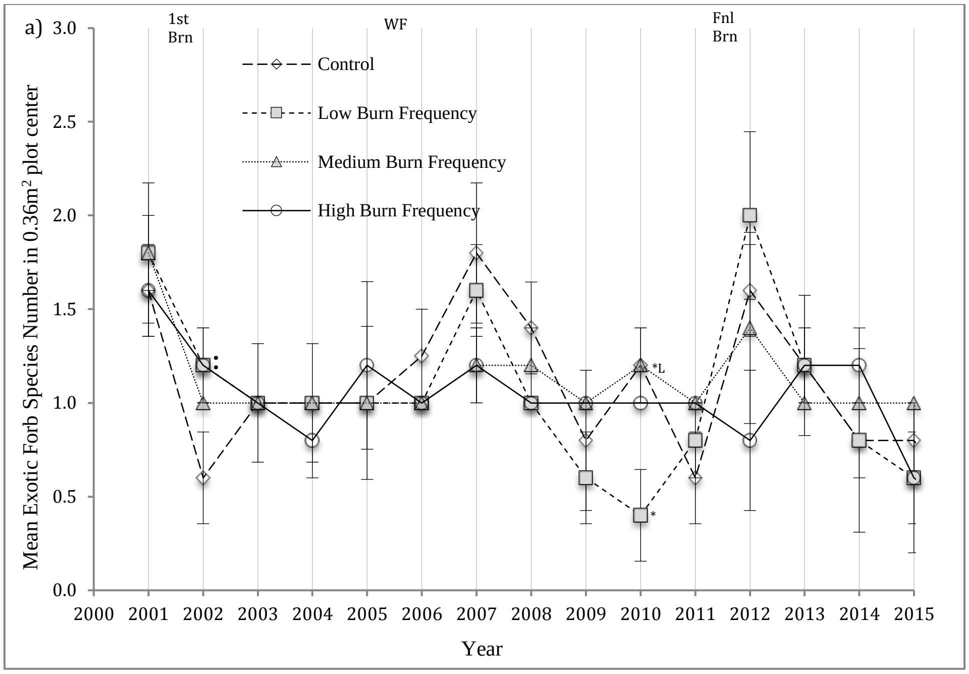


Fig. 7 Burn frequency effect on a) mean exotic grass species number and b) mean percent exotic grass cover in the 0.36m^2 plot center. Error bars are one standard error, n=5 except for control treatment in 2006, where n=4. See Fig. 2 for significance levels and notes.



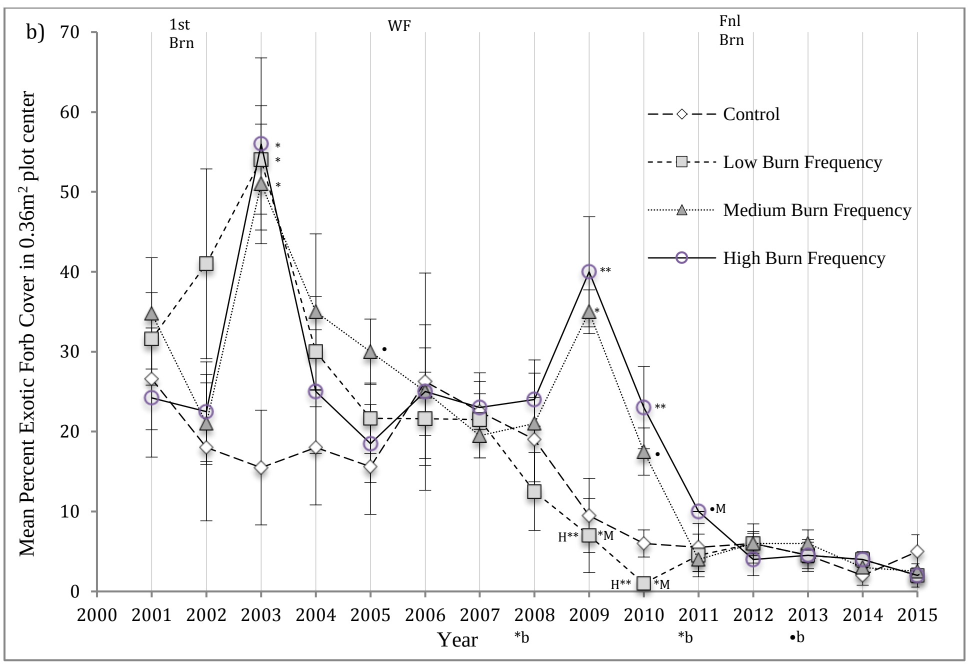


Fig. 8 Burn frequency effect on a) mean exotic forb species number and b) mean percent exotic forb cover in the 0.36m^2 plot center. Error bars are one standard error, n=5 except for control treatment in 2006, where n=4. See Fig. 2 for significance levels and additional notes.

Proffered potential cover photos. Late spring prescribed burns conducted on the pine bluegrass grasslands at Lawrence Livermore National Laboratory's Site 300.