Title

Invasive Plants, Fire Succession, and Restoration of Creosote Bush Scrub in Southern California

Author

Steers, Robert Jeremy

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Invasive Plants, Fire Succession, and Restoration of Creosote Bush Scrub in Southern California

A Dissertation submitted in partial satisfaction
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in

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by

Robert Jeremy Steers

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Dissertation Committee:
Dr. Edith B. Allen, Chairperson
Dr. Jodie S. Holt
Dr. Richard A. Minnich

The Dissertation of Robert Jeremy Steers is approved:

Jodie S Holt

Edith B. Allen

Committee Chairperson

University of California, Riverside

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ABSTRACT OF THE DISSERTATION

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by

Robert Jeremy Steers

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, December 2008
Dr. Edith B. Allen, Chairperson

Exotic annual plant species have invaded large regions of southern California deserts. Certain areas have been especially impacted, such as the western edge of the Colorado Desert adjacent to Mt. San Gorgonio, Banning Pass, and Mt. San Jacinto. This landscape is highly invaded due to relatively high winter rainfall compared to interior desert locales and elevated anthropogenic nitrogen deposition from urban areas to the west. Invasive annual grasses, in particular, are abundant here and have fueled disastrous wildfires in creosote bush scrub (CBS) since the 1970s. Invasive annual plants and fire pose major threats to the sustainability of CBS. The purpose of this dissertation was to document the impact of fire on CBS perennial and annual plant components. The ability of various restoration treatments to remove invasive annual plants and to promote native species in both burned and unburned contexts was also tested. Fire disturbance was shown to dramatically reduce shrub species richness and diversity. Fire also altered the vertical and horizontal vegetation structure of CBS. Total shrub density returned to unburned levels within a decade or two after fire due to recruitment by *Encelia farinosa*, a relatively small, short-lived shrub. Fire also increased the abundance of invasive annual plants. These changes may result in a vegetation type that is more fire prone than unburned CBS. Post-fire increases in invasive annual plants were also shown to decrease native annual plant cover and species richness. However, if invasive annuals were removed after fire, then native annual plant abundance and richness increased greatly, resembling unburned, pristine stands. Positive responses to invasive plant removal were also documented by native annual plant assemblages in unburned CBS. Clearly, the combination of invasive annual plants and fire has a large negative impact on native plant components of CBS. Fortunately, there is great potential to reestablish native annuals if invasives can be controlled.

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INTRODUCTION

In the last century, exotic annual plants such as grasses (*Bromus madritensis*, *Schismus barbatus*, and *Schismus arabicus*), red-stem filaree (*Erodium cicutarium*), and Sahara mustard (*Brassica tournefortii*) have invaded large areas of creosote bush scrub (CBS) vegetation in desert landscapes of California (Minnich 2008). In localized areas invasive grasses have been especially problematic for fueling wildfires (Brooks and Matchett 2006, Brooks and Minnich 2006). One such area is the western edge of the northern Colorado Desert and southern Mojave Desert in Riverside and San Bernardino Counties. Fire is thought to be relatively common here due to elevated precipitation and anthropogenic nitrogen deposition that promote invasive grasses, and also because of increased human ignitions due to its location within a major wildland urban interface (Brooks and Esque 2002, Brooks and Matchett 2006, Rao 2008). This specific landscape will be referred to as 'Fire Cluster 1' throughout this introduction, after the work of Brooks and Esque (2002).

Previous investigations of fire disturbance in CBS of this region have shown dramatic impacts to native perennial plants, especially long-lived species such as *Larrea tridentata* (O'Leary and Minnich 1981, Brown and Minnich 1986). These studies were the first of their kind to document the impacts of fire on CBS. Due to the novelty of fire at the time of these studies, post-fire vegetation was only recorded up to five years. A more recent study in central Arizona has documented burned CBS vegetation up to 21 years since fire (Alford et al. 2005), but site-specific conditions, such as shrub species composition, may limit inference to Fire Cluster 1. Examining some of the oldest burned CBS stands in Fire Cluster 1 (about 30 years since fire) would broaden our understanding of successional processes and help guide conservation efforts in this increasingly disturbed landscape.

Secondary succession to climax CBS is thought to take hundreds to thousands of years in the absence of invasive plants (Lovich and Bainbridge 1999, Vasek 1983). Because invasive annual plants can competitively interfere with native plants (Brooks 2000, DeFalco et al. 2007), successional timelines to climax could be lengthened or trajectories could be altered. In worst case scenarios, the grass-fire cycle (D'Antonio and Vitousek 1992) suggests that invasive annual grasses will self perpetuate in a positive fire feedback loop, ultimately resulting in type conversion to annual grassland. Measuring stands that have burned multiple times could validate this model. Finally, studies that focus on the impact of fire on species richness are critical since biodiversity is important for the conservation of these shrublands, and especially for developing restoration approaches. These are focal points of Chapter 1 of this dissertation, which surveyed CBS stands with differing ages since fire in addition to two stands that had experienced multiple fires.

Understanding the impact of fire on native annuals is especially imperative as this component of CBS is responsible for much of the vascular plant diversity these shrublands are known for (Jennings 2001). Little information exists regarding the impact of fire on native annuals (Cave and Patten 1984, Brown and Minnich 1986, Brooks 1999a, Brooks 2002) compared to perennials (O'Leary and Minnich 1981, McLaughlin and Bowers 1982, Brown and Minnich 1986, Bazzell 1988, Alford et al 2005, Brooks and Minnich 2006, among others). While invasive annual plants can displace native annuals from desert landscapes without the presence of wildfires, disturbances generally exacerbate plant invasions (*reviewed by* Hobbs and Huenneke 1992 and Theoharides and Dukes 2007). Therefore, it is important to determine if fire disturbance in CBS also promotes invasive plant abundance, as predicted (D'Antonio and Vitousek 1992, Brooks et al. 2004), especially since invasive species are so effective at displacing native annual plants (Minnich 2008). While not all areas of the desert are highly invaded like Fire Cluster 1, evaluating annual plant dynamics after fire in this location will be applicable in other localized areas impacted by fire since the same suite of invasive plants is found throughout much of the southwestern United States (Hickman 1996). Chapter 2 of this dissertation focuses on native annual plant dynamics after fires utilizing some of the same sites that were sampled for Chapter 1. Chapter 2 also uses the unburned stands to correlate soil variables, in two multiple linear regressions, with the dependent variables, invasive plant cover (%) and native annual species richness (m^{-2}). This was done since invasive plant abundance is usually greater in relatively fertile soils (Brooks 1999b, Davis et al 2000, Bashkin et al. 2003) and invasive plant cover and native annual species richness showed stronger negative correlation than any other combination of invasive plant and native plant measures from unburned stands. Lastly, invasive plant removal in burned and unburned contexts can provide a better understanding of the interaction between fire and invasive plants on native annual plants. Such experiments have been carried out in Chapters 3 and 4.

Previous desert research has shown that invasive plants are highly competitive with annual species. Invasive annual grasses, *Erodium cicutarium*, and *Brassica tournefortii* can all individually reduce native annual abundance in desert environments (Brooks 2000, Schutzenhofer and Valone 2006, Barrows et al. 2008). When one of these invaders is removed, remaining invasive species usually increase (Brooks 2000, Barrows et al. 2008). Studies from cismontane annual communities have also shown similar patterns (Allen et al. 2005, Cox and Allen 2008, Cox and Allen *in press*). Overall, these studies suggest that the greatest native annual plant responses will not occur unless all invasives are removed. Therefore, in Chapters 3 and 4, total invasive plant removal treatments were implemented to better understand pre-invasion native assemblages and to establish restoration potentials.

For practical purposes, achieving invasive annual grass and forb control when mixed with native grasses and forbs can be extremely difficult since target species are very similar to desired species. However, invasive plant control is a necessary step in the ecological restoration of CBS since they are so problematic. While Bainbridge (2007) and others (Grantz et al. 1998, Lovich and Bainbridge 1999, Walker and Powell 2001) have demonstrated a number of promising techniques to restore perennial components of CBS, no work has been done to restore native annual plant assemblages in CBS to my knowledge. However, many examples of annual plant restoration studies in cismontane vegetation can be used to determine successful approaches that are applicable to desert environments (Cione et al. 2002, Cox and Allen 2008, among others). Based on previous studies from cismontane California (Pavlick et al. 1993, Cione et al. 2002, Allen et al.

2005, Cox and Allen 2008, Marushia and Allen *in press*), Fusilade II was identified as a promising restoration tool, which was implemented in burned and unburned CBS stands in both Chapters 3 and 4.

Another promising restoration approach implemented in this dissertation was based on phenological differences between invasive annuals and native annuals. Because invasive desert annuals have a more rapid phenology than native annuals (Burk 1982, Jennings 2001) and usually germinate earlier (personal observation), a non-specific treatment that removes all plants during a short timeframe when invasives have germinated and are vulnerable but natives are still in seed could also be successful. This particular strategy was implemented in Chapter 3. Since Chapters 2 and 3 provide the first examples of annual plant restoration techniques from the desert, hopefully they will be useful for land management and in the development of future restoration methods.

Other approaches for controlling invasive annuals to restore native plant assemblages could also be effective in desert environments. For example, other restoration strategies explore resource manipulation (Zink and Allen 1998, Baer et al. 2004), native plantings utilizing a trait-based approach (Pywell et al. 2003, Bakker and Wilson 2004), or altering ecosystem processes, such as the fire regime (Moyes et al. 2005, DiTomaso et al. 2006), all with the goal of controlling invasive species, promoting native species, and returning ecosystem properties and functioning. Obviously, burning CBS to control invasive grasses like *B. madritensis*, for instance, would be counterproductive since *E. cicutarium* and *Schismus spp*. respond positively after fire (Brooks 2002) and fire severely impacts long-lived shrubs (Brooks and Minnich 2006).

In general, utilizing many types of weed control strategies in an integrated approach may be required, but their effectiveness will be context specific.

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CHAPTER 1. Impacts of single and multiple fires on creosote bush scrub of southern California.

ABSTRACT

The impacts of fire on creosote bush scrub (CBS) vegetation and post-fire successional processes have received attention recently as fire has become locally common throughout the Mojave and Sonoran Deserts, especially along roads and wildland/urban interfaces. One area of particular concern is western Coachella Valley, which forms the northwestern extent of the Colorado Desert. This is a major wildland/urban interface area significantly impacted by atmospheric nitrogen deposition, concomitant fuel alterations from invasive annual grasses, and increased ignition frequencies from human activities. CBS vegetation takes much longer than more mesic vegetation types to re-establish after fire, and the majority of desert species lack traits that promote resiliency to fire disturbance. Because exotic species that invade this habitat and encourage fire are also aggressive fire-followers, type conversion of CBS to invasive annual grassland is a major concern. Previous research in this area has only investigated once burned stands for up to five years since fire. This study documents the post-fire recovery of CBS from seven sites that represent a 2 to 28 year old chronosequence, plus two other stands that had burned twice. The goals of this study were to determine the impact of fire on shrub richness and diversity, overall vegetative structure, and successional processes. Field surveys revealed that fire significantly reduced shrub richness and diversity, and fire also reduced structural heterogeneity. Total shrub cover

and density returned or exceeded unburned levels at least 20 years after fire, although species composition was almost entirely *Encelia farinosa*, a short-lived shrub. Longer-lived shrubs indicative of unburned vegetation, like *Larrea tridentata*, *Ambrosia dumosa*, and *Krameria grayi*, failed to recover. In addition, species richness and diversity of shrubs were decreased again from a second fire even though once burned stands were already depauperate. Because *E. farinosa* recruitment from seed was so high in twice burned stands, *Encelia* shrublands appear to be a highly resilient vegetation type to fire disturbance. Burned CBS vegetation will likely take hundreds of years before it resembles unburned CBS. However, because the study area is highly invaded by annual grasses, the fuel properties of *Encelia* shrublands appear more conducive to fire, and fire occurrence is frequent, *Encelia* shrublands may form an alternate stable state in this region.

INTRODUCTION

Alterations to fire regimes can be especially damaging to ecosystem sustainability since native components have specific adaptations and traits that allow them to be successful under a certain regime. When regimes are altered in either direction, it can be catastrophic (*reviewed in* Brooks et al. 2004). Historically, fires have been relatively absent or extremely rare in creosote bush scrub (CBS) but the frequency and extent have increased significantly during the last 40 years as alien annual grasses and human ignition sources have become increasingly more common (Brooks and Esque 2002, Brooks and Matchett 2006).

As fire becomes more common in CBS, especially in localized areas (Brooks and Esque 2002), this type of disturbance dramatically alters the landscape. Since most native shrub components of CBS lack traits that enable resiliency to fire disturbance (Brooks and Minnich 2006), fires can result in long-lasting alterations to vegetation. In addition, invasive species common to the desert, such as *Bromus madritensis*, *Schismus* spp, and *Erodium cicutarium*, are aggressive fire followers in the immediate post-fire growing season or at least regain-exceed their pre-fire abundance within several years after fire (Brown and Minnich 1986, Minnich and Dezzani 1998, Brooks 2002, Brooks and Matchett 2003, Keeley et al. 2005, Steers dissertation – Chp. 2). Since these invasive annual grasses are also competitive with mature shrubs (Melgoza et al. 1990, Holzapfel and Mahall 1999, DeFalco et al. 2007), the combination of fire and the particular suit of invasive plants are threats to desert ecosystems. The impact of multiple fires is especially of interest since an invasive grass – fire cycle (D'Antonio and Vitousek 1992) has been reported from desert vegetation of the southwest (Brooks and Esque 2002, Brooks and Matchett 2006). Besides anecdotal evidence of type conversion to invasive annual grassland following repeated fires, examples and information are lacking in the literature about the consequences of multiple fires on CBS perennials. However, we do know that impacts will largely depend on initial species composition and fire intensities (Bazzell 1988).

As fire disturbance becomes more common in CBS, additional studies are needed to examine the effects of fire on native CBS vegetation. In the particular region where this study took place, the relevant literature has investigated no CBS burns older than five years (O'Leary and Minnich 1981, Brown and Minnich 1986) and no stands that have experienced more than one fire, besides anecdotal evidence (Brown and Minnich 1986). The primary objective of this study was to build upon the short-term findings of these previous studies in order to determine the impact of fire on shrub diversity and the degree of perennial native vegetation recovery in CBS after single and multiple fires. Specifically, I evaluated short-term (2 years) to relatively long-term (28 years) fire succession from stands that experienced single fires and the short-term impact of multiple fire on two stands that experienced their first fire about 19 or 20 years ago and their second fire two years ago. I also examined changes to vertical and horizontal vegetation structure that resulted from fire. My hypotheses are that native perennial plant cover, density, and diversity will be lower in burned than unburned CBS, regardless of time since fire (tsf), that certain functional groups, like succulents, will be disproportionately impacted by fire, and that the more frequently CBS burns, the lower the native plant measures of richness and diversity will be. As fires continue to claim increasing amounts of CBS habitat, understanding the impact of fire over longer periods of time or after multiple fires per site will be critical to conserving these shrublands in fire prone regions of the southwest.

METHODS

STUDY AREA

The study sites used in this experiment were located on the western edge of the Colorado Desert, in western Coachella Valley (Figure 1). Sites were on flat to low sloped areas located on valley bottoms and bajadas composed of creosote bush scrub (CBS). Degraded desert scrub\coastal scrub that had mostly been replaced by invasive grasses and *Encelia farinosa* (O'Leary and Minnich 1981, Brown and Minnich 1986) surrounded the study area on lower slopes of the Peninsular Range to the south and the Transverse Range to the north. Further west in the Bannning Pass, near Cabazon, the vegetation transitioned into cismontane types. East of the study area in Coachella Valley, CBS dominated the landscape. Since the 1970s, fire frequency in this area has increased dramatically (Brown and Minnich 1986, Brooks and Esque 2002). The increase in wildfires in this area is thought to be due to a combination of high rates of atmospheric nitrogen deposition that promote fine fuel loads large enough to carry fire even in years with average precipitation (Rao 2008, Allen et al. 2009), and increased opportunities for human-caused fires since the study area is part of a significant wildland/urban interface (WUI) immediately adjacent to major southern California metropolitan areas. Average precipitation in the study area is also relatively high since it is located at the edge of the desert, which would promote intra-annual build up of herbaceous fuels (Brooks and Matchett 2006). To the east of the study area, average precipitation in the city of Palm Spring is 13.1cm while to the west, at Cabazon, average precipitation is 39.9cm (WRCC 2008).

SITE DETERMINATION

Eight study sites that included burned CBS and a respective unburned stand of CBS were sampled for this study. These eight sites were identified based on stereoscope validation of fire perimeters from aerial photographs of the study area taken from 1949 to 2005, and from direct observation for sites burned in the summer of 2005. For each burned stand per site, only unburned vegetation was utilized as the paired unburned stand if it contained similar pre-fire shrub cover to the burned stand (based on aerial photography), was located on similar slopes and soil conditions, and was located opposite of a fuel break to the paired burned stand. This was done to minimize differences in fuel between paired stands at the time of fire. All paired stands per site were ground-truthed to ensure they met criteria. Please see Steers (dissertation – Chp. 2) for full details on the methods used to select study sites in the area. Eight sites were selected for this study. Seven sites were utilized that ranged in year burned from 1979 to 2005 with a time since fire (tsf) of 2, 2, 9, 12, 20, 24 and 28 years. In addition, one other site that had burned twice (19&2) was also utilized. Site **19&2** had burned twice, 19 and 2 years ago, but the second fire consumed all of the area that had burned once within soil and vegetation coverage similar to the unburned stand so only two paired stands could be surveyed, an unburned and twice burned stand. Site **20** also included a twice burned stand (tsf: 20&2) that did not completely overlap the burned once stand, resulting in three paired stands, an unburned, once burned, and twice burned stand. The names of the eight sites correspond to their tsf. Two of the burned once sites experienced fire in the same year (two years before sampling) and were given the suffix ‘a’ and ‘b’ to distinguish between each other.

VEGETATION SAMPLING

At each site, a stratified random sampling design was used to collect perennial plant cover, height and density from six sampling units in both the burned and paired unburned reference vegetation. Sampling units consisted of a 100m line transect and 5 x 100m belt transect on the right side of the line transect, facing upslope. Transects were oriented perpendicular to elevation contours and placed in CBS vegetation. Desert wash habitat was specifically avoided since it can be more productive and can include perennials that are capable of resprouting from the base following disturbances. The line transects were used to measure cover of live and dead perennial plants. Also, any live plant that crossed the line transect was measured for height at the tallest point on the plant. If different individuals of the same species were clumped together so that no interspace along the line transect separated the individuals in the clump, then only the tallest individual per clump was measured for height. The belt transects were used to measure density by species.

For every seedling encountered in the belt transect, the microhabitat (understory or interspace) where it occurred was recorded in addition to its height and width at the widest point. For stands that had burned in the summer of 2005, seedlings were defined as plants that had germinated after the fire, which was apparent when compared to resprouts or fire survivors/escapees. For stands that had burned longer ago than in 2005, *Larrea tridentata* individuals with a height ≤ 30cm and a width ≤ 15cm at the widest point were called seedlings. For all other shrubs, seedlings were classified as those with ≤ 15cm height by 10cm width. For cacti, only species that were ≤ 10cm height by 10cm width were recorded as seedlings. Differences in the classification of seedlings between recently burned stands and other stands were implemented since *E. farinosa* seedlings in recently burned stands sometimes grew very quickly, exceeding dimensions that would normally distinguish them as seedlings. Study sites were sampled in the spring of 2007.

For stands that had burned in 2005 (**2a**, **2b**, **19&2**, and **20&2**) shrub and cacti seedlings, resprouts, or fire survivors/escapees were also documented for each species in line transects and belts. Seedlings were defined as above. Resprouts were those individuals whose canopies were completely or partially removed by the fire and contained new shoot growth from the base of the shrub stem. Survivors were classified as individuals whose canopies were at least still partially alive and exhibited no new shoot growth from the base. Resprouts and survivors were not determined for the other sites in this study since they had burned at least 9 years since sampling time and distinguishing resprouts from shoot survivors was difficult for certain species this long after fire.

DATA ANALYSES

For comparing the structure of the vegetation between paired burned and unburned stands, interspace cover, total live and dead plant cover (excluding overlap), live shrub cover (excluding overlap), dead shrub cover (excluding overlap), live herbaceous perennial plant cover (excluding overlap), live shrub density, dead shrub density, and live herbaceous perennial plant density were calculated for each sampling unit and then averaged per stand. For the purposes of this study, when shrub density or cover is referred to, it includes both shrubs and cacti unless stated otherwise. Shrub heights of each species were calculated based on the average height across all unburned stands in the study area. When comparing the variation in shrub height between paired burned and unburned stands, the standard deviation of shrub height was calculated based on all heights recorded per paired stand.

Site **28** was utilized to further compare the horizontal structure of burned versus unburned vegetation since it was the oldest burned stand and exhibited mature *E. farinosa* shrubland structure based on maximum longevity of this shrub (Goldberg and Turner 1986). For each line transect at this site, the average number of perennial vegetation patches (continuous perennial plant intersection) per line transect were calculated per stand, in addition to average perennial plant patch length per transect and average interspace length per transect. Clumpiness was calculated as the ratio of total cover of perennial plants summed per line transect, with no correction for overlapping shrubs, to the total number of patches per line transect. Clumpiness could be considered homologous to average perennial patch length except that it accounts for overlap. Since greater perennial plant overlap occurred in unburned stands compared to burned stands, this was important to distinguish. Finally, interspace and perennial plant cover from transect #1 of both paired stands were graphically displayed to demonstrate the one-dimensional structure of burned versus unburned vegetation and their potential for carrying fire. For all horizontal vegetation structure calculations from site **28**, perennial plant cover included live and dead vegetation.

Species richness, Shannon diversity (*H'*) (Shannon and Weaver 1963), and the probability of interspecific encounter (Δ_1) (Hurlbert 1971) were calculated based on live shrub and cacti density data per sampling unit. To improve normality for statistical tests, arcsine transformations were performed on all cover and Δ_1 data. Also, density and richness were square root transformed. Unburned and paired burned stands were compared statistically using ANOVA. For site **20**, Fisher's LSD test was also used to determine statistical differences between each of the three paired stands.

The cover and density of live individual species were also summed by line (with no regard for overlap) or belt transect. Cover and density data from the most common species across the study area (*Ambrosia dumosa*, *Encelia farinosa*, *Krameria grayi*, and *Larrea tridentata*), in addition to the sum of all cacti species, were left untransformed and statistically compared between paired unburned and burned stands using the Kruskal-Wallis test for nonparametric data. JMP® 7.0.2 (SAS Institute, Inc. Cary, NC) was used for all statistical analyses at $\alpha = 0.05$. All species nomenclature follows Hickman (1996).

RESULTS

Across the study area, 23 shrub and cacti species were documented (Table 1). All the unburned stands were dominated by *L. tridentata* (highest cover of all species) with a high density of *A. dumosa* and sometimes *K. grayi*; typical of the *Larrea-Ambrosia* microphyllous scrub that is common throughout the Colorado Desert (Ezcurra et al. 1987). Average *L. tridentata* cover among all unburned stands was about 10%. Average *A. dumosa* density among all unburned stands was about 24 individuals per 500m², which was also the highest of all species. *Ambrosia dumosa*, *E. farinosa*, *K. grayi*, and *L. tridentata* were the most common shrubs across the study area, occurring in every unburned stand, except *E. farinosa* was absent from site **9** and *K. grayi* was absent from site **2a** (Tables 1 and 2). Additional common shrubs across unburned stands of the study area were *Echinocereus engelmannii*, *Ferocactus cylindraceus*, *Ephedra californica*, and *Opuntia basilaris*, among others (Table 1).

Impact of Fire on Vegetation Structure

Fire disturbance increased interspace cover for stands with a tsf of 12 years or less (Table 3). For stands with a greater tsf, interspace either showed no difference compared to paired unburned stands or was reduced (Table 3). Live shrub cover was low for at least 12 years after fire (Table 3). At the three oldest burns, sites **20**, **24**, and **28**, live shrub cover was either greater than the paired unburned stand for site **20**, or was not different (Table 3). The reestablishment of live cover in older burns was due to *E. farinosa* (Table 1 and 2). Typically, unburned stands had greater dead shrub plant cover and density than their respective paired burned stands except in the oldest burned stands (Table 3).

Average shrub heights based on all unburned stands across the study area showed that *L. tridentata* was the tallest shrub, at about 1.7m, while most other shrubs and all cacti averaged less than a meter in height (Table 4). Average shrub height of all species per stand per site was lower in burned stands compared to their paired unburned stands (Figure 2). Based on the standard deviation of shrub height per paired burned and unburned stands, variation in shrub height was usually dramatically reduced in burned stands, resulting in decreased structural heterogeneity after fires (Figure 2).

For site **28**, the horizontal distribution of perennial cover was also evaluated. As mentioned previously, site **28** was chosen for this analysis since it was the oldest stand and represented the structure of *Encelia* shrublands at maturity. Total perennial plant cover and interspace cover between paired burned and unburned stands did not differ (Table 3). No differences were found for average number of vegetation patches (F (1, 10) = 0.9869, $p = 0.3439$, Figure 3) or average interspace length (F (1, 10) = 0.0704, $p = 0.7961$, Figure 3). However, greater average patch size (F (1, 10) = 15.4236, $p = 0.0028$) and greater clumpiness (F (1, 10) = 23.2218, $p = 0.0007$) both occurred in the unburned stand (Figure 3). The graphical representation of the one-dimensional structure of perennial vegetation in burned and unburned stands showed that the vegetation in the burned stand appears more uniform and contains more patches that are smaller in length (Figure 3), which makes sense since perennial plant density is much greater in the burned stand, averaging 53.4 more perennial plants per $500m^2$ than in the unburned stand (Table 3).

Species Specific and Functional Group Responses to Fire

In recent fires (2 years since fire), *A. dumosa*, *K. grayi*, and *L. tridentata* decreased in cover and density (Tables 1 and 2). *Encelia farinosa* also exhibited reduced cover at site **2b** but not at site **2a** (Table 2). *Encelia farinosa* density was not affected by fire within the first two years (Tables 1 and 2). Dominant, long-lived shrubs were still severely impacted by fire even in the older burns. *Ambrosia dumosa* and *K. grayi* cover and density remained lower in paired unburned stands up to 28 years after fire. However, due to overall low cover and density in some stands, statistical differences were not always detectable for these species. *Larrea tridentata* cover and density were always lower than paired unburned stands regardless of tsf (Tables 1 and 2). Relative density and cover values also exhibited similar impacts to fire disturbance (Figures 4 and 5).

Average cacti density and cover also decreased after fires. Sites **2a** and **2b** showed decreases in cacti density ($\chi^2 = 9.504$, $p = 0.0021$; $\chi^2 = 7.2052$, $p = 0.0073$, respectively), dropping from 3.7±1SE and 3.2±0.9SE individuals per 500m^2 to zero individuals, respectively. Cacti density at site **12** decreased ($\chi^2 = 5.2537$, $p = 0.0219$) from 1.2±0.5SE to zero individuals per 500m^2. At site **20**, both cover and density of cacti decreased ($\chi^2 = 11.0056$, $p = 0.0041$; $\chi^2 = 16.1288$, $p = 0.0003$, respectively). Cacti cover dropped from 0.5%±0.1SE in the unburned stand to near elimination (0%±0.04SE) in the once burned stand (tsf 20) and to zero detection in the twice burned stand (tsf 20&2). Cacti density dropped from 9.7±1.1SE individuals per 500m^2 in the unburned stand to zero individuals in both the once burned and twice burned stands. Site **28**, which had the greatest cacti abundance of all sites, also significantly lost cover and density of cacti after fire ($\chi^2 = 9.4661$, $p = 0.0021$; $\chi^2 = 8.3958$, $p = 0.0038$, respectively), dropping from 0.9%±0.3SE to zero cover and from 22.8±2.5SE individuals to just 1.5±0.7SE individuals per 500m^2. Overall, sites with relatively high cover and density of cacti experienced the greatest decreases when burned (Figures 4 and 5).

The data strongly suggest that most shrub species and all cacti species are severely reduced by fire, especially in regard to density (Table 1). Cover measures were less able to detect as many types of species but also support this finding (Table 2). The species with the greatest positive response to fire was *E. farinosa*, which increased greatly in 12 year old or older burned stands. Other shrubs, such as *Bebbia juncea*, *Hymenoclea salsola*, and *Psorothamnus arborescens* var. *simplicifolius*, appeared less impacted relative to other shrubs (Table 1). However, it is difficult to draw conclusions about their individualistic responses to fire disturbance since they were less common. The increase in herbaceous perennial plant density in two of the oldest burned stands suggests that over time, species with this habit may respond positively to disturbance (Table 3). The positive response by herbaceous perennial vegetation was mostly due to increases in *Croton californica* at site **24** and by *Ditaxis neomexicana* and *Mirabilis bigelovii* at site **28**. In general, *Stephanomeria pauciflora* also responded positively as did *Stillingia linearifolia* where they occurred (Table 1).

Richness, Diversity, and Interspecific Encounter after One Fire

Total shrub richness was reduced by fire at every study site (Figure 6). Comparisons of Shannon diversity between paired stands per site also revealed decreases across all burned stands. Decreases in Shannon diversity for sites **2a** and **2b** were not as strong due to much lower density of live plants in these stands (Table 3) and a consequent increase in evenness. Measures of the probability of interspecific encounter (PIE) were even more sensitive to the low density of shrubs in burned stands **2a** and **2b** (Figure 6).

Despite much lower species richness in these burned stands compared to their respective unburned stands, PIE did not differ between the burned and paired unburned stands for these two recently burned sites. However, all other paired burned and unburned stands exhibited lowered PIE in the burned stands (Figure 6).

Impact of Multiple Fires

At site **20**, the twice burned stand (20&2) had greater interspace cover and less live and dead shrub cover compared to the other two paired stands (UB and 20), which was expected (Table 3). However, live shrub density was much greater than the other two paired stands, primarily due to prolific seedling recruitment following the second fire by *E. farinosa* (Figure 7). Compared to all other stands that had burned 2 years prior in the summer of 2005, seedlings contributed massively to the live plant density at this site (Figure 7). Structural heterogeneity based on shrub height was also lower in the twice burned stand than the once burned stand (Figure 2). *Larrea tridentata* and other shrubs besides *E. farinosa* were almost eliminated following the second fire (Table 1). Therefore, it was no surprise that shrub richness, Shannon diversity, and probability of interspecific encounter were all reduced each time a stand burned at this site (Figure 4).

At site **19&2**, the twice burned stand also had greater interspace cover and decreased live cover of shrubs (Table 3). There was no difference in live density between the twice burned and paired unburned stands because of increased *E. farinosa* seedling recruitment after the second fire (Figure 7). Also, like the twice burned stand at site **20**, the twice burned stand at site **19&2** experienced almost complete elimination of shrubs other than *E. farinosa* (Table 1) and reduced structural variation in shrub height after fire (Figure 2). The twice burned stand at site **19&2** also exhibited lowered richness, Shannon diversity, and PIE compared to the paired unburned stand (Figure 6). Finally, 70 individuals (43.5% of all shrubs encountered) in the twice burned stand at site **19&2** were fire survivors (Figure 7), suggesting that the overall fire intensity in this stand was relatively low compared to the other twice burned stand at site **20**, which only had 16 (0.4%) unburned shrubs. Despite possibly lower fire intensity, the cover and richness data demonstrate that this second fire still had a large negative impact at site **19&2**. Unfortunately, I could not determine if these decreases would have been significantly lower compared to a paired, once burned stand because such a stand was not available.

Shrub Seedlings and Microhabitat

A total of 4479 *E. farinosa* seedlings were encountered from all study sites. All were found in twice burned stands except 29 occurred in once burned habitat and only one occurred in an unburned stand. Most of these seedlings were found in the twice burned habitat at site **20** (Figure 7). One *H. salsola* seedling was found in once burned habitat at site **28**. Three *L. tridentata*, two *Ferocactus cylindraceus*, and two *Opuntia echinocarpa* seedlings were also found, all of which were in unburned habitat except that one of the *L. tridentata* seedlings was found in the burned stand at site **28**. Of the *E. farinosa* seedlings encountered, 95% were observed in open, interspace microhabitat, 4.8% were documented from the understories of dead or live *E. farinosa* shrubs, and the rest were found in the live or dead understories of other shrubs. The *H. salsola* seedling was also found in the open. For all other species, seedlings were only found in the understory of dead or live shrubs.

DISCUSSION

The impact of fire on the shrub and cacti species in the study area will be relevant to more interior CBS shrublands since so many species or genera in the study area have wide distributions throughout the arid southwest (Hickman 1996). Increases in *E. farinosa* abundance after fire may be less relevant, but this will depend on whether other sites contain this species. The positive or advantageous response of *E. farinosa* to disturbance has also been documented in other desert regions, such as Upland Sonoran vegetation of Arizona, USA (Cave and Patten 1984), desert scrub of Sonora, Mexico (Turner 1990), and desert scrub of the eastern Mojave Desert (Abella et al. 2007). Vasek (1983) has listed other perennials that react opportunistically to disturbance that could also respond positively to fire (see O'leary and Minnich 1981) and may be more important elsewhere in the southwest.

Hopefully, a potentially unique feature of the study area that will not be applicable elsewhere is the high abundance of invasive annual plants that dominate the landscape (Steers dissertation – Chp. 2). The relatively high amount of precipitation, anthropogenic nitrogen deposition, consequent plant invasions, and elevated human ignitions create major challenges for conserving this landscape. These important factors must also be considered when comparing these results to other desert regions and especially when using these data to predict fire successional trajectories elsewhere.

Regardless of differences, taking advantage of the rich fire disturbance history of the study area will aid our understanding of the consequences of fire, especially in regard to succession and impacts to plant diversity.

Impact of Single Fires

The short-term impact of single burns on CBS vegetation of the study area has been previously investigated up to 5 years tsf, at five separate sites in two separate studies (O'Leary and Minnich 1981, Brown and Minnich 1986). The increase in interspace cover and reduction in shrub cover and density that I observed for stands with a tsf of 2 years was similar to what was found in 1983 for 3 year old burns (Brown and Minnich 1986). In addition, Brown and Minnich (1981) observed increased *E. farinosa* cover and density relative to other shrubs. They also documented *E. farinosa* seedling densities that were orders of magnitude greater than other shrub species and concluded that burned stands would convert to *Encelia* dominated shrublands capable of persisting for decades.

My observations in relatively older stands (12 – 28 years since fire) confirm the predictions of Brown and Minnich (1986). However, if *E. farinosa* is not a component of the pre-fire community, then type conversion to an *Encelia* shrubland will not occur. For example, *E. farinosa* was absent from the unburned vegetation at study site **9**. Consequently, this plant was not present in the post-fire community and instead, the shrub components were composed almost entirely of just several *L. tridentata* individuals that appeared to be resprouts. The vegetation could best be described as an invasive annual grassland*Larrea* savanna. Shrub seedlings were absent and the resulting invasive grass dominated vegetation appeared very stable. Alternatively, O'Leary and Minnich (1981) have shown that where *H. salsola* is abundant in prefire stands, it becomes dominant following fire. *Hymenoclea salsola* was also absent from site **9**.

The observations from site **9** are important because they suggest that where CBS shrublands lack propagules of early colonizers (Vasek 1983), the potential for type conversion to invasive annual grassland may be much higher. The results from this site and the others also suggest that whether the post-fire community is dominated by *Encelia* or invasive grasses, the reestablishment of other shrubs typical of CBS can be virtually non-existent. However, even though species richness, diversity, and probability of interspecific encounter are all significantly reduced compared to unburned stands for at least 30 years after fire and likely to be reduced for centuries, this is might be expected considering the slow population dynamics of CBS (Cody 2000) and the long time periods required for its development (McAuliffe 1988).

The lack of seedlings observed in this study is reflective of the low rainfall preceding the vegetation surveys. Despite my relatively liberal definition of seedlings, very few were observed other than those of *E. farinosa* in burned vegetation. Seedbank analyses from six of the eight study sites also showed a depauperate shrub seedbank in both burned and unburned stands of the study area (Steers dissertation – Chp. 2). However, for the purposes of projecting future changes in composition that the *Encelia* dominated shrublands will undergo, the lack of seedlings encountered, especially in older burned stands, raises predictive confidence. We can conclude that besides small increases in herbaceous perennials, *Encelia* dominated shrublands show little trend toward change. In the oldest burned stand at site **28**, one *L. tridentata* seedling was found under an *E. farinosa* shrub, which hints that these shrublands may eventually return to CBS, assuming additional fires do not occur. But overall, *Encelia* dominated shrublands appear very stable.

Depending on the severity of disturbance, Lovich and Bainbridge (1999) determined that desert shrublands can take hundreds of years to return to predisturbance conditions. So again, it is of no surprise that after about thirty years, burned stands still show very little resemblance based on species composition to unburned stands. Another important determinant of post-fire recovery is the effect of fire intensity (Bazzell 1988, Brooks 2002). It is very unlikely that all of the study sites experienced the same fire intensity when they burned. However, despite likely differences in intensity, all stands appear to have been severely compromised by fire, and where *E. farinosa* was present, these sites converted to an *Encelia* dominated shrubland. Also, regardless of initial species composition, although it did not differ dramatically between sites, the decrease in species richness and diversity measures for all burned stands were major and are a long-term consequence of fire.

Alterations to Fuel Properties in Burned CBS

Based on the examination of stands that experienced single fires, it appears that recovery to pre-fire species composition and diversity will be on the order of centuries. If additional fires within burned stands can be prevented, then trajectory towards recovery can proceed. Unfortunately, due to high amounts of invasive annual plant abundance in the study area, especially in burned stands (Steers dissertation – Chp. 2), the potential for increased fire frequency in already burned CBS is high, following the invasive grass – fire cycle (D'Antonio and Vitousek 1992). The replacement of *L. tridentata* and other evergreen desert shrubs with *E. farinosa*, a short-lived (Goldberg and Turner 1986) and shallow rooted (Nobel and Jordan 1983), drought to semi-drought deciduous shrub (Cunningham and Strain 1969), may also profoundly alter the fire regime besides changes due to invasive annual grasses.

Encelia farinosa plants are relatively short, hemi-spherical shrubs with relatively large leaves. They are highly sensitive to water stress and rapidly alter their phenology at the onset of drought (Smith and Nobel 1977). They produce their largest leaves during the winter wet season, which desiccate from lower portions of the branches up to the tips as summer drought progresses (Cunningham and Strain 1969). Moisture content of *E. farinosa* can be very low early in the dry season. Because of these traits, shrublands dominated by this species are probably more susceptible to fire earlier in the summer dry season than the majority of species found in unburned CBS. Also, the spatial distribution of *E. farinosa* in burned shrublands appears more regular than in unburned CBS, resulting in altered horizontal fuel properties that may lessen the importance of herbaceous fuel loads necessary to carry fire. Larger patch size and more clumpiness in unburned stands were confirmed by field observation from all sites. The conclusion that *Encelia* shrubland are more flammable because of greater shrub fuel continuity compared to unburned CBS is also supported by the greater perennial plant densities that are found in mature *Encelia* shrublands versus their paired unburned stands. Increased shrub density will likely decrease the importance of herbaceous fuels needed to carry wildfire even though invasive plant abundance also increases following fire (Steers dissertation – Chp. 2).

Although changes due to dominance by *E. farinosa* may promote fire, overall fire intensity if these stands were to burn a second time might be reduced since *E. farinosa* does not accumulate organic matter (Muller 1953) or support high amounts of herbaceous species in their understories like *L. tridentata* (Went 1942, Muller 1953), which contribute to high fire intensities (Brooks 2002). Overall, increased invasive annual plant abundance, an increased fire season due to early onset invasive grass and *E. farinosa* flammability, and changes in the spatial distribution of shrubs all result in a community that is likely more vulnerable to repeated fire. Therefore, despite the fact that full type conversion to invasive annual grassland is generally not occurring, an invasive plant – fire feedback is still in place within the study area. Interestingly, in perennial grasslands where shrub encroachment occurs, fire has been a key disturbance that reduces *L. tridentata* colonization and prevents heterogeneous/patchy distribution of perennial vegetation and soil resources (Kieft et al. 1998, Van Auken 2000).

Impact of Multiple Fires

Compared to sites with stands that had burned for the first time in 2005, seedling densities of *E. farinosa* in twice burned stands were magnitudes greater. Therefore, the formation of an *Encelia* dominated shrubland should occur much more rapidly in the twice burned stands than in stands that burn for the first time. Both of the twice burned stands in this study had a similar fire return interval of about 20 years so the effects of a shorter or longer interval are unknown. Short fire return intervals can be very damaging to cismontane coastal scrub vegetation by promoting invasive plant invasion that leads to type conversion (Minnich and Dezzani 1998, Keeley et al. 2005, Syphard et al. 2006), eliminating shrubs before they reach reproductive maturity, and reducing energy stores needed for resprouting (Zedler et al. 1983, Westman and O'Leary 1986, Haidinger and Keeley 1993). However, in the vicinity of Riverside, California, degraded coastal scrub also converts to *Encelia* shrublands that are highly invaded by exotic annuals. Despite experiencing shorter fire intervals than 20 yrs, these more coastal *Encelia* shrublands have been stable since *E. farinosa* is a prolific seeder (Steers personal observation). Therefore, based on more western locales, CBS converted *Encelia* shrublands may persist in the desert study area for a long period of time even if fire return intervals are shortened, at least up to a point. While *Encelia* dominated shrublands appear to be more resilient to fire disturbance than CBS, this resiliency is of little importance if succession to CBS is desired.

With a successional trajectory aimed at resembling unburned CBS, multiple fires are extremely problematic. Significant decreases in shrub richness, diversity, and probability of interspecific encounter were documented each time CBS burned at site **20**. In addition, both stands that had burned twice (20&2 and 19&2) contained very few shrubs besides *E. farinosa*. Multiple fires basically led to monoculture stands of *E. farinosa* with an herbaceous component dominated by invasive grasses and forbs (Steers dissertation – Chp. 2). Because *Encelia* shrublands may be more fire prone than unburned CBS yet more resilient to fire, these shrublands could persist much longer than human life spans since they appear to be an alternate stable state under current conditions. Based on this study, the biggest threats from multiple fires are reinforcement of *Encelia* dominance, increased time it will take until succession to climax CBS, and the elimination of most shrubs other than *E. farinosa* as measured by shrub density, cover, richness, and diversity indexes. Impacts to other taxa are probably also severe.

Areas for Future Research

Several hypotheses may explain the lack of shrub reestablishment observed in burned stands. First, shrub seeds may be eliminated by fire (propagule limitation). Alternatively, competition with invasive annual plants could prevent shrub seedling recruitment and reduce the survival rate of resprouts (competitive exclusion). Third, establishment of long-lived shrubs is a rare phenomenon in general (Barbour 1969, Boyd and Brum 1983) and inadequate time may have passed to observe recruitment. Forth, the removal of nurse plants and/or alterations to "fertile islands" by fire may result in safe site limitation, preventing successional processes from advancing. For example, *E. farinosa* understories do not accumulate understory debris like *L. tridentata* and *A. dumosa* (Muller 1953). Evaluating the importance of each of these hypotheses will provide essential information for understanding the future of CBS in invaded and fire prone regions. Allelopathic exudates from *E. farinosa* leaves have been shown to cause mortality to plants (Gray and Bonner 1948) and could also explain why a lack of shrub reestablishment has been observed. However, these allelopathic chemicals are inactive under field conditions typical of the study area (Muller 1953).

Initial species composition and fire intensity will greatly affect successional processes (Bazzell 1988). Understanding how these differences play out across the desert landscape and consequently result in different successional assemblages will be of great importance for managing CBS in the southwest. Furthermore, a mechanistic understanding of shrub establishment for multiple species is necessary for reinstating shrub diversity and structural complexity. Other ecologically important characteristics of CBS, like fertile islands (Dean et al. 1999, Carrillo-Garcia et al. 2000, Bolling and Walker 2002, El-Bana et al. 2003), horizontal shrub distribution (Barbour 1969, Phillips and MacMahon 1981, Huenneke et al. 2001, Schenk and Mahall 2002, Schenk et al 2003), vertical heterogeneity of the canopy (this study), or below ground organization of roots (Mahall and Callaway 1991, Wilcox et al. 2004, Schenk 2005) may be 'keystone structures' (*sensu* Tews et al. 2004) that are critical for biodiversity. We still do not understand what keystone structures, if any, maintain higher biodiversity in CBS vegetation. Until these are understood or keystone species identified (Power et al. 1996), restoration efforts may fail to maximize biodiversity. Keystone arthropods (Whitford 2000) and vertebrates (Ernest and Brown 2001) have been identified from desert shrublands of the southwest, but no plants of the study area have been singled out as such. Clearly, fire resulted in major changes to the structure of CBS. Exactly how these structural changes will impact biodiversity and ecosystem processes is mostly unknown.

Management Implications

Preventing fire is critical for preserving these shrublands. The most ecologically beneficial way to accomplish this would be through the removal of invasive annual plants from the study area, which increase horizontal fuel connectivity between widely spaced shrubs and fuel wildfires (Brooks 1999). Because invasive plants can competitively inhibit native perennials in unburned CBS (DeFalco et al. 2007) and other burned arid ecosystems (Melgoza et al. 1990), control of these invaders is important regardless of their fire promoting traits. Removal of invasive annual grasses and forbs for the first three post-fire years in CBS significantly increased perennial plant abundance by the third year (Steers dissertation – Chp. 3). Invasive plant removal in the study area would decrease overall fire frequency and release native plants from competition, a double benefit. Similar recommendations have also been made for fire prone CBS of the eastern Mojave Desert (Brooks et al. 2007).

If increasing the rate of succession after fire is desired, then a combination of invasive plant control and shrub plantings would be ideal. Recently, Bainbridge (2007) has summarized perennial plant establishment techniques in desert environments and offered useful approaches to restoring CBS. Shrub plantings in highly disturbed desert scrub can speed the rate of succession (Abella et al. 2007). However, due to the negative effects of annual plants on shrubs (Holzapfel and Mahall 1999), disproportionately so by invasive species (DeFalco et al. 2007, Steers dissertation – Chp. 3), the control of invasive annuals in addition to shrub plantings would probably be the most successful approach. Successful techniques for restoring post-fire annual assemblages in CBS have also recently been developed (Steers dissertation – Chp. 3). Assuming allelopathy by *E. farinosa* is too low in the field to cause harm to other native species (Muller 1953), taking advantage of the abundance of *E. farinosa* that occur in post-fire stands and using them as nurse plants may also be more cost effective and successful than installing artificial shading. Utilizing a nurse plant is critical since most long-lived desert shrub and cacti seedlings have increased recruitment success in understory microhabitat (Sherbrooke 1989, Flores and Jurado 2003).

The maximum life span of *E. farinosa* has been reported at 32 years (Goldberg and Turner 1986). In the next decade many *E. farinosa* individuals in the older burned stands will likely die if they have not done so already. Once dead, *E. farinosa* shrubs begin to break up and accumulate windblown debris, developing microsites more suitable to shrub establishment for longer-lived species. For example, Went (1942) found higher annual species richness, composed of 'understory obligates,' under dead *E. farinosa* compared to live *E. farinosa*. Utilizing dead *E. farinosa* shrubs in combination with other shrub planting techniques (Bainbridge 2007) may be one successful approach for restoring shrub diversity in burned CBS. The link between biodiversity and ecosystem functioning is tightly coupled for some ecosystems (Loreau et al. 2001) and although evidence for CBS has not been explicitly synthesized, the large body of literature from this vegetation type suggests that CBS is a complex ecosystem and biodiversity is critical to maintaining its functioning. Active restoration will be necessary to prevent additional fires and direct succession towards healthy structure and functioning.

CONCLUSIONS

My hypothesis that native perennial live plant cover and density would be lower in burned than unburned CBS, regardless of tsf, was rejected since stands at least 20 years old reached or exceeded pre-fire cover and density levels. However, this increase was due almost entirely to *E. farinosa*, which responds positively to fire in this study area. Besides *E. farinosa*, I found that almost all other shrub species decreased in abundance from fire disturbance, regardless of likely differences in fire intensities between sites. I also found that certain functional groups, like succulents, were severely impacted by fire, similar to other studies in desert shrublands (O'Leary and Minnich 1981, McLaughlin and Bowers 1982, Cave and Patten 1984, Brown and Minnich 1986, Alford et al 2005, Brooks and Minnich 2006). Assuming the chronosequence approach utilized in this study was suitable for all species groups, herbaceous perennials showed positive responses to fire but these were not detected until over twenty years after fire disturbance, in contrast to Cave and Patten (1984) who observed increases in the season immediately after fire in Arizona.

My hypothesis that shrub diversity would be lower in burned than unburned CBS, regardless of tsf, was not rejected. Return of pre-fire richness and diversity appears to be on the order of centuries. Most importantly, the hypothesis that the more frequently CBS burns, the lower the native plant measures of richness and diversity was also not rejected. Despite severe reductions in richness after a first fire, a second fire can still significantly decrease shrub richness, diversity, and the probability of interspecific encounter. However, sites that experienced second fires were so species depauperate it seems unlikely at the scale used in this study that further significant decreases would be detected after a third fire. In conclusion, single and multiple fires are major threats to CBS sustainability. Active management and restoration that target vegetation structure and species diversity appear essential for the conservation of CBS in fire prone regions of the southwest.

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FIGURE AND TABLES

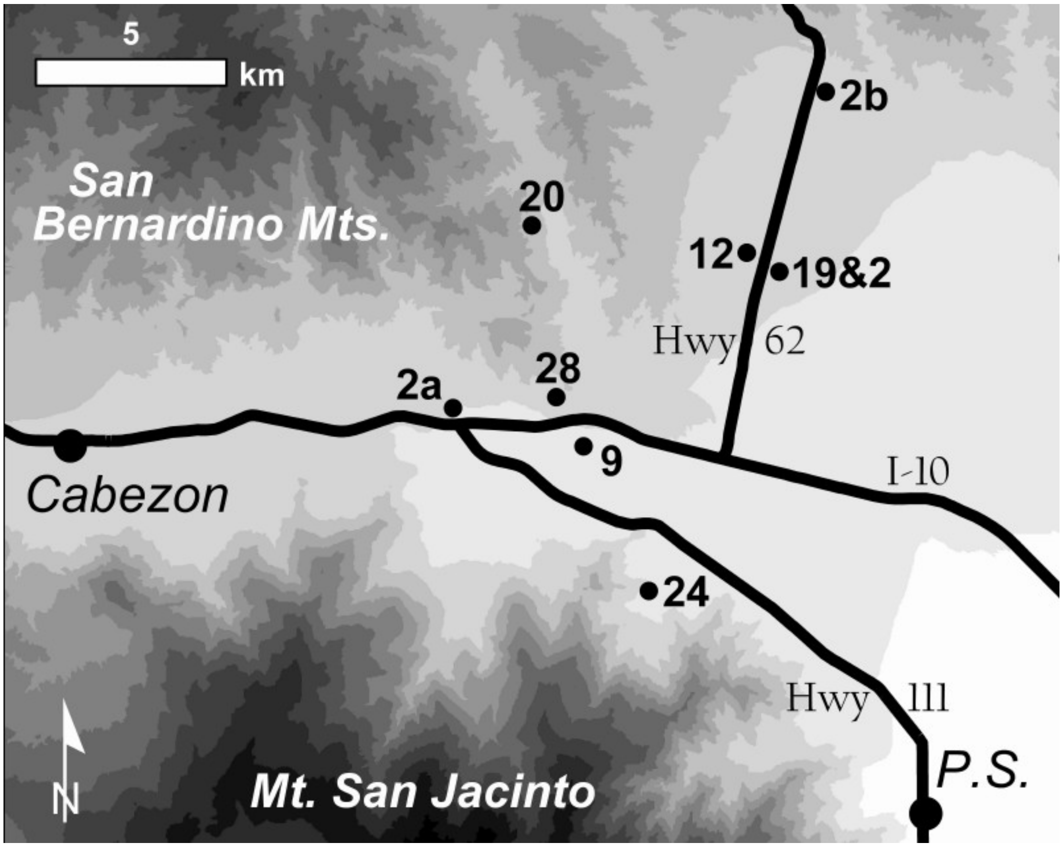

Figure 1.1 Study area in Riverside County, CA showing the names and locations of the study sites. Study sites were named after the number of years since their first fire occurred, except site 19&2 was named for both fires that occurred. P.S. stands for the city of Palm Springs. Darker colors represent increasing elevation.

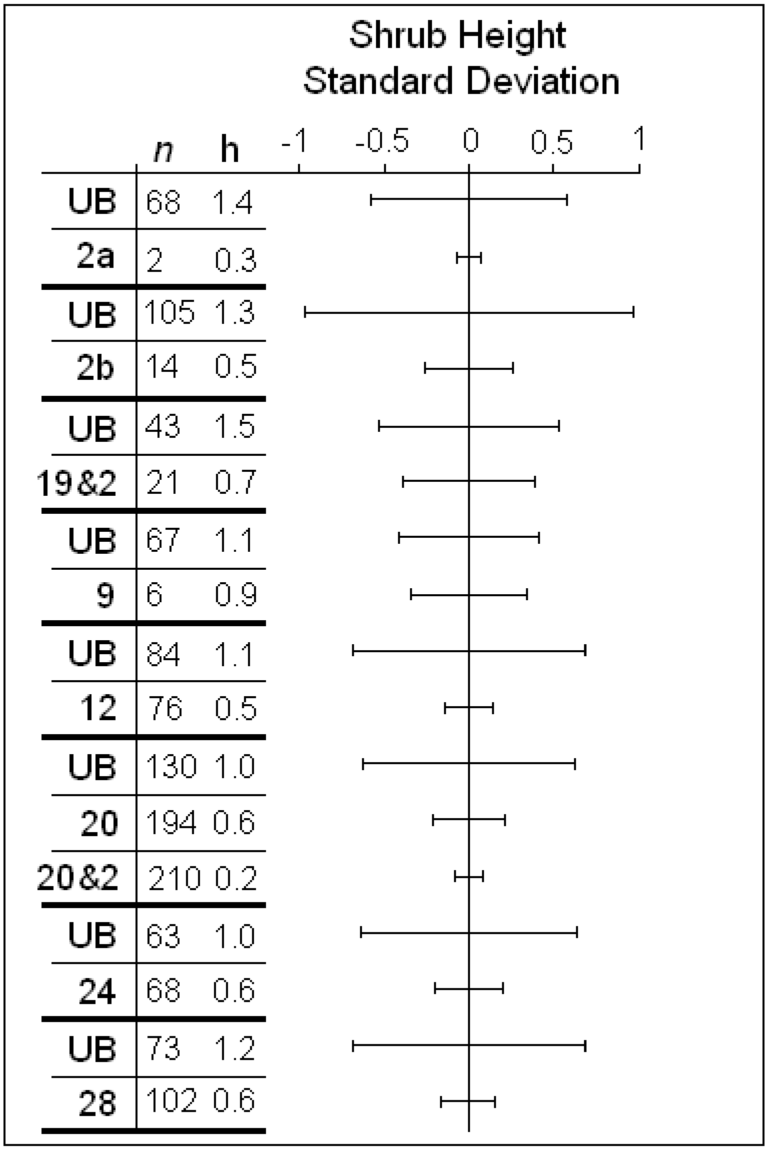

Figure 1.2 Structural heterogeneity of stands based on the standard deviation of shrub height. *n* = the total number of shrub heights measured per stand; h = the average height based on *n* shrubs per stand.

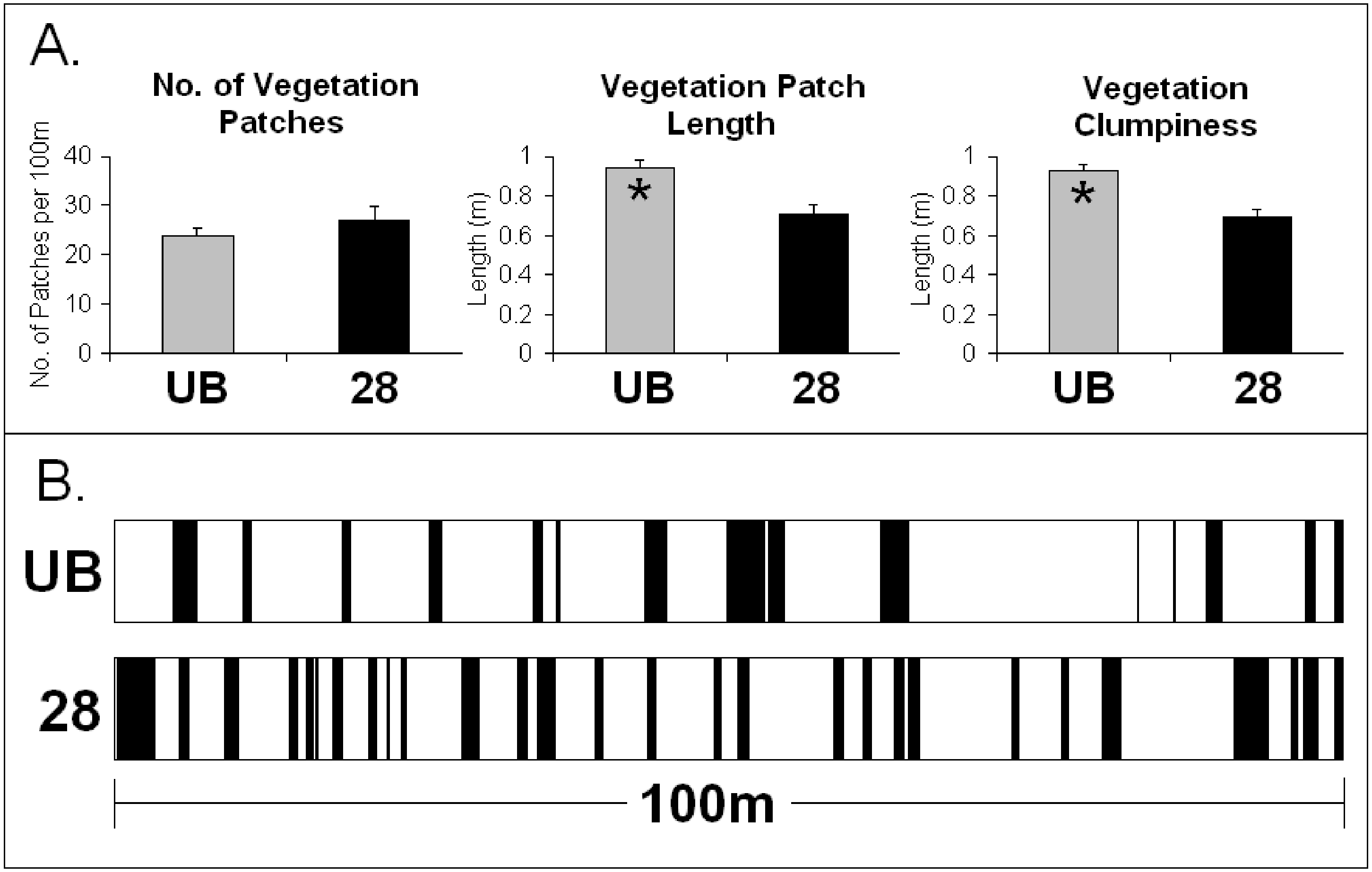

Figure 1.3 Impacts of fire on horizontal spatial properties of perennial vegetation from site **28**. A. Graphs comparing average number of vegetation patches, average size of vegetation patches, and vegetation clumpiness between unburned (UB) and burned (28) stands. Asterisks indicate significant differences between paired stands. B. One dimensional replication of perennial vegetation (black) and interspace (white) cover along transect #1 from both the unburned (UB) and burned stands (28).

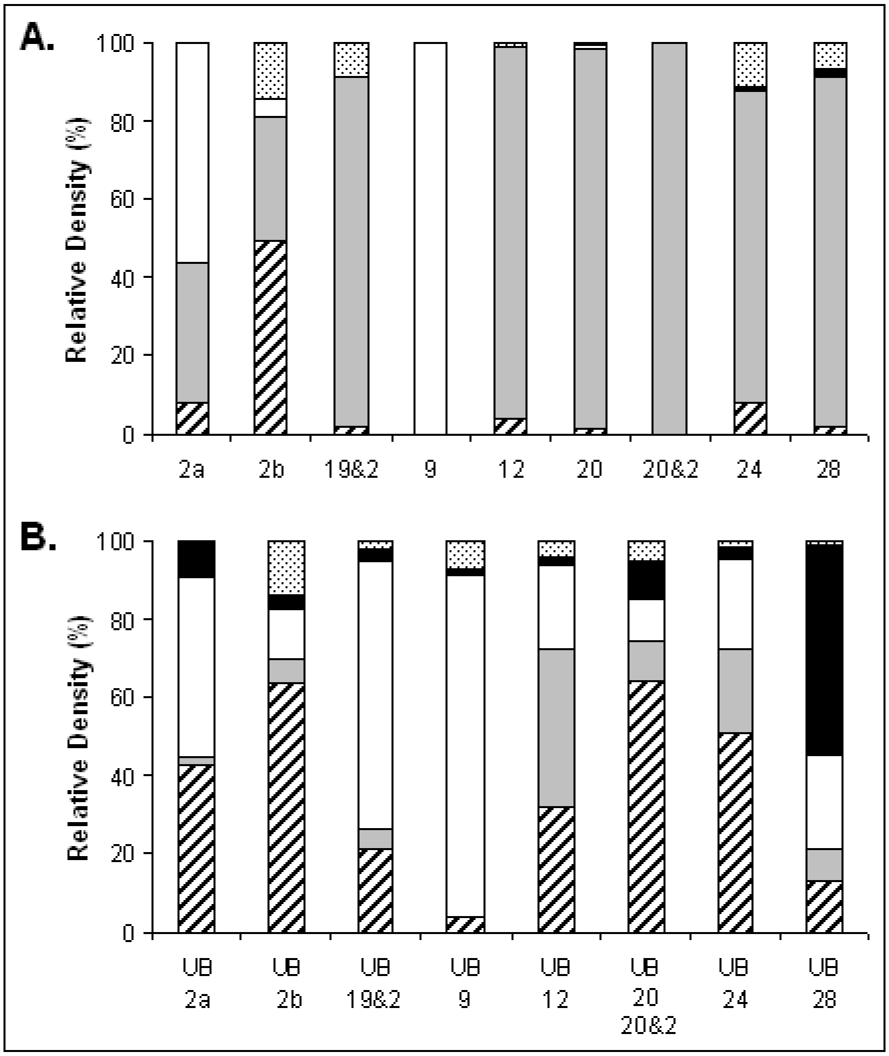

Figure 1.4 Relative density of live shrubs and cacti in paired burned and unburned stands. A. Relative density of burned stands. B. Relative density of unburned (UB) stands listed by corresponding burned stand. *Ambrosia dumosa* relative density is represented by diagonal lined bars, *Encelia farinosa* by grey bars, *Larrea tridentata* by white bars, cacti by black bars, and other shrubs by speckled bars.

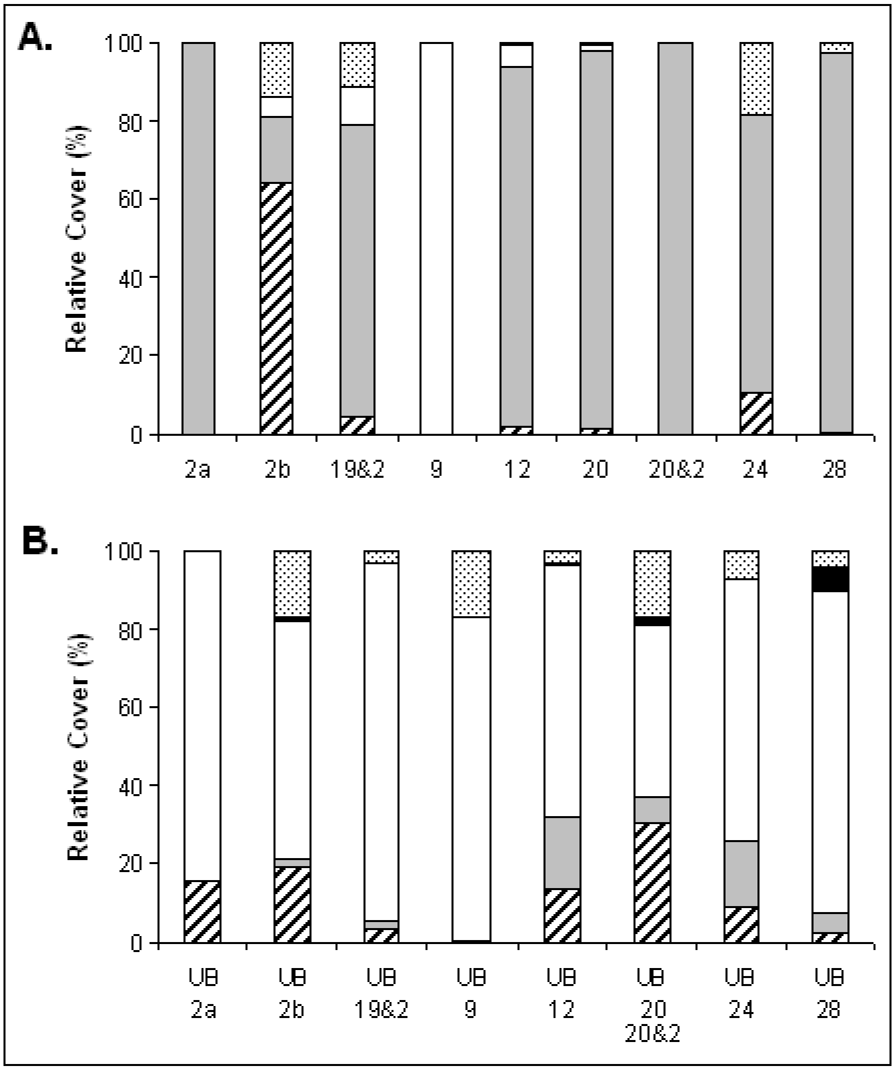

Figure 1.5 Relative cover of live shrubs and cacti in paired burned and unburned stands. A. Relative cover of burned stands. B. Relative cover of unburned (UB) stands listed by corresponding burned stand. *Ambrosia* dumosa relative cover is represented by diagonal lined bars, *Encelia farinosa* by grey bars, *Larrea tridentata* by white bars, cacti by black bars, and other shrubs by speckled bars.

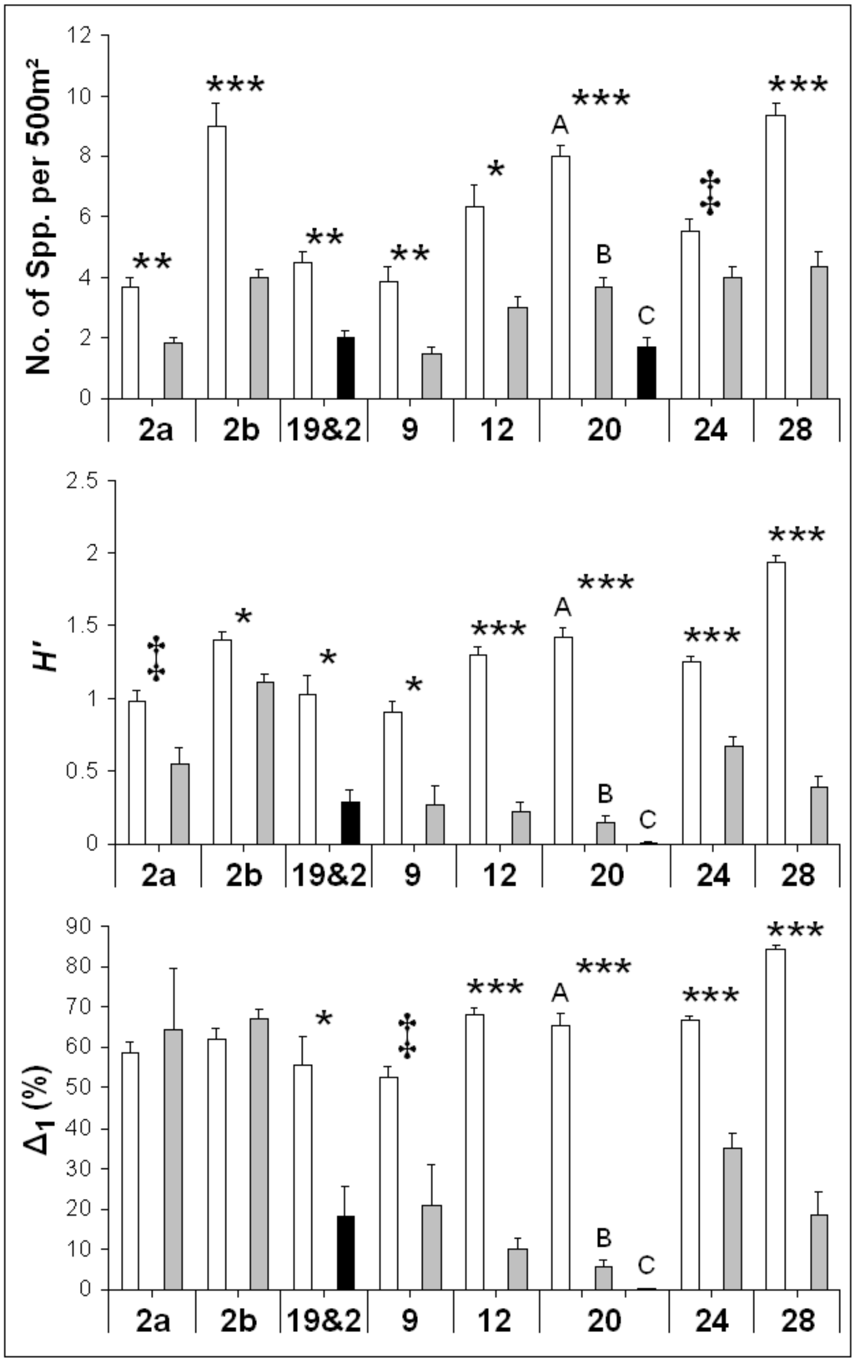

Figure 1.6 Average live shrub and cacti species richness per 500m², Shannon diversity (*H'*) per 500m², and probability of interspecific encounter (Δ_1) per 500m² (as a percentage). Symbology above paired unburned (grey) and burned (black) stands per site represent significant differences, where ‡, *, **, *** represent significance at $\alpha = 0.05$, 0.01, 0.001, 0.0001, respectively. Also for site 20, letters indicate significant differences between each of the three paired stands at $\alpha = 0.05$ based on the LSD test.

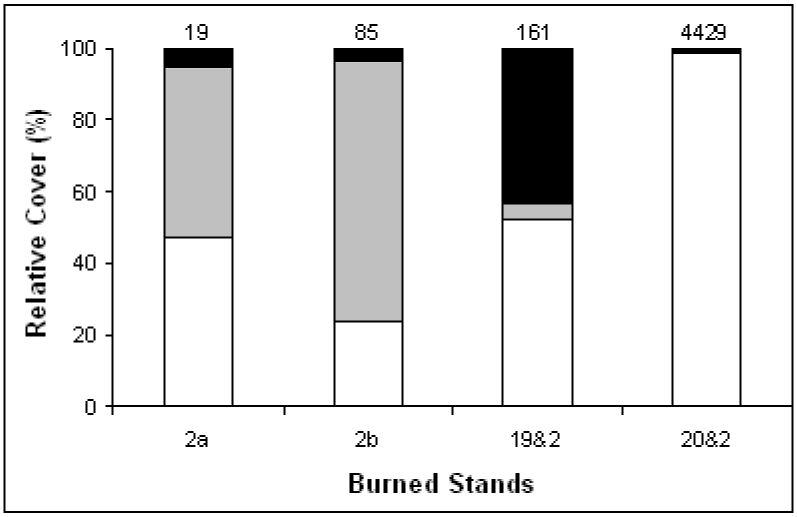

Figure 1.7 Relative density of seedlings (white), resprouts (grey), and fire survivors (black) from the four stands that most recently burned. Numbers above each bar indicate *n*.

Table 1.1 Average live density (500m^{-2}) of perennial species in paired unburned and burned stands per study site. Species in bold were statistically analyzed to compare their density values between paired stands per site. Density values in bold indicate significant differences at α = 0.05 between paired unburned (UB) and burned (named by tsf) stands per site. Significant differences at α = 0.01, 0.001, and 0.0001, were represented by the symbols *, **, and ^, respectively.

Family	Species	UB	2a	UB	2b	UB	19&2	UB	9
SHRUBS AND CACTI									
Asclepiadaceae	*Asclepias subulata*								
Asteraceae	*Acamptopappus sphaerocephalus*			0.3					
	Ambrosia dumosa	**16.5***	0.2	**53.3***	6.7	**5***	0.5	1.2	
	Bebbia juncea			0.2			1.7		
	Encelia farinosa	0.8	1.5	5.2	3.8	0.2	**24.8***		
	Hymenoclea salsola			1.2					
	Viguiera parishii								
Cactaceae	*Echinocereus engelmannii*	0.8		0.2				0.2	
	Ferocactus cylindraceus	0.2		0.2		0.5			
	Mamillaria tetrancistra			0.2					
	Opuntia basilaris			0.8					
	Opuntia bigelovii								
	Opuntia echinocarpa	2.7		1.8				0.2	
Capparaceae	*Isomeris arborea*								
Ephedraceae	*Ephedra californica*			7.5	1	0.2		2.2	
Fabaceae	*Acacia greggii*			0.3					
	Psorothamnus arborescens			1.5	1.2				
Krameriaceae	***Krameria grayi***			**6.5***	0.7	**3.7***		**11.5***	0.8
Lamiaceae	*Salazaria mexicana*					0.5			
Liliaceae	*Yucca Schidigera*			0.2					
Polygonaceae	*Eriogonum fasciculatum*					0.2			
Rutaceae	*Thamnosma montana*			0.2					
Zygophyllaceae	***Larrea tridentata***	**16.8***	1.5	**10.5***	0.7	**15****		**25***	4.7
HERBACEOUS PERENNIALS									
Asteraceae	*Stephanomeria pauciflora*			0.3		0.2	0.2		1
Cucurbitaceae	*Cucurbita palmata*				0.3				
Euphorbiaceae	*Croton californica*								
	Ditaxis neomexicana				2.3				
	Stillingia linearifolia				0.2				
Malvaceae	*Sphaeralcea ambigua*								
Nyctaginaceae	*Mirabilis bigelovii*			0.2		0.8	0.2	0.2	
Solanaceae	*Datura wrightii*								

Table 1.1 Continued on next page

Table 1.1 Continued…

Family	Species	UB	12	UB	20	20&2	UB	24	UB	28
SHRUBS AND CACTI										
Asclepiadaceae	*Asclepias subulata*	0.2								
Asteraceae	*Acamptopappus sphaerocephalus*	1.5								
	Ambrosia dumosa	**20.5***	3	**62.7^**	3.2	0.2	**26.7**	6.5	**5.7**	2
	Bebbia juncea	0.2	0.5							0.5
	Encelia farinosa	26.3	**94.5***	9.8	281	**737.3^**	12.5	**60.7***	3.5	**82.5***
	Hymenoclea salsola		0.2				0.2	2		6
	Viguiera parishii			1.2	1.3	0.5				
Cactaceae	*Echinocereus engelmannii*			2.5					2.2	0.5
	Ferocactus cylindraceus	0.7		0.2					8.8	0.2
	Mamillaria tetrancistra								0.5	
	Opuntia basilaris	0.2					0.2		2.7	0.5
	Opuntia bigelovii	0.2						0.7	2.2	
	Opuntia echinocarpa	0.2		7			1.2		6.5	0.3
Capparaceae	*Isomeris arborea*							0.2		
Ephedraceae	*Ephedra californica*			3.3					0.3	0.3
Fabaceae	*Acacia greggii*									
	Psorothamnus arborescens						1	4.8		
Krameriaceae	***Krameria grayi***	**1.3**		**16.3^**	0.3		**4.5***		3	
Lamiaceae	*Salazaria mexicana*									
Liliaceae	*Yucca Schidigera*	0.3	0.2	0.5		0.2			0.2	
Polygonaceae	*Eriogonum fasciculatum*	0.2								
Rutaceae	*Thamnosma montana*	0.5								
Zygophyllaceae	***Larrea tridentata***	**13****	0.2	**10.3^**	3		**9.7***	0.3	**10***	0.3
HERBACEOUS PERENNIALS										
Asteraceae	*Stephanomeria pauciflora*	0.5	1.5				0.5	3.2		0.5
Cucurbitaceae	*Cucurbita palmata*									
Euphorbiaceae	*Croton californica*						0.3	25.5		
	Ditaxis neomexicana		0.2						2	4.8
	Stillingia linearifolia		4.5							
Malvaceae	*Sphaeralcea ambigua*							0.2		
Nyctaginaceae	*Mirabilis bigelovii*	0.5	0.3	0.7		1.7			2.3	6.5
Solanaceae	*Datura wrightii*							0.2		

Table 1.2 Average cover (%) of live perennial species in paired unburned and burned stands per study site. Species in bold were statistically analyzed to compare their cover values between paired stands per site. See Table 1 for symbol interpretation for statistical differences between paired stands. The '<' symbol represents cover values less than 0.1%.

Family	Species	UB	2a	UB	2b	UB	19&2	UB	9	UB	12	UB	20	20&2	UB	24	UB	28
SHRUBS AND CACTI																		
Asclepiadaceae	*Asclepias subulata*									0.2								
Asteraceae	*Acamptopappus sphaerocephalus*									<								
	Ambrosia dumosa	**1.8***		**3.9**	0.8	0.3	<	<		**1.9***	0.3	**6.3****	0.4		0.9	1	0.4	<
	Bebbia juncea						0.2				<							
	Encelia farinosa		0.1	**0.4**	<	0.2	**2.3**			2.5	**9.8***	1.3	**27.1****	4.4	1.7	**6.6**	0.6	**12.6**
	Hymenoclea salsola															0.2		0.3
Cactaceae	*Echinocereus engelmannii*											0.3						
	Ferocactus cylindraceus									<							0.2	
	Mamillaria tetrancistra																<	
	Opuntia basilaris			<													<	
	Opuntia bigelovii									<							<	
	Opuntia echinocarpa			0.2								0.2	<		<		0.5	
Ephedraceae	*Ephedra californica*			1.6				0.1				0.3						<
Fabaceae	*Psorothamnus arborescens*			0.8	0.3							0.2			0.2	1		
Krameriaceae	***Krameria grayi***			**1.5**		0.3		**2.1***		<		**2.9****			0.7		0.7	
Rutaceae	*Thamnosma montana*									0.2								
Zygophyllaceae	***Larrea tridentata***	**11***		**13.1***	<	**8***	0.1	**9***	0.6	**9***	0.6	**9****	0.6		**7.1***		**11.1***	<
HERBACEOUS PERENNIALS																		
Asteraceae	*Stephanomeria pauciflora*															0.1		<
Euphorbiaceae	*Croton californica*															0.7		
	Stillingia linearifolia										<							
	Ditaxis neomexicana																0.1	<
Nyctaginaceae	*Mirabilis bigelovii*									<	<	<					<	<
Solanaceae	*Datura wrightii*															<		

Table 1.3 Vegetation structure. Average cover (%) and density values (500m^{-2}) in paired unburned and burned stands per study site. Values in bold indicate significant differences at $\alpha = 0.05$ between paired unburned (UB) and burned (named by tsf) stands per site. Numbered superscripts between paired stands at site **20** indicate significant differences based on LSD tests. The '<' symbol represents cover values less than 0.1%.

	UB	**2a**	**UB**	**2b**	**UB**	**19&2**	**UB**	**9**	**UB**	**12**	**UB**	**20**	**20&2**	**UB**	**24**	**UB**	**28**
Interspace Cover (%)	75.7	**92**	66.4	**85.1**	85.1	**93.4**	81.6	**90.9**	75.2	**86.4**	65.7^{1}	48^{2}	**85**^{3}	85.4	89	78.4	81.5
Live and Dead Perennial Cover (%)	**24.3**	8	**33.6**	15	**14.9**	6.6	**18.4**	9.1	**24.8**	13.6	34.3^{1}	**52**^{2}	15.1^{3}	14.6	11	21.6	18.5
Live Shrub & Cacti Cover (%)	**12.8**	0.2	**21**	1.1	**8.7**	2.7	**11.3**	0.6	13.8	10.8	20.2^{1}	**28.2**^{2}	4.4^{3}	10.6	8.9	13.6	13.1
Dead Shrub & Cacti Cover (%)	**11.9**	8	14.2	13.8	6.4	3.9	7.2	8.5	**11.4**	3	15.1^{1}	**27.4**^{2}	11.1^{1}	**4**	1.4	8.1	5.4
Live Herbaceous Perennial Cover (%)									<	<	<				**0.9**	0.2	0.2
Live Shrub and Cacti Density (500m-^{2})	**37.8**	3.2	**90.3**	14	26.2	27	**40.2**	5.5	65.2	98.5	113.8^{1}	288.8^{2}	**738.2**^{3}	55.8	75.2	46.3	**93.2**
Dead Shrub and Cacti Density (500m-^{2})	**86**	24.2	**68**	36.7	69.2	38	44.8	38.2	**87.5**	30	105.7^{1}	131^{1}	**190.5**^{2}	**75.5**	25	80	79
Live Herbaceous Perennial Density (500m-^{2})			1.5	2.8	1	0.3	0.2	1	1	6.5	0.7^{1}	^{1}	**1.7**^{2}	0.8	**29**	4.3	**11.8**

Table 1.4 Average shrub height by species for all unburned stands. *n* = the total number of shrub heights measured per species. The standard error (SE) for species height is also shown.

Species	***n***	**Height (m)**	**SE**
A. sphaerocephalus	1	0.45	
A. dumosa	152	0.57	0.01
A. subulata	1	1.28	
E. farinosa	61	0.58	0.02
E. engelmannii	3	0.31	0.02
E. californica	14	0.78	0.06
F. cylindraceus	6	0.46	0.09
K. grayi	51	0.64	0.02
L. tridentata	315	1.72	0.03
M. tetrancistra	1	0.09	
O. basilaris	3	0.22	0.05
O. bigelovii	3	0.46	0.22
O. echinocarpa	13	0.76	0.05
P. arborescens	7	1.25	0.16
T. montana	1	0.41	

CHAPTER 2. Post-fire annual plant dynamics on the western edge of the Colorado Desert.

ABSTRACT

Fire in creosote bush scrub (CBS) may become more common in the future as exotic annual grasses continue to invade this habitat and alter fuel characteristics. These grass species not only promote fire but are also aggressive fire-followers. Field observations indicate that invasive plants may cause type conversion of CBS into exotic annual grassland based on the invasive plant –fire regime. Six sites that had burn ages from 3 to 29 years ago, including one site that had burned twice, and their respective, paired, unburned reference stands, were surveyed for annual plant cover and species richness. Multilinear regression revealed a positive correlation between invasive grass abundance and soil nitrogen among unburned reference stands, which suggests that nitrogen deposition may exacerbate invasion and fire disturbance in the study region. Recently burned stands exhibited increased invasive annual grass abundance after fire due to a positive *Schismus* spp. response. *Erodium cicutarium*, an invasive forb, also significantly increased following fire while native annual plant cover and species richness were reduced. The impact of two fires per stand was especially severe, with significant reductions in native annual plant richness each time a stand burned, and significantly lower native diversity and increased homogenization of the native annual community in the twice burned stand. Based on analyses of current geographical distribution of annual plant species found in recently burned stands, annuals whose current ranges extended well into cismontane vegetation types were less impacted by fire than annuals restricted

to transmontane vegetation, which historically experience less fire disturbance. Biogeographic derivation (Arcto-Tertiary, Madrean, etc.) of the native annual plants was not important in explaining positive or negative responses following fire. Because most native annuals in the study area are assumed to be adapted to fire disturbance based on their current distributions in more fire prone plant communities of cismontane California, losses in native annual plant abundance and richness after fire may best be explained by competitive exclusion by invasive annuals. However, more interior desert locales that are primarily composed of transmontane restricted annual taxa may be more sensitive to fire per se. Overall, fire in the context of invasive annual plants is detrimental to native annual plant assemblages in CBS. Burned stands generally formed near monotypic stands of *Encelia farinosa* shrubland with an herbaceous component dominated by invasive plants.

INTRODUCTION

Invasive annual grasses in western North American shrublands can alter the fire regime by increasing the frequency, intensity, extent, and seasonality of fire (Brooks et al. 2004). In creosote bush scrub (CBS), these invasive grasses differ fundamentally from the dominant native annual forbs that they often displace. For example, invasive annual grasses dry out earlier than most native annual forbs and also have persistent standing biomass throughout the dry season, unlike most native annuals (Brooks 1999). One problematic result of grass invasion for CBS vegetation is longer-lasting horizontal fuel connectivity between widely spaced shrubs (Brooks et al. 2004). In addition, invasive grasses can also form higher density assemblages than native vegetation (Steers dissertation – Chp. 3), thus increasing the fuel packing ratio and consequently, fire intensity.

Due to the invasiveness of alien annual grasses and their fire-promoting traits, D'Antonio and Vitousek (1992) referred to the phenomenon of invasive grass – fire feedback as the 'grass/fire cycle.' Recently, Brooks et al. (2004) expanded this concept as the 'invasive plant – fire regime cycle' to include other invasive species lifeforms. The main premise of these models, as they relate to CBS, is that invasive grass invasion will promote fire by altering fuel characteristics of a site, which will then affect the fire regime, and will consequently promote invasive annual grasses in a positive feedback loop. The end result, in worse-case scenarios, is type-conversion to invasive annual grassland similar to what has been observed throughout much of the Great Basin (*reviewed in* D'Antonio and Vitousek 1992). However, while evidence clearly demonstrates how invasive grasses have promoted fire in CBS, few examples of increased invasive annual grass abundance, post-fire, exists for CBS in the literature (see Cave and Patten 1984, Brown and Minnich 1986, Brooks 2002). Also, examples of type-converted CBS shrublands as persistent, stable invasive grasslands are non-existent to my knowledge.

The primary foci of most studies examining fire in CBS have been the perennial components of the vegetation. Previous studies have documented reductions in cacti and the dominant long-lived shrub components (O'Leary and Minnich 1981, McLaughlin and Bowers 1982, Brown and Minnich 1986, Bazzell 1988, Alford et al 2005, Brooks and

Minnich 2006). However, most of these studies did not measure annual vegetation or did so at a crude resolution, except see Cave and Patten (1984) and Brooks (2002). Because native annual species differ in many ways from the long-lived shrub components of CBS, it is likely that the impact of fire on annual plants could vary greatly from that observed on the shrubs. The Mojave and Sonoran Deserts are geologically recent in origin (Pliocene-Pliestocene), yet many of the shrub components are thought to have evolved in more ancient xeric ecosystems during the Paleogene. In contrast, many of the annual plants have evolved more recently (Holocene) (Thorne 1986). A high percentage of California desert annual species also occur in cismontane California (Raven and Axelrod, 1995). The persistence of some desert annuals in cismontane vegetation types that are more prone to fire disturbance suggests that fire tolerance may be relatively high for the annual habit compared to desert shrubs.

Fire disturbance has been historically rare in CBS until invasive annual grasses and human ignition sources became increasingly more common in recent times (Schmid and Rogers 1988, Brooks and Esque 2002, Alford et al. 2005, Brooks and Matchett 2006). The goal of this study was to document the impact of fire on native and invasive annual plants by investigating a number of burns that ranged in time since fire (tsf) and had burned more than once. Specifically, I wanted to determine if fire promotes invasive annual abundance and if there was evidence for type-conversion to invasive annual grassland. Annual vegetation was sampled in the field and from seedbank assays in a glasshouse. Seedbank assays were utilized since above ground plant performance is linked to propagule abundance (Olano et al 2005, Cox and Allen 2007). Also, seedbank assays are useful in desert environments since high interannual variability of rainfall can have a large effect on above ground annual species composition between years (Freas and Kemp 1983, Philippi 1993, Pake and Venable 1996). Finally, I investigated species-specific responses to fire in order to determine which annuals are more or less impacted by this type of disturbance. The response of these annual plants to fire was then compared based on each species biogeographic derivation/origin and their current floristic province affinity/geographic distribution.

METHODS

STUDY AREA

The study area was located on the western edge of the Coachella Valley in Riverside County, CA (Figure 1). This valley forms the extreme northwest portion of the Colorado Desert and transitions into the Mojave Desert to the north, and into cismontane vegetation of the California Floristic Province towards the west and south. The primary vegetation in this region is CBS on the valley bottoms with pockets of degraded desert\coastal sage scrub or desert chaparral on north facing slopes of Mt. San Jacinto. Degraded desert scrub also exists on lower slopes of the San Bernardino Mts. and then transitions into chaparral at higher elevations. A rich post-1960 fire chronosequence exists for the CBS vegetation that dominates the valley and eastern reaches of the Banning Pass and several burned sites have been investigated previously (O'Leary and Minnich 1981, Brown and Minnich 1986). The high fire frequency in CBS of this area is primarily due to persistent invasive grass biomass, thought to be promoted by relatively high rainfall compared to other desert locales to the east, and by heavy anthropogenic nitrogen deposition that originates upwind in the Los Angeles Basin (Fenn et al. 2003, Rao 2008, Allen et al. 2009). Average precipitation in the city of Palm Spring to the east of the study area is 13.1cm while to the west, at Cabazon, average precipitation is 39.9cm (WRCC 2008). Creosote bush scrub reaches its western-most extent in the Banning Pass near the eastern border of Cabazon.

STUDY SITE DETERMINATION

In the spring of 2006, potential study sites were selected based on stereoscope validation of fire perimeters from a series of aerial photographs of the study landscape, spanning from 1949 to 2005. Aerial photos were obtained from Riverside County Flood Control and Water Conservation District, Coachella Valley Water District, and UC Riverside Science Library. The year when examined aerial photos were taken include the following: 1949, 1957, 1974, 1980, 1984, 1985, 1986, 1987, 1989, 1990, 1995, 1996, 1998, 2000, and 2005. Dates of the fires at each site were first determined from the aerial photos, but historic Los Angeles Times articles via ProQuest© (http://www.proquest.com), personal communication with R. Minnich (UC Riverside), and personal observations for all fires that occurred in 2005 were also used to date the year of fire. At two of the study sites utilized, the year of fire was only narrowed down to a 2 yr period. Since fires in desert vegetation are more common following winter seasons with above average rainfall (Brooks and Matchett 2006), the wetter of the two possible burn years is reported in this experiment as the assumed burn year.

Respective unburned reference stands for all of the burned stands were also identified from aerial photographs in the spring of 2006. All paired unburned reference sites existed in similar areas of shrub cover to pre-fire conditions based on aerial photographs. They were also located opposite of fuel breaks (dozer-lines, dirt roads, or paved roads) to minimize fuel differences at the time of fire. Over twenty unique sites that had burned were identified in the study area from aerial photography, but after ground-truthing each site in July and August of 2006 only six sites were selected for this study. Sites dismissed from the study were done so mostly because of a lack of suitable unburned reference vegetation. Other reasons for dismissal were because of recent grazing history (determined in the field), irregular soil type (based on NRCS soils maps or % sand, silt, and clay analyses), or to minimize climatic variation. The six sites selected ranged in year burned from 1979 to 2005 with a time since fire (tsf) of 3, 3, 10, 13, 21, and 29 years. In addition, one of these sites also included an area that had burned twice (tsf: 21&3 yrs). The names of the sites correspond directly to tsf. Two of the sites that had burned in the same year were given the suffix ‘a’ and ‘b’ while the third site that had burned in the same year had also burned 21 years ago (see above). Please see Figure 1 for site names and locations within the study area.

SOIL AND VEGETAION SAMPLING

In August and September of 2006, 6 sampling units were implemented in a stratified random design in both the unburned and paired burned reference vegetation at all six sites. Sampling units consisted of one circular modified-National Weed

Management Association (mod-NAWMA) plot (Figure 2) (Stohlgren et al. 2003). Slope and aspect were measured from the center of each plot using a SUUNTO® Tandem compass/clinometer. Soil was also collected for chemical, physical, and seedbank analyses. For nutrient analyses, four soil samples per mod-NAWMA plot were taken up to 5cm depth with a 2.5cm diameter corer and pooled into one composite sample per plot. The four samples were taken at the center and at three edge locations (7.32m from plot center), at 30, 150, and 270 degrees from plot center. For soil seedbank samples, four cores per plot were also sampled similarly to the nutrient samples except 5cm diameter cores were used instead. One core with the same dimensions used for seedbank samples was taken at the center of the plot for bulk density, coarse fraction (>2mm), and soil texture measures. All soil sampled was taken at a 5cm depth. Soil pH from the four pooled soil samples taken with the 2.5cm diameter core was measured using a Fisher Scientific® Model 50 pH meter. The same soil samples were then analyzed for carbon (C) nitrogen (N), NH_4^+, and NO_3^- by the UC Davis Analytical Laboratory (http://groups.ucanr.org/danranlab) in addition to % sand, silt, and clay from the 5 cm diameter core.

Soil seedbank samples were assayed by growing them out in a glasshouse and counting the number of seedlings per species (Cox and Allen 2007). Pooled samples were sieved through a 6x6 mm mesh, making sure not to remove any seeds, and then the all of the remaining material for each sample was spread out on 20 x 20cm styrofoam trays. Soil depth in each tray ranged from 1 to 2cm. Trays were kept moist and seedlings were removed when identifiable or at a stage where they could be transplanted safely to conetainers to await identification. Watering continued in all trays until no new seeds germinated and then trays were left to dry. Once the soil in each tray was dry, it was mixed before the next watering cycle. Three cycles of watering and drying took place from September 2007 to May 2008. By the third cycle, negligible amounts of germinated annuals appeared so further cycles were not implemented. Throughout the watering, trays were reorganized several times to minimize localized effects within the glasshouse.

In the winter wet-season of 2006-07, insufficient rainfall prevented the germination of annual plants at the study sites and no vegetation measurements were taken. In the wet season of 2007-08, precipitation was about average and vegetation was sampled throughout March 2008 during peak flowering in each established mod-NAWMA plot (Figure 2). Percent cover by species and species richness were measured in three $1m^2$ (1 x 1m) quadrats per mod-NAWMA plot, located 4.57m from plot center at 30, 150, and 270 degrees. Species richness was measured within each of the three $1m^2$ quadrats per mod-NAWMA plot and also within each mod-NAMWA plot (out to a 7.32m radius from plot center).

DATA ANALYSES

Vegetation at each of the six study sites was categorized into invasive grass cover, invasive forb cover, total invasive cover, native annual cover, herbaceous perennial cover, and native shrub cover at the $1m^2$ scale (in quadrats). For all analyses, shrub data included species in the Cactaceae. Species richness of invasive annuals, native annuals, and shrubs was also calculated at both the $1m^2$ and mod-NAMWA plot scales. These parameters were used to compare the unburned stands of the six study sites. Linear regression was also used to determine correlations between shrub and native annual richness, and invasive and native annual richness at both scales.

To determine relationships between invasive plant cover and soil characteristics, a multilinear regression based on standard least squares was utilized. First, a correlation matrix found significant ($p < 0.05$) collinearity among several independent variables. Total N exhibited collinearity with total C ($R^2 = 0.9086$), NH_4^+ ($R^2 = 0.6089$), and NO_3^- ($R^2 = 0.3849$). Percent sand exhibited collinearity with percent silt ($R^2 = -0.9692$) and percent clay ($R^2 = -0.8439$). Variables exhibiting collinearity were removed from the model. The final reduced rank model included the following variables: total N, percent sand, pH, coarse fraction, bulk density, percent bare ground cover, percent rock cover, and percent litter cover. The same reduced rank model was then used to analyze native annual species richness (/m²) as the dependent variable. The two dependent variables, invasive annual plant cover and native annual richness (/m²), were chosen for multivariate analyses because they exhibited the strongest negative correlation ($R^2 = -0.7982$) among all combinations of invasive and native vegetation variables at both scales.

To compare the soil and vegetative variables between unburned and paired burned stands, ANOVA was utilized at $\alpha = 0.05$. Fisher's LSD test was also used to determine differences between the unburned (UB), burned (21), and twice burned (21&3) stands at site **21**. When comparing shrub cover, Kruskal-Wallis tests were used instead, since this data was not normally distributed.

Additional vegetation variables were also utilized to investigate the impact of repeated burns using data from site **21**. At the 1m^2 scale, Shannon Diversity (*H'*) was calculated based on native annual richness and cover by species (Shannon and Weaver 1963). Also, native annual plant similarity (*S*) was calculated from the three 1m^2 frames per mod-NAMWA plot for multiple-plot community coefficients based on a modification of the Sorenson index (Diserud and Ødegaard 2007), using the equation: $S = (3/2)((ab + ac + bc - abc)/(a + b + c))$, where *a* is the number of species in plot frame A, *b* is the number of species in plot frame B, etc… and *ab*, *ac*, *bc*, and *abc* are the number of species shared between plot frames A and B, A and C, B and C, and A, B, and C, respectively. Annual plant diversity and similarity at the $1\ \text{m}^2$ scale in addition to other basic parameters described previously were compared between all three burn conditions using ANOVA with the LSD test at $\alpha = 0.05$.

To determine the impact of fire on seedbanks, individuals recorded were grouped by invasive grass, invasive forb, native annual, and shrubs. The densities of plants in these groups, in addition to native annual plant richness, were square root transformed to improve normality. Statistical analyses were performed by site using ANOVA, with LSD tests where appropriate at $\alpha = 0.05$.

Species-specific responses to fire were evaluated between paired unburned and burned sites for the three sites with the most recent burns, **3a**, **3b**, and **21** (tsf 21&3). Only sites that had burned in the summer of 2005 were utilized even though some fires older than 3 years of age still had severely decreased native plant richness compared to their respective paired unburned stands. After above average precipitation in 2004-05 and increased fire activity the following summer (2005), the wet season of 2005-06 was below average. Then in 2006-07 there was very little precipitation (NCDC 2008) and no germination of annual plants in CBS of the study area (Steers, personal observation). Due to the lack of precipitation after the fires in 2005, species-specific differences in the post-fire communities are assumed to be attributed to within-stand effects from fire and less influenced by dispersal of propagules from surrounding unburned vegetation. Species-specific effects of the recent fires were investigated by comparing the cover of each species by burn class (unburn, burn, and twice burned) for the three sites separately. Only species that exhibited at least 0.1% cover in any one of the burn classes per site were included in the analyses. Plant cover data for annual species were arcsin transformed and statistically analyzed using ANOVA or ANOVA with a LSD test for the one site with the three burn classes. Species that still exhibited nonnormal data after transformation were analyzed using the Kruskal-Wallace test.

All of the species from these three sites were also compared based on their biogeographic derivation/origin and their current geographic range. Species were categorized by biogeographic derivation (Arcto-tertiary, Madrean, Californian, or Desert) based on summaries by Raven and Axelrod (1995). Species were then categorized by their current geographic distribution using species range descriptions in the most current flora of California (Hickman 1996). Two categories were used for geographic range, transmontane and cismontane. Species classified as transmontane were restricted to transmontane vegetation or only entered the California Floristic Province in dry locales such as Tehachapi (Teh), San Jacinto Valley (SnJV), and eastern margins of the interior

Coast Range (SCoRI) where precipitation is desert-like (see Hickman 1996). Species categorized as cismontane were those species found at the study site that had ranges extending well into mesic cismontane locales, not counting the dry, desert-like regions described above. After species were grouped according to the categories listed above, the percent change in cover of each category based on the average cover value of a category in the unburned stand was determined per burned stand per site. When comparing percent change of biogeographic derivation, annuals derived from the 'Desert' were left out of the analyses since only three species made up this group and responses were outliers based on very strong post-fire increases in *Plantago ovata*. The positive response to fire by *P. ovata* has been documented previously in the study area (Brown and Minnich1986) and in Upland Sonoran Desert Scrub of Arizona, USA (Cave and Patten 1984). Species responses to fire were statistically evaluated by biogeographic derivation and current geographic range using ANOVA and LSD analyses as described previously. All species nomenclature follows Hickman (1996).

RESULTS

Vegetation of Unburned Reference Stands

The CBS of the study site was dominated by *Larrea tridentata* and *Ambrosia dumosa* was usually sub-dominant. *Ambrosia dumosa*, *Krameria grayi*, *Encelia farinosa*, and several species of Cactaceae exhibited a high amount of die-back, possibly due to the droughts of 2001-02 and 2006-07 (*sensu* Paddock 2006, Miriti et al. 2007; NCDC 2008). Various shrub species typical of Colorado desert CBS were documented as well as several herbaceous perennials (Table 1). In addition, 54 native annual species were recorded (Table 2). Most invasives encountered in the field surveys and seedbank assays were annual plants that were ubiquitous throughout the study area, such as *Brassica tournefortii*, *Erodium cicutarium*, *Schismus spp*, and *Bromus madritensis* (Table 2).

At the mod-NAWMA scale (168.3m²), the unburned stand at site **21** had the greatest invasive annual species richness with a mean of 4.7 invasive annuals per plot (Table 2). Unburned stands **3b** and **21** had the highest average native annual richness at 25.3 and 20.7 species, respectively. Both sites, in addition to site **29**, had the greatest average native shrub species richness per mod-NAWMA plot (Table 1). In general, sites with the highest native annual richness appeared to have the highest invasive annual richness at this scale (Table 2). When this relationship was analyzed across all sites, invasive annual and native annual richness showed positive correlation ($R^2 = 0.27$, $p < 0.0001$). Shrub richness and native annual richness also showed positive correlation at this scale ($R^2 = 0.18$, $p = 0.0001$).

At the 1m² scale, site **21** still had the greatest average invasive species richness at 3.6 spp. per m² (Table 3). Similarly, sites **3b** and **21** still had the highest average native annual species richness at 11.3 and 5.9 species per m², respectively (Table 3). Shrub richness between study sites at the 1m² scale also maintained a somewhat similar relationship to the larger plot scale except site **29** shrub richness dropped substantially in relation to the other sites, probably due to the high amount of cacti at this site that were less detectable at this smaller scale (Tables 1 and 3). Invasive annual and native annual richness were no longer correlated at this scale ($R^2 = 0.03$, $p = 0.1633$), and neither were shrub richness and native annual richness ($R^2 = 0.01$, $p = 0.3801$).

Invasive annual plant cover throughout the study area was very high, mostly attributed to invasive forbs, primarily *Erodium cicutarium* and *Brassica tournefortii* (data not shown). Invasive grasses were also substantial at some sites (Table 3). For example, site **3b** had the greatest invasive annual plant cover at 63%. Overall, however, invasive grasses only accounted for 34% of total invasive annual coverage across all unburned stands while invasive forbs accounted for 66% of total invasive coverage (data not shown). Native annual cover was less than invasive annual cover at every site except **3b** (Table 3). Herbaceous perennial cover was low (< 0.1%) at all unburned stands (data not shown) and live shrub cover ranged from about 3 to 19% between all of the unburned stands (Table 3).

Correlations of Soil and Vegetation in Unburned Stands

Multivariate analyses of soil factors with invasive annual plant cover as the dependent variable (DV) resulted in a significant model ($R^2 = 0.7829$, $p < 0.0001$). Percent cover of bare ground was the most important covariate for this model, exhibiting a strong negative correlation with invasive annual plant cover (Table 4). Soil pH was also negatively correlated with the DV. The only covariate with a positive correlation to the DV was total N (Table 3), which, due to its positive multicollinearity with total C, NH_4^+, and NO_3^-, was used as a surrogate for soil fertility. The second multivariate analyses, using native annual richness ($/m^2$) as the dependent variable, also exhibited a significant model ($R^2 = 0.598$, $p = 0.0007$). Percent cover of bare ground was the only significant covariate with this model and was positively correlated with native annual richness (Table 4).

Impact of Fire on Soils and Vegetation

Some soil parameters differed between burned and unburned reference stands while others did not seem effected by fire or time since fire (Table 3). Total N and C were usually greater in unburned stands compared to their paired burned stands at sites with more recent fires but the opposite was found at sites with the oldest fires. Extractable nitrogen (NH_4^+ and NO_3^-) did not show consistent patterns between paired burned and unburned stands. However, soil pH was consistently greater in paired burned stands, especially at sites that had recently burned. Also, percent cover of bare ground increased if a site had burned. The increase in bare ground of burned stands became more significant as time since fire increased. Litter cover had an opposite trend, where the greatest difference in this parameter between unburned and burned stands was found at sites that had more recently burned, and older stands showed no differences (Table 3).

Invasive grass cover was greater in burned stands than in respective unburned stands, especially for sites that have burned more recently (Table 3). In burned stands, relative invasive grass cover was highest immediately after a fire and then decreased as time since fire increased, while invasive annual forbs became relatively more abundant as time since fire increased (Figure 3). Both of these trends occurred despite assumed differences between sites in relative abundance of invasive grass, invasive forb, and native annual species at the time of fire (Figure 3). Fire reduced native annual cover at the $1m^2$ scale at sites **3a** and **21** (Table 3). Native annual plant richness at the $1m^2$ scale was also reduced by fire at sites **3b**, **13**, and **21** (Table 3). At the mod-NAWMA scale ($168.3m^2$), native annual richness was decreased by fire at sites **3a**, **13**, and **21** (Figure 4).

Live shrub cover was decreased by fires that had occurred three years prior (Table 3). However, shrub cover did not show differences between burned and unburned stands by 10 years after fire. The increase in shrub cover at some of the sites was due almost entirely to *Encelia farinosa* (Table 3). It appears that if *E. farinosa* is present at a site, then it will become the dominant shrub component of burned stands. If an *E. farinosa* dominated site reburns (see tsf "21&3"), shrub cover will return rapidly (Table 3) due to *E. farinosa* seedling recruitment and to a lesser extent, resprouting (Steers dissertation – Chp. 1). Shrub richness was also compared between paired burned and unburned stands. At the $1m^2$ scale, only sites **3a** and **3b** experienced decreased shrub richness in the burned stands ($p = 0.0157$, $p = 0.0033$, respectively), while all other sites showed no differences between paired stands (data not shown). However, at the mod-NAWMA scale, regardless of time since fire, shrub richness was always reduced in paired burned stands compared to unburned reference stands (Figure 4).

Impact of Repeated Fire on Vegetation

To further evaluate the impact of repeated fire on CBS vegetation beyond what has been previously examined (Table 3), additional analyses were performed on vegetative parameters from site **21**, which had a portion of area burned in 1988 and then burned again in 2005 (tsf 21&3). ANOVA with a LSD test revealed no difference in total invasive annual plant cover between the unburned, burned once (tsf 21) and twice burned (tsf 21&3) stands (Figure 5). However, absolute and relative invasive grass cover was highest in the twice burned stand (Table 3 and Figure 5).

When comparing the native vegetation, native annual plant cover and species richness at the 1 m^2 scale were reduced in both of the burned stands compared to the unburned stand (Table 3 and Figure 5). The stand that had burned twice did not have decreased native cover or richness compared to the stand that had only burned once. However, native annual plant diversity (Shannon Diversity – *H'*) was lower in the twice burned stand compared to the other two stands (Figure 5). Also, only in the twice burned stand was native annual plant similarity (Sorenson Index - *S*) greater than the unburned stand, suggesting that the more a stand burns, the more homogenized the native annual plant vegetation becomes at the 1m^2 scale (Figure 5). In other words, there is more dissimilarity or variety of annual species contributing to native cover and richness in unburned vegetation compared to burned vegetation, and especially compared to twice burned vegetation. At the larger mod-NAMWA scale (168.3m^2), native annual species richness decreased each time a stand burned, while shrub richness was reduced severely the first time it burned but showed no further decrease the second time it burned (Figure 5). However, measures of shrub richness at a large scale (500m^2) than the mod-NAWMA plots at this site show significant reductions in shrub richness after each burn (Steers dissertation – Chp. 1).

Seed Bank Assays

A total of 16,571 seedlings belonging to at least 31 species germinated during the study. About 94% of the germinated plants were *Schismus* spp. *Bromus madritensis* were very uncommon. The invasive forb, *Erodium cicutarium* made up about 2.1%, with 349 individuals counted, while *Brassica tournefortii* individuals only numbered at 87. Seventeen native annual species made up about 3.2% of the total seedlings counted. *Ambrosia dumosa*, *E. farinosa*, *L. tridentata*, and one unknown cactus that died prematurely made up seventeen seedlings in the shrub category. Besides one individual of the unknown cacti and three other unknown plants that died prematurely, all other individuals encountered were identified. Five species not encountered in the field surveys were assayed from the soil seedbank samples, including one individual each of the nonnative plants *Arabidopsis thaliana* and *Portulaca oleracea*. The other new species were natives, including three individuals of *Aristida adscensionis*, two of *Conyza canadensis*, and one each of *Gnaphalium californicum* and *Epilobium ciliatum*.

Analyses of the seedbank assays, which were taken at a scale of 78.5cm², showed less difference between paired unburned and burned stands than field survey data at the 1 m^2 and mod-NAWMA scales for invasive annual grass, invasive annual forb, native annual plant abundance, and native annual richness. At site **21**, the twice burned (21&3) stand had greater invasive annual grass density than the paired, burned once (21) and unburned stands (Figure 6). Site **29** also had greater invasive annual grass density in the unburned stand compared to the paired burned stand. Invasive annual forb density was greater in unburned stands than paired burned stands at sites **3a** and **10** (Figure 6). No differences in native annual plant density were found in the seedbank assays (Figure 6). At this smallest scale, native annual plant richness also showed no differences between burned and unburned stands at any of the sites (data not shown).

Responses of Native Annual Species to Fire

The percent cover of four invasive annuals and 26 native annuals was compared between paired unburned, burned, and twice burned (if applicable) stands for three sites in the study area that had experienced recent fires (Table 5). Among the invasive forbs, *Brassica tournefortii* responded both positively and negatively to fire while *Erodium cicutarium* only increased in cover in response to fire. Among the invasive grasses that were analyzed, *Bromus madritensis* decreased after fire while *Schismus* spp. increased. In general, most native annual plants species decreased in cover after fires (Table 5) and in frequency at the mod-NAWMA plot scale (Table 2). Of note, species that were restricted to understory microhabitats showed very strong decreases in cover in burned sites (Table 5), possibly due to lethal fire temperatures in these relatively productive microsites (Brooks 2002). In addition, the most dominant native annual in unburned stands at all sites, *Chaenactis fremontii*, also showed large decreases in cover in response to fire. *Emmenanthe penduliflora*, a common fire follower in cismontane shrublands (Keeley and Fotheringham 1998), showed increased cover with each burn at site **21**.

While most native annuals decreased in cover in response to the fires, some species were not as reduced as others, and some species even increased. To better understand these variable responses to fire, native annuals were split into several categories based on their biogeographic derivation/origin and their current geographic range (see Table 5 for categorizations). When comparing the response of native annuals by their biogeographic derivation, I found inconsistent responses (Table 6). For example, cover of species with a Madrean derivation increased in response to fire at site **3a**, while at the other two sites, Madrean species exhibited the lowest decrease in cover compared to all other biogeographic derivations. However, when comparing species responses to fire based on current geographic range, there were consistent responses between all three sites (Table 6). The abundance of species with ranges that extend well into cismontane California (CFP) were less impacted by fire than species primarily restricted to the deserts. This difference was enhanced greatly when native annuals associated with understory microhabitats were excluded from the analyses (see Table 5 for categorizations), thus minimizing variation attributed to elevated understory microhabitat fire intensity (Brooks 2002) (Table 6).

DISCUSSION

Vegetation of Unburned Reference Stands

For unburned stands, invasive annual grasses and forbs were ubiquitous across the study area and were dominant components of the annual assemblages, except site **3b** had slightly greater relative native cover than invasive plant (grass and forb) cover. Among all unburned sites combined, invasive grass cover was lower than invasive forb cover. Based on a separate experiment nearby (Steers dissertation – Chp. 4), more unique native annual species were recorded in unburned CBS during spring 2008 than in any of the three preceding seasons (unpublished data), which included one of the wettest on record (2004-05). Thus, this study may have missed documenting the upper potential of invasive annual grass abundance, resulting in a conservative view of the impact of fire on this species group. Alternatively, 2007-08 may have been an exceptional season for documenting the impact of fire on native annual plant diversity since native annuals were unusually abundant.

Relatively lower invasive grass cover observed in the spring of 2008 was partially due to preceding drought years that limited the abundance of *B. madritensis* over large areas of low elevation desert scrub such as in Coachella Valley (Salo 2004, Minnich 2008). All of the study sites that had burned 10 years ago or older were largely fueled by *B. madritensis* (Brown and Minnich 1986, Minnich *personal communication*). However, all of the fires in 2005, after *B. madritensis* abundance had decreased substantially, were primarily fueled by *Schismus* spp. (Steers *personal observation*).

The lower than expected relative cover of invasive annual grass in the spring of 2008 may be attributed to a possible decline in *Schismus* spp. that started in 2006, the first of two consecutive drought years. Based on data about 7km northeast of Palm Springs, taken at peak season in late January of 2006, about 30% of understory and interspace *Schismus* spp. experienced premature death or were severely stressed from drought (unpublished data). Therefore, a large amount of grass individuals may have died without replenishing the seedbank or at least experienced decreased fitness. In the following growing season (2006-07), precipitation events were never large enough to initiate germination, which could have further decreased *Schismus* spp. in the seedbank, similar to what occurs for B. madritensis (Salo 2004). Although seedbank samples in this study were collected over a year before the field vegetation sampling took place, invasive grass density in the seedbank assays was magnitudes greater than forb density. Therefore, the low relative cover of invasive annual grasses in the field was likely due to factors other than a lack of propagule abundance in the seedbank. Gutterman's (2003) finding that *Schismus arabicus* has a long-lasting seedbank in the Negev Desert also supports this conclusion. Alternatively, what I observed as a 'forb' year in 2008 could be a combined result of the timing of precipitation and temperature during germination that favored forbs over grasses (*sensu* Pitt and Heady 1978).

Correlations of Soil and Vegetation in Unburned Stands

In the first multiple linear regression of soil variables and invasive plant cover, total N was the only soil variable that exhibited a positive correlation. This finding strongly suggests that fertile sites may be more prone to invasion than relatively resource poor sites. It may also suggest that N deposition could increase invasive plants in this desert region, as supported by experimental manipulations (Brooks 2003, Allen et al. 2009). The second multivariate analysis examining soil variables with native annual richness (m^{-2}) revealed a correlation with only one soil variable, cover of bare ground, which was positive. In the first model, invasive plant cover experienced the strongest correlation of all variables with bare ground, which was negative. Because invasive plants directly limit native abundance and richness in burned or unburned CBS (Brooks 2000, Schutzenhofer and Valone 2006, Steers – Chps. 3 & 4), areas with high bare ground, less soil fertility, and consequently less invasive plant abundance appear to be acting as refugia for native species in the study area. Similar conclusions that relatively resource poor sites act as refugia for native annuals have been drawn from other highly invaded annual communities (Harrison 1999, Gea-Izquierdo et al. 2007).

Impacts of Single and Multiple Fires

Fires in the study area resulted in a few significant and/or long-lasting effects on soil parameters. Soil pH increased after fire, which is consistent with other studies from different vegetation types (*reviewed in* Raison 1979). The increase in cover of bare ground in all burned stands across the study area may be attributed to losses in shrub cover once sites are burned; however, the oldest burned sites had shrub cover at least as great as their respective paired unburned stands. It is not clear why bare ground increased with time while shrub cover (almost entirely *E. farinosa*) also increased. A possible consequence of fire in these arid shrublands could be higher rates of soil erosion, which would promote bare ground in a desertification-like process (*sensu* Belnap 1995). Such erosion may have been exacerbated in the older stands since they had a slightly steeper slope.

This study revealed that fires promote invasive annual grass abundance, which matched predictions based on the invasive plant – fire regime cycle (Brooks et al. 2004). The increase in invasive grass was especially evident at sites with a high proportion of native annual cover in paired unburned stands. Fire increased invasive annual grass cover within the first three years after a fire. This increase was due almost entirely to

Schismus spp. which has also been shown to increase after fire in CBS and other semi-arid shrublands (Cave and Patten 1984, Minnich and Dezani 1998, Brooks 2002). The potential for a consequent fire may be greatest within this time frame. However, since the study area is already heavily invaded by annual grasses and forbs, the potential for wildfire seems to be high regardless of previous fire history.

A goal of this research was to seek evidence for type-conversion to invasive annual grassland due to fire. Type-conversion of the annual component of CBS in the study area has mostly already occurred. Native annual assemblages have largely been displaced by a simple mix of invasive annual grasses and forbs in the absence of fire disturbance (this study). Because *Encelia farinosa* increases after fires and can form shrublands sometimes greater in cover than paired unburned stands, full type conversion to invasive annual grassland will not result unless *E. farinosa* is absent. Aside from several *L. tridentata* resprouts, this is basically what occurred at site **10**. However, since all other sites contained *E. farinosa*, *E. farinosa* shrublands are expected to form over time in these particular burned stands if they have not done so already (Steers dissertation – Chp. 1). *Encelia farinosa* dominated shrublands appear very stable and resilient to additional fires, as evidenced by the high amount of *E. farinosa* cover in the twice burned stand at site **21**. These shrublands will probably last for decades (Brown and Minnich 1986) or longer, (*implied from* Vasek 1983, Lovich and Bainbridge 1999). While invasive annual plant abundance eventually decreases after fire in cis-montane shrublands as the shrub canopy closes in (Keeley 2005), arid shrublands like the CBS and the *Encelia* dominated shrublands in post-fire stands of CBS of this study area do not form closed canopies and will never be able to limit invasive plants in this way. Regardless of whether or not CBS converts to invasive annual grassland, fires in this study area clearly promote invasive annual plants and can severely decrease native annual richness both in the first few years following fire and decades later when *E. farinosa* is dominant.

Even though the study area already has decreased native annual plants due to high abundance of invasive plants, fire disturbance can still significantly decrease this already marginalized native plant component. Brooks (2002) has reported that understory fire temperatures for *L. tridentata* can be lethal to annual species while interspace temperatures are much less hot and seem to have no effect. A portion of the decrease in native annual richness observed in this study is likely due to sensitivity of some native annuals to relatively high fire temperature in understories. This was especially evident for annuals that were primarily observed to occur almost exclusively in unburned, understory microhabitats of the study area. Although, these species were never totally eliminated from stands once they burned (Steers *personal observation*). Native annual plants in more fire prone communities, like chaparral, can also be negatively impacted by fire where the shrub canopy coverage (fuel) is high relative to gaps (Davis et al. 1989, Moreno and Oechel 1991, Tyler 1995, Odion and Davis 2000). In this study, fire temperatures in understories and interspaces of each burned stand were unknown and could have differed between sites. However, the resulting annual plant communities at all burned stands had a high resemblance to each other despite potential differences in fire intensity and in pre-fire annual species composition. Unfortunately, sites with the highest native abundance experienced some of the largest relative increases in invasive plants once burned, demonstrating how problematic fire disturbance is for CBS both directly, through killing some native annual seeds, especially in understories, and indirectly, through promoting certain invasive species like *Schismus* spp. and *E. cicutarium*.

A large percentage of the native annual plants sampled in this study, regardless of biogeographic derivation, are components of cismontane vegetation types like grasslands, coastal scrub, and chaparral (Hickman 1996), which experience relatively greater fire frequencies than CBS shrublands. These annuals are capable of persisting in cismontane vegetation despite the relatively greater impact of fire there (*implied from* Keeley and Keeley 1981, O'Leary and Minnich 1981, Rundel 1998, Brooks and Matchett 2006). In this study, these same species were less affected by fire than the annual species restricted to transmontane vegetation that burns relatively much less frequently. Unlike most of the shrub components of CBS that lack traits that enable resiliency to fire disturbance (Brooks and Minnich 2006), many native annual plants of the study area should be resilient to fire disturbance based on their current distributions even though there might be ecotypic differences between cismontane and transmontane populations.

I propose that fire *per se* is not necessarily detrimental to native annual plant assemblages in the study area, besides directly reducing some plant seed density in understories, but that fire disturbance in the context of invasive annual plant invasion is. I hypothesize that the decreases in native annual plant abundance and richness were primarily driven by increased invasive plant abundance that was promoted by fire disturbance and not solely due to fire itself, via sensitivity to the effects of this particular disturbance type. For example, post-fire removal of invasive plants in CBS of nearby Morongo Valley (~ 5km northeast) resulted in native annual assemblages that were similar in structure and species composition to relatively uninvaded, ‘pristine’ annual assemblages of unburned CBS for both interspace and understory microhabitats (Steers dissertation – Chp. 3). However, interior CBS shrublands that are composed of a greater proportion of strict transmontane annuals may be more sensitive to fire disturbance. Because the study area was located on the western edge of the desert, the proportion of native annual plant species common to cismontane vegetation was probably much greater than what would be found in locales further east. Results from this study must be considered with this context in mind.

CONCLUSIONS

Fires in CBS promote invasive annual grasses, especially within the first few years after fire due to increases in *Schismus* spp. *Bromus madritensis* decreases immediately after fire, as has been shown previously (Brooks 2002). Relative invasive annual plant abundance increases in burned stands and remains very high for at least 29 years after fire, the oldest burned site measured in this study. Fire dramatically reduces native annual and perennial species richness. If a burned stand experiences a second fire, then native annual richness can be significantly reduced again, compared to a paired once burned stand. Species diversity also significantly decreases, leading to a highly simplified assemblage dominated by invasive plants. Shrub components in this study area are especially sensitive to fire and show little resiliency, except for *E. farinosa*, which can become dominant after fires. If *E. farinosa* is absent from a site and no other desert shrubs colonize, then fire can result in type conversion to invasive annual grassland. The impact of fire is severe for CBS of the study area. For native annual plants in particular, fire is a major threat because it promotes invasive annual plants that can displace them. The impact of multiple fires on native annuals is especially severe.

The sustainability of CBS in the study area will be heavily dependant on preventing fire. However, invasive annual plants may likely continue to diminish native annual components even in the absence of fire. Invasive plant removal will favor natives through decreased competition (Brooks 2000, Schutzenhofer and Valone 2005, Steers dissertation – Chp. 4) and limiting fire disturbance (Brooks et al. 2004). Invasive plant removal in unburned stands or immediately after fire should also dramatically increase native annual abundance and richness (Steers, dissertation – Chps. 3 & 4). Because native annual richness is linked to the spatial and structural heterogeneity of CBS shrublands (Schmida and Whittaker 1981), some native species may not find suitable habitat until the shrub components are returned, regardless of invasive plant removal. Natural shrub reestablishment of the dominant species may take hundreds of years (Vasek 1983, Lovich and Bainbridge 1999) and may require active restoration (Bainbridge 2007).

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FIGURES AND TABLES

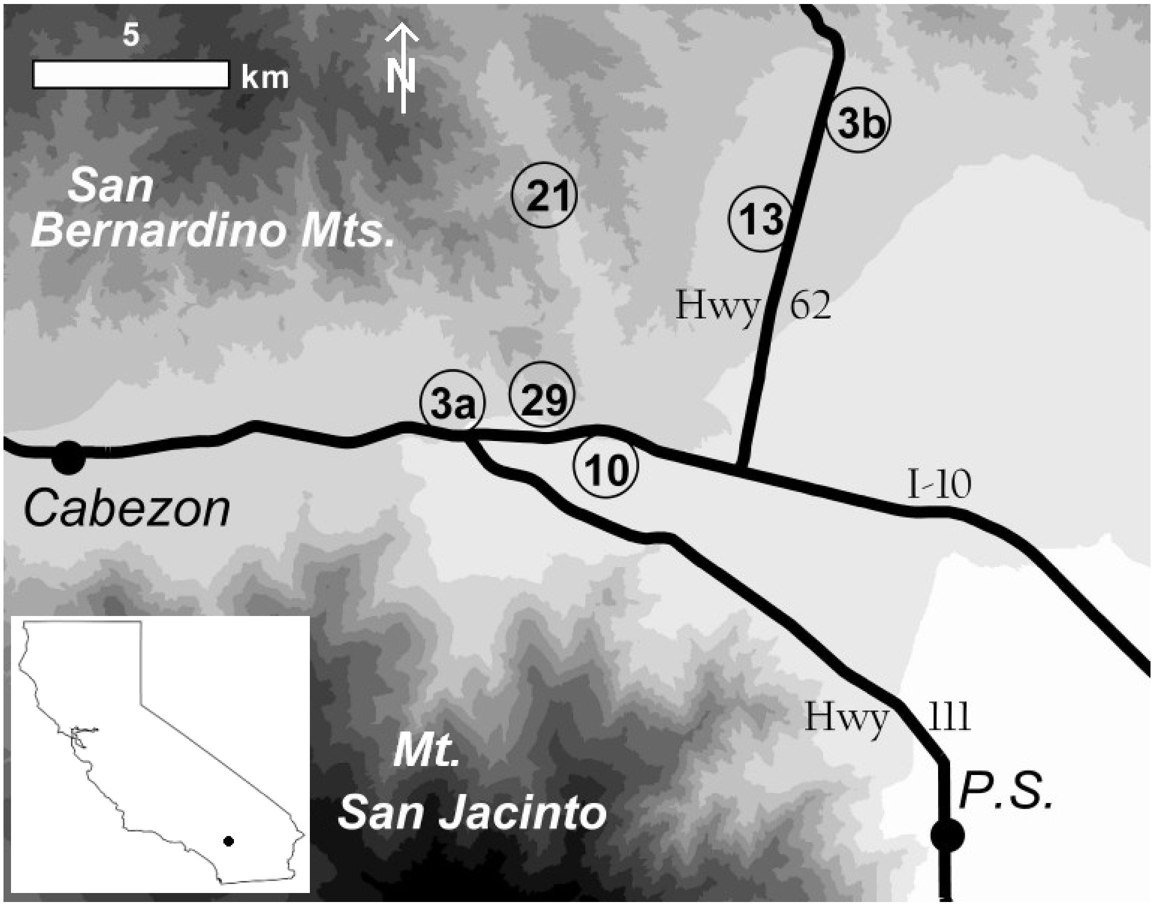

Figure 2.1 Study area showing study sites that are named after the number of years since they burned or first burned based on field vegetation sampling in spring 2008. P.S. represents the city of Palm Springs. Dark colors indicate increasing elevation.

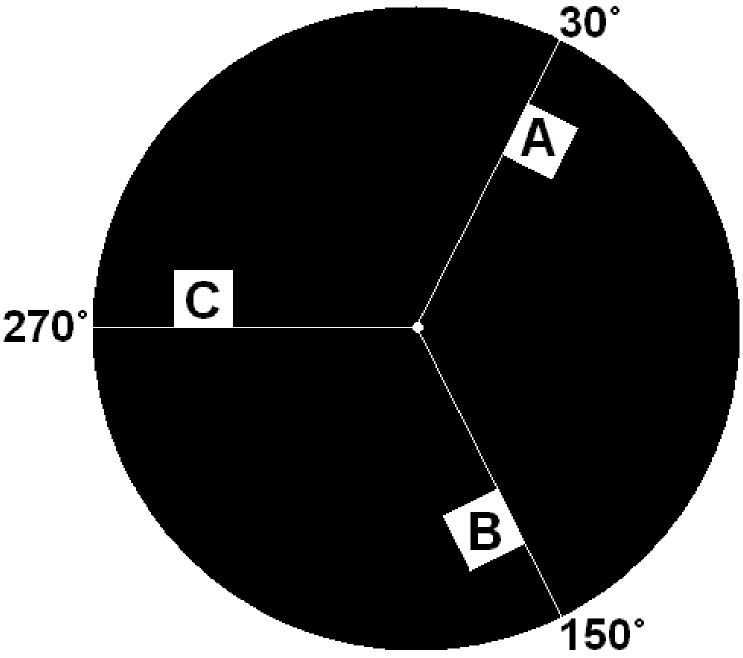

Figure 2.2 Graphical representation of the mod-NAWMA plot used for field surveys. The three 1m² plot frames, A, B, and C, start 4.57m from plot center along the indicated compass headings. The radius of the plot is 7.32m and the surface area is 168.3m².

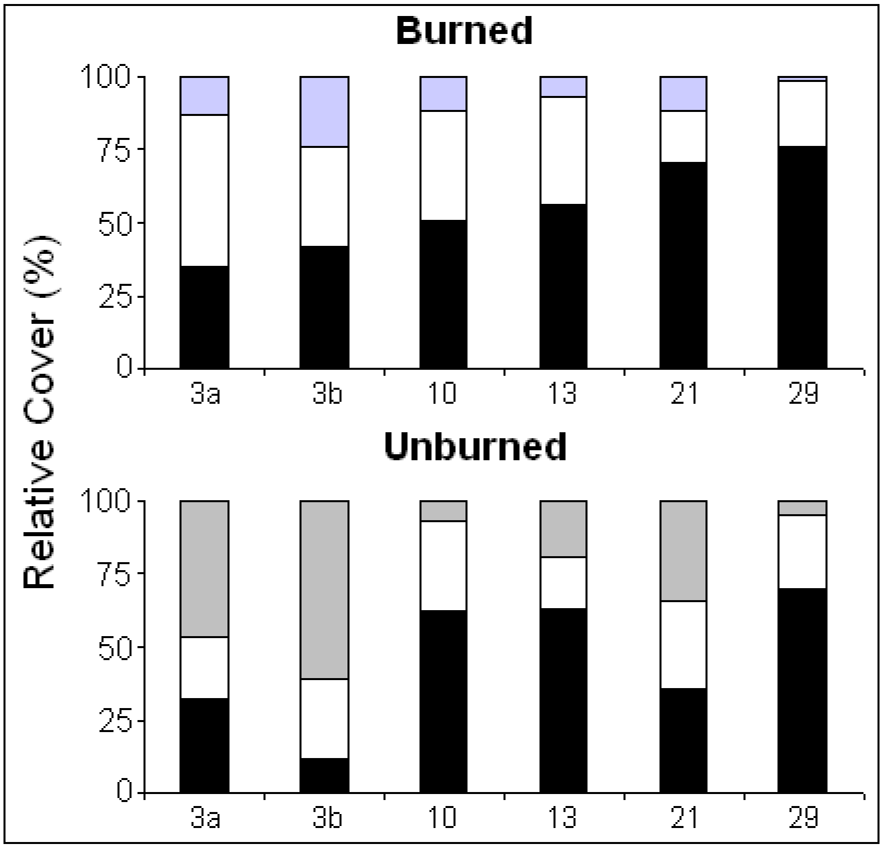

Figure 2.3 Relative cover of invasive annual forbs (black), invasive annual grasses (grey), and native annual plants (white) in paired burned once and unburned stands.

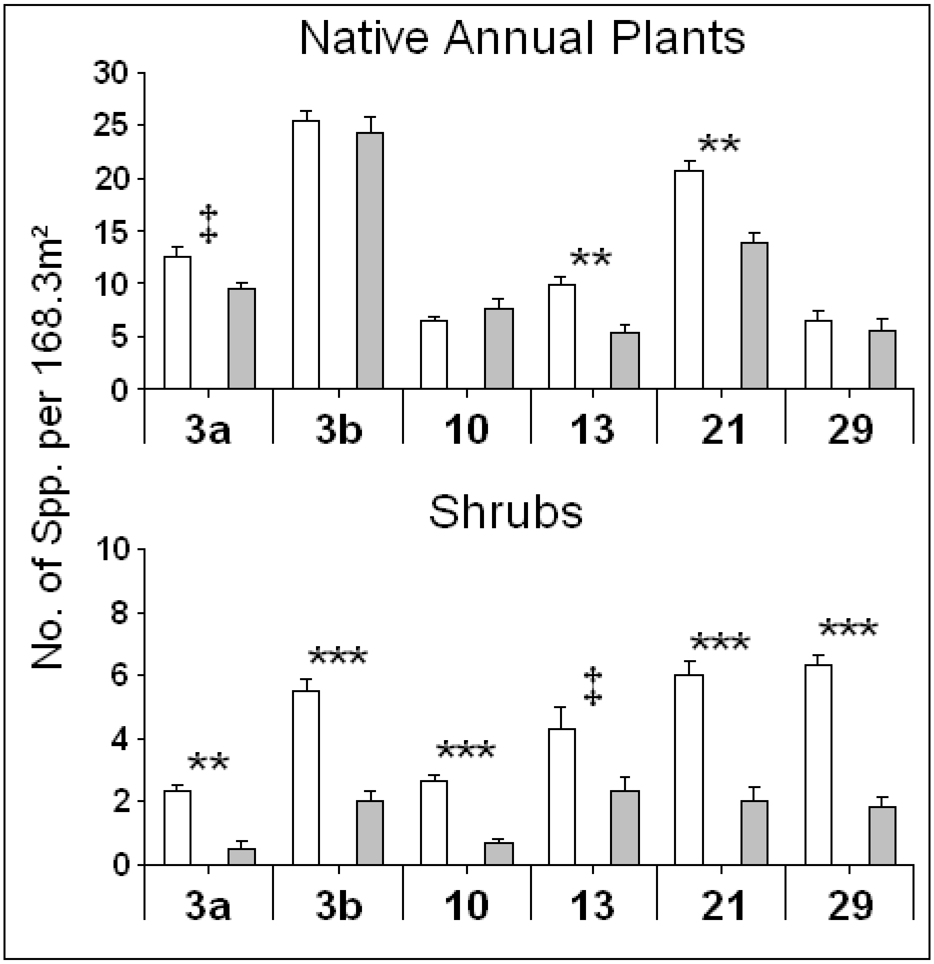

Figure 2.4 Species richness of native annual plants and shrubs at each of the six study sites, in unburned (white bars) and paired burned once (grey bars) stands of CBS at the mod-NAWMA plot scale (168.3m²). Symbols above paired stands per site indicate significant differences at the following levels of α: 0.05 = ‡, 0.001 = **, and 0.0001 = ***.

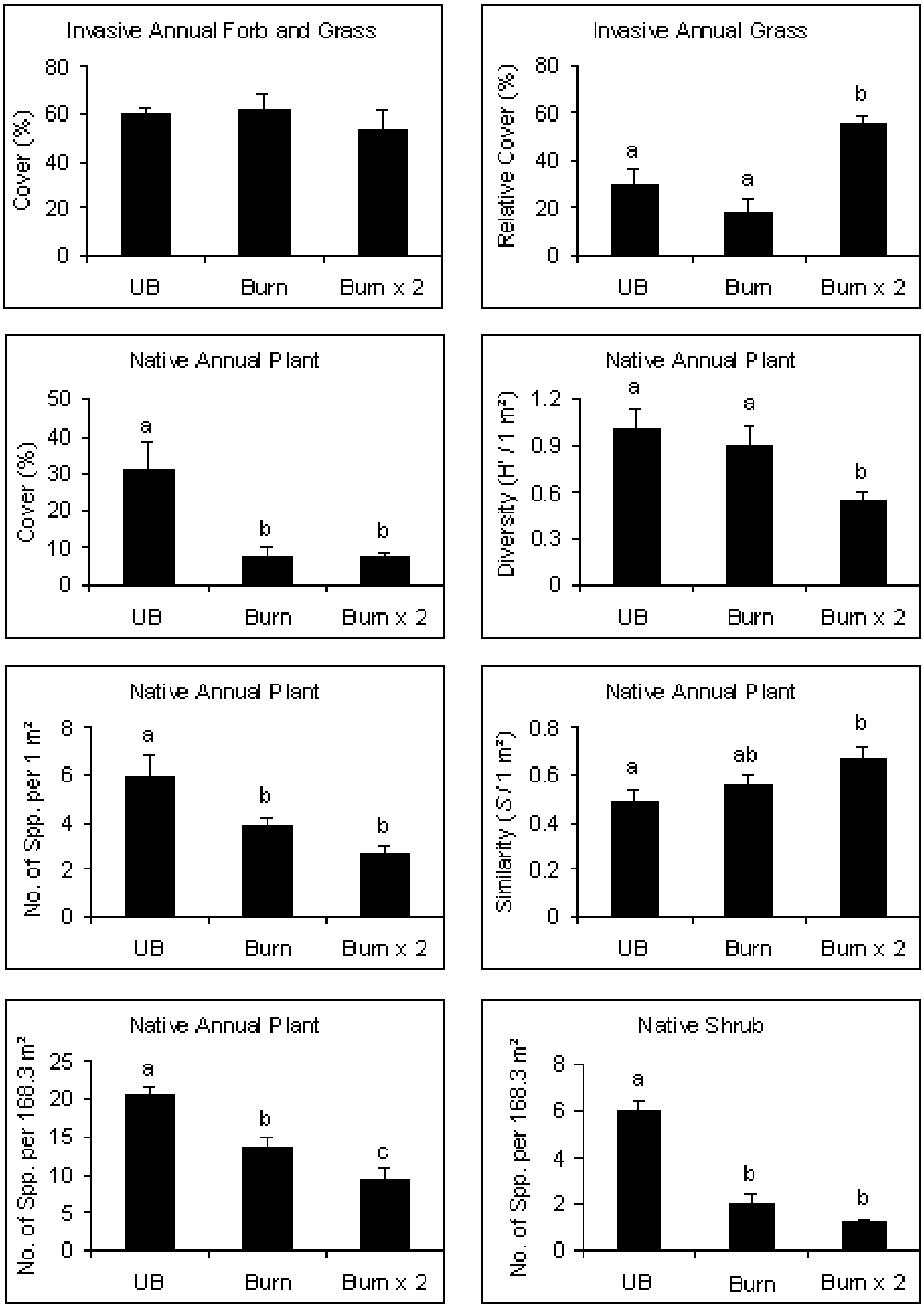

Figure 2.5 Effect of one (tsf 21) and two fires (tsf 21&3) on various vegetative parameters at site **21**. Values in each graph are averages per paired stand per site. Differences in letters between paired burned stands per vegetative parameter indicate significant differences based on ANOVA and LSD tests. For the graph of annual plant similarity per m², the ANOVA was nonsignificant ($p = 0.0752$) while the LSD test was significant ($p = 0.0232$ for unburn vs. burn x 2).

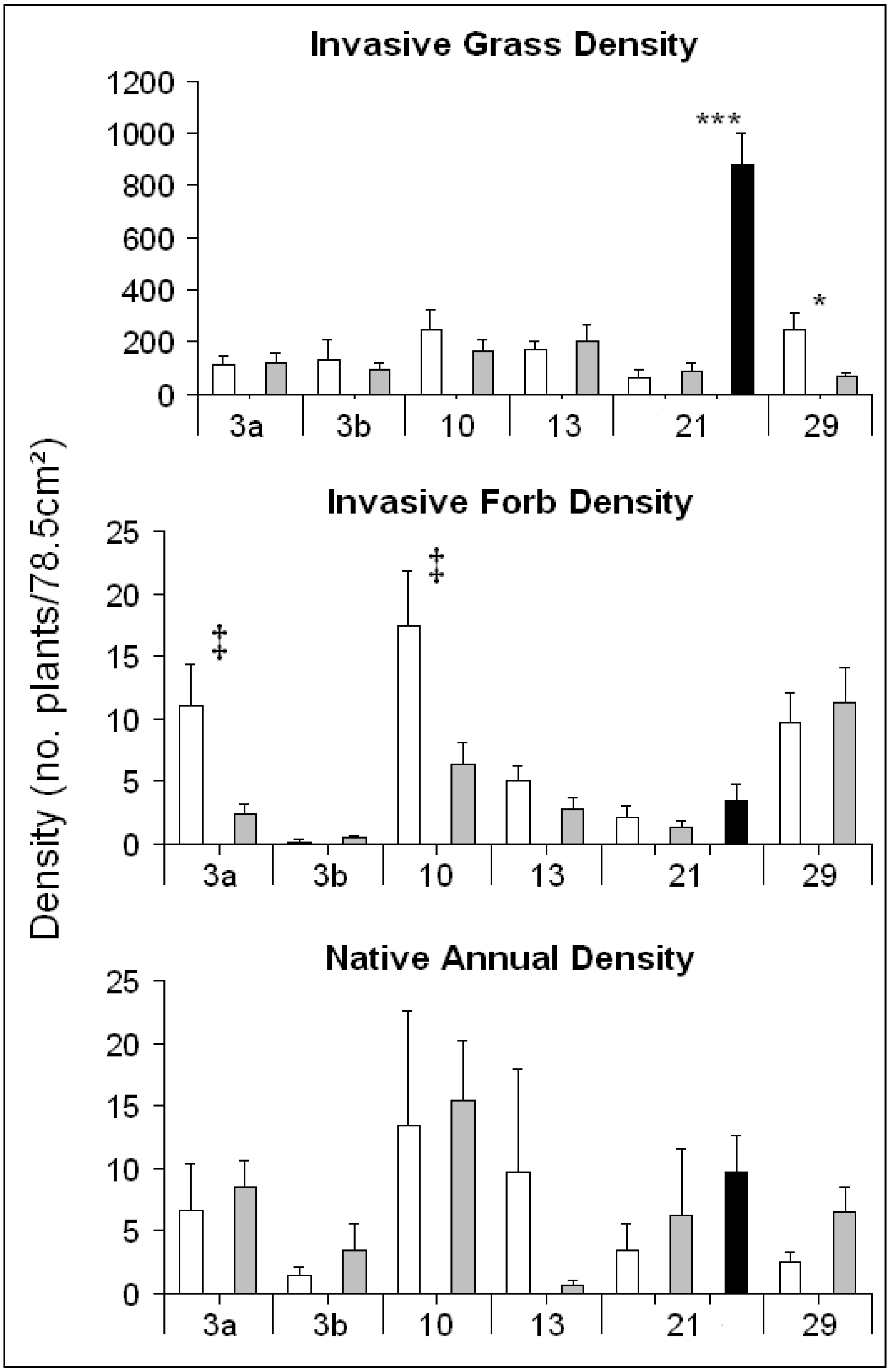

Figure 2.6 Seedbank density per 78.5cm² of three annual functional groups: invasive annual grass, invasive annual forb, and native annuals. Unburned, burned once, and twice burned stands are represented by white, grey, and black bars, respectively. Symbols above paired stands per site indicate significant differences at the following levels of α: 0.05 = ‡, 0.01 = *, and 0.0001 = ***.

Table 2.1 Frequency of perennial species found in the six mod-NAWMA plots per stand per site. For all six study sites, UB represents the unburned stand while the paired burned stand is listed to the right, named after the year since fire. Species found in all six plots per stand were given a frequency score of 6, species found in five of the six plots were given a score of 5, etc…

Family	Species	UB	3a	UB	3b	UB	10	UB	13	UB	21	21&3	UB	29
HERBACEOUS PERENNIALS														
Asteraceae	*Stephanomeria pauciflora*				1		2	1	4			2		1
Cucurbitaceae	*Cucurbita palmata*				1									
Euphorbiaceae	*Chamaesyce polycarpa*				1								1	4
	Ditaxis neomexicana												1	1
	Stillingia linearifolia								1					
Liliaceae	*Dichelostemma capitatum*			1	2								3	
Nyctaginaceae	*Mirabilis bigelovii*			1	3		1	5	3	3		1	3	6
Poaceae	*Pleuraphis rigida*												1	
Selaginellaceae	*Selaginella bigelovii*									2				
TOTAL HERBACEOUS PERENNIAL FREQUENCY				2	8		3	6	8	5		3	9	12
AVR. RICHNESS PER MOD-NAWMA (168.3m²)				0.3	1.3		0.5	1	1.3	0.8		0.5	1.5	2
SHRUBS AND CACTI														
Asclepiadaceae	*Asclepias subulata*							1						
Asteraceae	*Acamptopappus sphaerocephalus*							1						
	Ambrosia dumosa	6		6	6	3		5	5	6	2	1	6	1
	Bebbia juncea								2					
	Encelia farinosa	1	1	4	4			6	5	4	6	6	5	6
	Hymenoclea salsola			1					1					1
	Viguiera parishii									1	1			
Cactaceae	*Echinocereus engelmannii*	1								4			1	
	Ferocactus cylindraceus								1	1			6	2
	Mamillaria tetrancistra												1	
	Opuntia basilaris												1	
	O. bigelovii												3	1
	O. echinocarpa			2						6			2	
Ephedraceae	*Ephedra californica*			5		1		1		2			1	
Fabaceae	*Psorothamnus arborescens*			3	1									
Krameriaceae	*Krameria grayi*			4		6		4		5			6	
Liliaceae	*Yucca schidigera*			2						1				
Polygonaceae	*Eriogonum fasciculatum*							1						
Rutaceae	*Thamnosma montana*							1						
Zygophyllaceae	*Larrea tridentata*	6	2	6	1	6	4	6		6	3		6	
TOTAL SHRUB AND CACTUS FREQUENCY		14	3	33	12	16	4	26	14	36	12	7	38	11
AVR. RICHNESS PER MOD-NAWMA (168.3m²)		2.3	0.5	5.5	2	2.7	0.7	4.3	2.3	6	2	1.2	6.3	1.8

Table 2.2 Frequency of annual species in the six mod-NAWMA plots per stand per site. See Table 1 for scoring description.

Family	Species	UB	3a	UB	3b	UB	10	UB	13	UB	21	21&3	UB	29
INVASIVE FORB														
Asteraceae	*Sonchus oleraceus*												1	
Brassicaceae	*Brassica tournefortii*	6	6	6	6	6	6	6	6	6	6	6	6	6
Geraniaceae	*Erodium cicutarium*	6	6	6	6	6	6	6	6	6	6	6	6	6
INVASIVE GRASS														
Poaceae	*Bromus diandrus*					1								
	B. madritensis	4		6	5	1		6	2	6	6	3	4	1
	B. tectorum									4	1	1		
	Hordeum murinum	1	1											
	Schismus spp.	6	6	6	6	6	6	6	6	6	6	6	6	6
TOTAL INVASIVE PLANT FREQUENCY		23	19	24	23	20	18	24	20	28	25	22	23	19
AVR. RICHNESS PER MOD-NAWMA (168.3m²)		3.8	3.2	4	3.8	3.3	3	4	3.3	4.7	4.2	3.7	3.8	3.2
NATIVE ANNUALS														
Asteraceae	*Chaenactis fremontii*	6	6	6	6	1	1	3	1	6	6	2	3	4
	Eriophyllum wallacei		1	1	1									
	Filago californica	6	6	1		6	6			6	5	4	6	4
	F. depressa			6	6					2				
	Lasthenia californica		1					1	1	5	3	5		
	L. coronaria			1	2									
	Malacothrix glabrata	6	6	6	6	6	5	4	2		3	3	2	3
	Rafinesquia neomexicana	2		6	5			3		6				
	Stephanomeria exigua	5	3		1							2	1	2
	Stylocline gnaphaloides	1		4	4					6	1			
	Uropappus lindleyi										1	1		
Boraginaceae	*Amsinckia menziesii*									6	1	1		
	Cryptantha angustifolia				3									
	C. circumscissa			3	3									
	C. decipiens			1										
	C. intermedia	2		6	6			6	4	5	6	5	1	6
	C. maritima			5				1						
	C. micrantha	1		3	5									
	C. nevadensis			1										
	Pectocarya heterocarpa	3	4	6	6	2	6	4	6	5			1	
	P. linearis	6	5	6	2	6	6	6	6	5	5	1	4	3
	P. platycarpa			4										
	P. recurvata	3	1	6	6			6	6	5	5	2	3	1

Table 2.2 Continued on next page

Table 2.2 Continued…

Family	Species	UB	3a	UB	3b	UB	10	UB	13	UB	21	21&3	UB	29
Brassicaceae	*Descurainia pinnata*										3	1		
	Lepidium lasiocarpum			6	4			1	1		3	1	1	
	Tropidocarpum gracile							1		1			4	1
Campanulaceae	*Nemacladus longiflorus*				1									
Caryophyllaceae	*Loeflingia squarrosa*	2	5	6	5		4			5				
Crassulaceae	*Crassula connata*	6	6	6	6	6	6	6	4	6	4	4	6	6
Fabaceae	*Lotus strigosus*	6	4	4	5	6	6			5		1	2	1
	Lupinus sparsiflorus									2				
Hydrophyllaceae	*Emmenanthe penduliflora*				3					6	6	6		
	Phacelia campanularia										2	2		
	P. distans	1		6	6			3		5	6			
	Pholistoma membranaceum	6		6	3			6		6	1		5	
Lamiaceae	*Salvia columbariae*			1				1				1		
Loasaceae	*Mentzelia involucrata*										1			
	Mentzelia sp.			2	1			1		2				
Onagraceae	*Camissonia californica*			5	6					6	6	6		1
	C. pallida	6	6	6	6	2	3	1		4	2	4		1
Papaveraceae	*Eschscholzia minutiflora*				2									
Plantaginaceae	*Plantago ovata*	1			6					6	6	3		
Poaceae	*Vulpia microstachys*									1				
	V. octoflora	6	1	6	5	4	3	1		6	6	1		
Polemoniaceae	*Eriastrum diffusum*			3	3									
	Eriastrum sp.			3	3									
	Gilia angelensis									1				
	G. maculata			2										
	Linanthus bigelovii			1						2				
	Loeseliastrum schottii			3	2									
Polygonaceae	*Chorizanthe brevicornu*	1	2	6	6			4	1	2				
	C. watsonii				2									
	Pterostegia drymarioides			2	3					1				
Portulaceae	*Calyptridium monandrum*			6	6						1	1		
TOTAL NATIVE ANNUAL FREQUENCY		76	57	152	146	39	46	59	32	124	83	57	39	33
AVR. RICHNESS PER MOD-NAWMA (168.3m²)		12.7	9.5	25.3	24.3	6.5	7.7	9.8	5.3	20.7	13.8	9.5	6.5	5.5

Table 2.3 Average values of soil and vegetative parameters per paired stand per site. Values in bold indicate significant differences based on ANOVA at α = 0.05. Differences in superscript letters between the three paired stands at site **21** indicate significant differences based on LSD tests at α = 0.05. The only discrepancy between ANOVA and the LSD test was for bare ground where ANOVA was nonsignificant (no bold) while the LSD test was significant (letters are present). Values in bold that include the suffix **k** indicate significant differences using Kruskal-Wallace tests for nonparametric data. The symbols *, **, and *** indicate significance of ANOVA or Kruskal-Wallace tests at α = 0.01, 0.001, and 0.0001, respectively. Aspect and slope variables were not statistically compared between paired stands.

Soil and Vegetation Variables	**UB**	**3a**	**UB**	**3b**	**UB**	**10**	**UB**	**13**	**UB**	**21**	**21&3**	**UB**	**29**
Aspect (deg.)	96	92	103	78	163	175	74	95	64	100	93	198	166
Slope (deg.)	1	1	2	1	2	2	1	1	5	6	6	4	4
Total N (%)	0.10	0.10	0.08	0.05	0.09	0.08	**0.12**	0.10	0.08^{1}	0.10^{12}	**0.13^{2}**	0.12	0.15
Total C (%)	0.84	0.89	0.76	0.56	0.99	0.75	**1.07**	0.83	0.75^{1}	0.96^{12}	**1.23^{2*}**	1.33	1.62
NH_4^+ (ppm)	11.9	13.4	8.3	7.7	13.0	14.1	15.6	18.0	13.1	13.7	14.2	**16.0**	10.6
NO_3^- (ppm)	**28.1**	18.0	7.6	7.6	19.1	14.5	13.9	9.9	11.3	11.9	14.6	16.1	17.2
Sand (%)	86	87	87	86	83	**86**	77	80	78	80	81	80	**86**
Silt (%)	12	11	12	12	14	11	19	16	17	17	15	**15**	11
Clay (%)	2	2	1	2	**3**	2	4	4	**5^{1}**	3^{2}	**5^{12}**	**5**	4
pH	7.7	**7.8**	7.3	**7.6**	7.2	7.4	7.4	7.5	7.4^{1}	**7.6^{2*}**	**7.7^{2*}**	7.0	7.0
Bulk Density (g/cm³)	1.36	**1.61**	1.6	1.57	1.43	1.58	1.14	1.24	1.29	1.15	1.15	1.36	1.25
Coarse Fraction (g/cm³)	0.14	0.16	**0.25***	0.11	0.26	0.23	0.4	0.46	0.31	0.42	0.49	0.48	0.48
Bare Ground Cover (%)	17	26	41	33	10	10	13	22	7^{1}	12^{12}	19^{2}	5	**12***
Rock Cover (%)	1	3	4	4	2	1	6	2	3^{1}	6^{1}	**12^{2}**	3	8
Litter Cover (%)	**8**	<1	3	2	1	1	**3***	1	4	6	2	2	3
Invasive Grass Cover (%)	19	**43****	17	**27**	34	38	16	29	26^{12}	12^{1}	**35^{2}**	29	23
Inv. Grass and Forb Cover (%)	49	77	25	**63*****	97	86	70	73	60	61	53	109	96
Inv. Grass and Forb Richness (/m²)	2.9	2.7	2.9	3.3	**3**	2.8	**3.3**	2.9	**3.6^{1*}**	3.1^{2}	2.7^{2}	2.9	3
Native Annual Cover (%)	**39***	10	32	20	6	12	16	5	**31^{1*}**	8^{2}	7^{2}	4	2
Native Annual Richness (/m²)	5.1	4.4	**11.3**	7.8	2.8	3.1	**2.9**	2.0	**5.9^{1*}**	3.8^{2}	2.7^{2}	0.8	0.7
Live Shrub and Cactus Cover (%)	**12k**	<1	**8k***	<1	3	<1	7	1	11	19	19	7	13
Encelia farinosa Cover (%)	<1	<1	<1	<1	0	0	<1	1	<1	**18k***	**16k***	<1	**13k***
Shrub and Cactus Richness (/m²)	**0.4**	0	**0.6***	0.1	0.2	0	0.4	0.4	0.7	0.9	0.8	0.2	0.5

Table 2.4 Results from two separate multilinear regressions from unburned stands based on the correlation of soils variables with two dependent variables, invasive annual plant cover (%) and native annual plant species richness (m^{-2}).

Model		Invasive Annual Plant Cover		Native Annual Plant Richness (m^{-2})	
		Estimate (SE)	p value (t ratio)	Estimate (SE)	p value (t ratio)
Fixed Effects	Intercept	323.666 (125.79)	0.0159 (2.57)		0.6917 (-0.4)
	Total N	298.533 (124.23)	0.0234 (2.4)		0.0553 (-2)
	% Sand		0.5367 (-0.63)		0.4652 (0.74)
	pH	-32.816 (13.77)	0.0245 (-2.38)		0.5912 (0.54)
	coarse fraction		0.9862 (-0.02)		0.8909 (-0.14)
	bulk density		0.2979 (1.06)		0.8197 (-0.23)
	% bare ground	-1.47412 (0.27)	<.0001 (-5.41)	0.147 (0.04)	0.0016 (3.5)
	% rock		0.0551 (-2)		0.6889 (0.4)
	% litter		0.4753 (-0.72)		0.4039 (-0.85)

Table 2.5 Average percent cover of annual plant species per paired stand per site. Only species with > 0.1% cover in at least one of the stands per site (**3a**, **3b**, and **21)** are included. Species cover values in bold indicate significant differences based on ANOVA at $\alpha = 0.05$. Differences in letters between the three paired stands at site **21** indicate significant differences based on LSD tests. Species values in bold that include the suffix **k** indicate significant differences using Kruskal-Wallace tests for nonparametric data. Species < 0.1% were not statistically analyzed individually, but include the following invasive grasses: *Bromus tectorum* and *Hordeum murinum*, and the following natives: *Chorizanthe watsonii* (M, trans), *Cryptantha angustifolia* (A, trans), *C. maritima* (A, cis), *C. micrantha* (A, cis), *Descurainia pinnata* (A, cis), *Eriophyllum wallacei* (C, cis), *Gilia maculata* (C, trans), *Lasthenia californica* (C, cis), *Lasthenia coronaria* (C, cis), *Loeflingia squarrosa* (M, cis), *Loeseliastrum schottii* (C, trans), *Mentzelia* sp. (D, ?), *Nemacladus longiflorus* (C, cis), *Pectocarya platycarpa* (A, cis), *Phacelia campanularia* (C, trans), **Pterostegia drymarioides* (C, cis), and *Urropappus lindleyi* (A, cis).

	UB	**3a**	**UB**	**3b**	**UB**	**21**	**21&3**
INVASIVE FORB							
Brassica tournefortii	17.4	10.6	7.3	12	**22.1**^{A}	**41.9**^{A}	5.2^{B}
Erodium cicutarium	12.9	23.4	1.3	**24.2**	11.2	7.3	13.4
INVASIVE GRASS							
Bromus madritensis	< 0.1		0.5	0.1	**4.1**^{A}	< 0.1^{B}	0^{B}
Schismus spp.	18.7	**43.3**	16.1	**26.7**	22.1^{AB}	11.9^{B}	**34.7**^{A}
NATIVE ANNUAL							
Amsinckia menziesii (A, cis)					**1k**		
Calyptridium monandrum (C, cis)			0.7	0.2			
Camissonia californica (C, cis)			0.3	0.2	0.1^{A}	1.1^{AB}	**2**^{B}
Camissonia pallida (C, trans)	0.3	0.6	0.5	0.4	0.1		< 0.1
Chaenactis fremontii (C, trans)	**24.8**	5.4	9.3	1.5	**5.7**^{A}	0.8^{B}	0^{B}
Chorizanthe brevicornu (M, trans)		< 0.1	**0.7k**	< 0.1			
Crassula connata (A, cis)	0.6	0.7	0.4	0.3	**1.3k**	0.1	< 0.1
Cryptantha intermedia (A, cis)			1.8	0.1		0.8	**1k**
Emmenanthe penduliflora (C, cis)					0.1^{A}	**3.3**^{B}	**2.5**^{B}
Eriastrum diffusum (C, cis)			1	0.3			
Filago californica (M, cis)	1.4	1.7			**0.6**^{A}	0^{B}	0.2^{AB}
Filago depressa (M, trans)			**1.3**	0.1	< 0.1		
Gilia angelensis (C, cis)					0.2		
Lepidium lasiocarpum (D, cis)			0.1	0.2			< 0.1
Lotus strigosus (M, cis)	0.1	0	< 0.1	< 0.1	< 0.1		< 0.1
Malacothrix glabrata (C, trans)	< 0.1	1.3	1.4	**7.6**			0.2
Pectocarya heterocarpa (A, cis)	< 0.1	0.3	1.8	6.6	**0.3**^{A}	0^{B}	0^{B}
Pectocarya linearis (A, cis)	1	0.3	**0.6**	< 0.1	**0.7k**	< 0.1	< 0.1
Pectocarya recurvata (A, trans)	0.6		6.9	1.3	**0.8**^{A}	0.1^{B}	0^{B}
**Phacelia distans* (C, cis)			0.4	0.4	**1.4k**	< 0.1	0
**Pholistoma membranaceum* (C, cis)	**10.1**		**4.4**	< 0.1	**13.2**^{A}	0^{B}	0^{B}
Plantago ovata (D, cis)	< 0.1			**0.5**	0.1	0.7	1.1
**Rafinesquia neomexicana* (C, trans)	0.1		**0.6k**		0.1		
Stephanomeria exigua (C, cis)	0.1	< 0.1					< 0.1
Stylocline gnaphaloides (M, cis)	< 0.1		< 0.1	< 0.1	**1.4k**		
Vulpia octoflora (A, cis)	0.1		< 0.1	< 0.1	**3.9k**	0.9	

* - species found to be understory obligates within the study area based on personal observations.

A, **C**, **D**, and **M** refer to species with an Arcto-Tertiary, Californian, Desert, or Madrean derivation, respectively.

cis or **trans** refer to species with a current distribution extending well into the California Floristic Province or a distribution primarily in transmontane California, respectively.

Table 2.6 Percent change in native annual plant cover after fire based on biogeographic derivation, current distribution, and current distribution excluding annual species found to be understory obligates (- EUO). For example, Cis- EUO represents the response of cismontane native annuals not counting species that were primarily restricted to shrub understories. Values were calculated as the average percent change of native annual cover in burned stands based on the respective average native annual cover values in paired unburned stands.

	3a	**3b**	**21**	**21&3**
Arcto-Tertiary	-46.4^{AB}	-26.1^{A}	-74.4^{A}	-87.0
Madrean	11.5^{A}	-88.3^{B}	-100.0^{B}	-90.1
Californian	-79.3^{B}	-43.9^{AB}	-74.8^{A}	-77.0
p – value	**0.0487**	0.0612	**0.0275**	0.5935
Cismontane	-77.9	-26.2	-71.0	-71.5
Transmontane	-71.4	-46.4	-86.0	-96.4
p – value	0.6867	0.462	0.2452	**0.0084**
Cis – EUO	-13.1	18.2	-27.6	-28.6
Trans – EUO	-71.3	-44.8	-85.7	-96.3
p – value	0.0754	0.1521	**0.0294**	**0.0036**

CHAPTER 3. Are desert annual communities resilient to fire in creosote bush scrub?

ABSTRACT

Exotic annual grasses have become increasingly important components of desert communities and have altered key ecosystem processes such as the fire cycle. After fire, these grasses are often dominant. Habitat degradation by invasive annuals in arid- and semi-arid shrublands has been well documented in the west, and restoration methods are needed to control invasive species and promote native succession following fire. Three treatments to control invasive annual grasses and forbs were implemented in the first three years following a fire in creosote bush scrub. Treatments included early-season mechanical removal (raking) of all annuals, grass-specific herbicide (Fusilade II), and Fusilade II plus hand pulling of exotic forbs. In the first year, all treatments reduced invasive annual grass abundance by about half but had little effect on native annuals. The lackluster performance in the first year was likely due to low and irregular distribution of rainfall during the growing season. In the second year, insufficient rainfall prevented the germination of any annual plants and no treatments were applied. In the third year, precipitation onset occurred later in the season and was above average. While the raking treatment was ineffective this year, treatments utilizing Fusilade II practically eliminated invasive grasses and forbs, and achieved native annual dominance that resembled the structure and composition of unburned, relatively un-invaded creosote bush scrub. These results indicate that burned creosote bush shrublands can be managed after fire to reduce invasive plants and decrease the chance of fire feedback. They also show that in the

absence of invasive grasses and forbs, the native annual community can be very resilient to fire disturbance.

INTRODUCTION

When wildfires occur in creosote bush scrub they are usually fueled by invasive annual grasses. Fire in these systems can be problematic for a number of reasons. First, these low productivity shrublands have long-lived dominant shrubs (Vasek 1980) and slow population dynamics with low turnover compared to the lifespan of humans (Cody 2000). Recovery after fire could take at least one hundred years depending on various factors, but probably much longer (Lovich and Bainbridge 1999). Second, most of the native shrub components lack traits that aid their recovery after fire and can be locally extirpated in worse-case scenarios (Brown and Minnich 1986, Brooks and Minnich 2006). Third, invasive annual grasses appear to be less impacted by fire than native components and often dominate the post-fire vegetation (Brooks and Esque 2002). Forth, experimental evidence suggests that invasive annual grasses competitively suppress native perennial (DeFalco et al. 2007) and annual species (Brooks 2000, DeFalco et al. 2003, Steers dissertation – Chp. 4). Finally, if invasive grasses dominate post-burn vegetation, they also increase the likelihood that the site will burn again in a process known as the invasive plant – fire regime cycle (Brooks et al. 2004). Unfortunately, native annual and perennial species richness will decrease again, the second time a stand of creosote bush scrub burns (Steers dissertation – Chp. 2). Therefore, fire and invasive species impacts on creosote bush scrub are substantial since burned stands will result in relatively poor habitat quality (Brooks and Esque 2002) and major changes to ecosystem processes (Brooks et al. 2004).

Obviously, the control and suppression of invasive annual grasses is of great importance in the conservation of creosote bush scrub. Due to the large-scale invasion of the southwestern deserts by invasive annual grasses, eradication seems impossible. Nevertheless, control of these invasive plants where important biological resources occur and/or in areas that are fire prone (see Brooks and Esque 2002, Brooks and Matchett 2006), would be greatly beneficial. Because fire is so detrimental, fire prevention through the control of invasive grasses would contribute the most towards their preservation. If, however, that is not possible and these shrublands do burn, post-fire restoration treatments are needed. Historically, fire in this arid vegetation type has been rare due to low productivity and lack of continuous fuels (Brooks and Minnich 2006). Consequently, limited information exists regarding restoration methods for burned creosote bush scrub.

While much of the focus on fire in desert shrublands is directed towards invasive annual grasses, invasive annual forbs are also problematic. *Erodium cicutarium* is ubiquitous in the southwest and is often a dominant annual plant after fires (Minnich and Dezzani 1998, Brooks 2002). While it is very competitive with native annuals (Brooks 2000, Schutzenhofer and Valone 2006), it fortunately does not have persistent standing biomass and does not contribute much to fuel (Brooks 1999a). *Brassica tournefortii* is also highly competitive with native plants (Barrows et al. 2008) and can be prolific after fires (Steers dissertation – Chp. 2). Unlike *E. cicutarium*, it can contribute fuel toward desert fires (Trader et al. 2006). Therefore, while the removal of grasses alone is probably sufficient to prevent the vast majority of invasive plant fire – feedback cases, the subsequent control of invasive forbs is also critical for the recovery of burned desert vegetation. Treatments that target both invasive grasses and forbs after fire will benefit native vegetation recovery the most.

The negative impact of fire on desert shrubs is well established (*reviewed in* Brooks and Minnich 2006). What is less clear is the impact of fire on the native annual components, which account for a large portion of the plant biodiversity in creosote bush scrub. This may partly be due to the fact that there are hundreds of annual species associated with creosote bush scrub and sensitivity to fire may be species specific. Native annual plant species richness often decreases after fire (Steers dissertation – Chp. 2), but it is unclear whether this occurs because desert annuals are poorly adapted to fire, like their shrub counterparts, or because of increased competitive exclusion from invasive grasses and forbs that proliferate after fire. The research reported here was conducted in order to evaluate the role of invasive species in decreasing native species richness after fires and the ability of the native annual community to regain dominance once invasives are removed. Experiments were conducted to test the effectiveness of several treatments to control invasive annuals, document the native annual community that resulted from complete invasive species removal, and compare the recovered community to a relatively un-invaded, unburned site with high species richness.

METHODS

STUDY SITES

The study site (34º02’55.23”N, 116º33’57.0”W) was located in burned creosote bush scrub vegetation within Big Morongo Canyon Preserve (BMCP), which is located on the western edge of the Little San Bernardino Mountains in Morongo Valley, San Bernardino County, CA. The study plots were placed in flat to moderately sloped (0-15º) terrain at an elevation of about 780m. BMCP is located near the western-most extent of creosote bush scrub in the Little San Bernardino Mountains, and it is also in a transition zone between the Colorado Desert to the South and the Mojave Desert to the north.

The fire at the study site occurred on June 22, 2005. Based on shrub skeletons and/or resprouts in the burned stand, and plants in an adjacent small patch of unburned vegetation opposite a fuel break, the pre-fire plant community was creosote bush scrub, co-dominated by *Larrea tridentata* and *Ambrosia dumosa*. Other shrubs included *Acacia greggii*, *Encelia actoni*, *Opuntia basilaris, O. echinocarpa*, *Psorothmanus arborescens*, *Vigueria parishii*, and *Yucca schidigera*, among others. The annual vegetation in the adjacent unburned stand was dominated by *Bromus madritensis* ssp. *rubens* in interspaces and especially in shrub understories, which likely was the primary fuel in the wildfire. *Schismus* spp. was also abundant in the interspaces. Nomenclature follows Hickman (1996).

Average precipitation (1948-1972) in the adjacent town of Morongo Valley is 19.6cm with average snowfall of 8.4cm (WRCC 2008). Approximately 85% of the average precipitation occurs from October through April during the winter wet season.

The fire in June 2005 followed one of the wettest seasons on record, based on data from the nearest weather station in Palm Springs, CA, which is 25km to the SSE. In October of 2005, a new weather station was set-up at BMCP; weather data during the study period was obtained from this station since the station in the town of Morongo Valley had been inactive since 1972. Precipitation during the experiment was 15.6, 1.2, and 18.9cm from October through April during the first three seasons (2005-06, 2006-07, and 2007-08) following the early summer fire in 2005. Precipitation in the first season kicked-off with a large storm that started on October 17, 2005 and produced 5.5cm of precipitation over a three-day period (Figure 1). Massive germination of annual plants commenced immediately. This was followed by no precipitation in November and only 0.08cm in early December, resulting in mortality as well as water stress for a large number of winter annuals. About 2.16cm of precipitation fell in the first two days of January, which helped surviving annuals rebound, but this was followed by 46 days without any precipitation. In February 2006, precipitation returned and occurred relatively uniformly through April, and surviving annual plants were able to reach flowering. In the second season, precipitation was insufficient for the germination of annual plants, and no invasive or native annuals were recorded (Figure 1). In the third and final season (2007-08), the first major precipitation event that induced annual plant germination occurred on November 30, 2007, 44 days later than in 2005 (Figure 1). Precipitation in the third winter wet season was about average (18.9cm) with no significant droughts between precipitation events. Consequently, annual plants appeared non-stressed from germination to flowering.

EXPERIMENTAL DESIGN

Three treatments were utilized: Herbicide (H), herbicide plus weeding of invasive forbs (W), and a raking treatment (R). The three treatments and a control (C) were implemented in a randomized, complete block design composed of twelve blocks. Four plots within each block were randomly assigned to treatments H, W, R, or C. Plots were 8x8m and centered on a mature, burned *Larrea tridentata* individual. Plots were designed to allow for the sampling of interspace and understory microhabitats. Two 0.5m^2 (1x0.5m) permanent sampling frame locations were marked with wooden stakes in interspace habitat at the two corners of the plots least influenced by shrubs, fertile islands, or disturbances. Another two 0.5m^2 permanent sampling frames were demarcated in understory microhabitat, under burned branches of the plot-central *L. tridentata* on the north and south side of the shrub. The two permanent sampling frame locations per interspace and understory microhabitats were used to collect vegetative data during the three year study. I applied treatments once a year, on the same plots locations, during the first three post-fire growing seasons, but no annual plants germinated in the second post-fire season so treatments were not applied that year (2006-07).

Control (C) plots were left un-manipulated. The entire 8x8m area of the H and W plots was broadcast sprayed with the grass-specific herbicide, Fusilade® II (Syngenta, Greensboro, North Caroline), at a rate of 15ml/64m^2. Herbicide Helper® (Monterey Lawn and Garden Products, Inc, Fresno, CA) was used as a surfactant, also at the rate of 15ml/64 m^2. H and H plots were sprayed with Fusilade II on January 13, 2006 and again on January 7, 2008 over the same exact areas that were treated in 2006. In W plots, *E. cicutarium*, the only non-native forb encountered, was also weeded to complement the grass-specific herbicide in removing all invasive annuals. Invasive forbs in W plots were weeded by hand to minimize damage to native forbs. Most of the tap root was usually removed during the weeding (*see* Schutzenhofer and Valone 2006). Weeding in 2006 and 2008 was done about one week after herbicide spraying, coinciding with the estimated time of grass mortality based on label specifications. Rather than weeding the entire 8x8m plots, *Erodium cicutarium* was weeded from W plots in two 1.5x1.5m squares that each encompassed one of the two 1x0.5m ($0.5m^2$) permanent sampling frames in the interspace habitat. In the understory, weeding was done in a 1.5x0.75m square that encompassed the $0.5m^2$ permanent sampling frame locations under the north and south sides of the central, burned *L. tridentata* individual; obviously, permanent sampling areas were weeded in this process.

I observed that invasive annual plants at the study site germinated immediately following the first significant rain and if precipitation arrived early, as it did the first post-fire season, then this phenomenon was heightened, with a great majority of germinated annuals being invasive species, especially *Schismus* spp. In practice, applying a non-species-specific treatment within this window of time would injure or kill invasives with minimal damage to natives. My observations of germination sequences were consistent with studies on flowering phenology, that show *E. cicutarium* and *Schismus barbatus* to flower relatively earlier compared to native annual plants (Burk 1982, Jennings 2001). Since native desert annuals exhibit seedling density-dependent inhibition of germination

(Inouye 1980), the purpose of this treatment was to remove invasive annuals that had germinated early to free space for remaining un-germinated natives to then take their place. The R treatment was implemented about two weeks after the first major rain event of each season, on November 3, 2005 and December 14, 2007, and it involved raking out all germinated annuals in the upper soil layer regardless of their identity. A scuffle hoe was used to rake out the plants and the soil was only disturbed up to a maximum 5cm depth. The entire area within and immediately surrounding a permanent sampling frame location was raked with the scuffle hoe, regardless of whether there were visible germinated plants present, creating an additional 0.5 m buffer of R treatment around every interspace and understory sampling frame.

VEGETATIVE SAMPLING

Vegetation at Treatment Application Time

Interspace baseline vegetative parameters were collected at treatment application time each year a treatment was applied. In H, W, and R plots, percent cover of invasive grass, invasive forb, and native annuals was measured when treatments were implemented. Cover in control plots was also recorded in 2008 at the time herbicide was applied. These measures were taken with $0.5m^2$ grided sampling frames that were placed in one of the two permanent interspace sampling frame locations per plot. In addition, the phenological stage of *Schismus* spp. and *E. cicutarium* was also recorded for the H treatment. This was done with twelve $0.125m^2$ (25x50cm) frames placed in the middle of the larger $0.5m^2$ frames used to collect cover data when plots were sprayed with Fusilade

II. Phenology was recorded as the percent of *Schismus* spp. or *E. cicutarium* individuals that were in fruiting and/or flowering stage.

Peak Season Annual Vegetation Sampling

Percent cover and richness of plant species were measured in 0.5m² grided sampling frames. Sampling was performed in the permanently designated locations for both interspace and understory microhabitats. Plant density was measured with 0.125m² frames that were placed in the middle of the 0.5m² frames used for cover and richness. Biomass of the most dominant invasive grass (*Schismus* spp.), invasive forb (*E. cicutarium*), and native forb (*Chaenactis fremontii*) was clipped in treated plots using 0.125 m² frames at varying levels of cover, from the lowest values to the highest values for each treatment and each microhabitat (interspace or understory) based on cover values from the 0.5m² frames. Twelve biomass samples were taken for each species x treatment x microhabitat and a regression of cover to biomass was calculated and used to determine biomass per m² based on actual cover values from the large (0.5 m²) sampling frames. To avoid destructive sampling, biomass was collected outside of the permanently marked large sampling frame locations but still in areas that were treated identically. For H and C treatments this could be anywhere else in the plot that had matching microhabitat conditions, but for W and R treatments, biomass could only be clipped in the large buffer zones around the permanently marked sample frame locations. Places where biomass had been collected were marked so that they would not be sampled again in the future.

Peak season annual plant measures, as described above, were taken in late March to early April both during 2006 and 2008.

DATA ANALYSES

ANOVA with an LSD test for multiple comparisons at $\alpha = 0.05$ was used to compare cover, richness, density, and biomass values among the treatments. ANOVA was also used to compare vegetative parameters between microsites or baseline and peak season measures at $\alpha = 0.05$. Data were transformed using arcsine($\sqrt{x}$) for cover, $\sqrt{(x + 0.5)}$ for density and species richness, and $\log_{10}(x + 1)$ for biomass when they would improve normality based on tests for Goodness of Fit. Kruskal-Wallis tests were used to compare perennial plant cover between treatments since this data was severely nonparametric even after transformation. JMP® 7.0.2 (SAS Institute, Inc. Cary, NC) software was used to conduct these analyses. PCA was also used to compare the annual assemblages that resulted from the W and C treatments in 2008 with an un-burned, relatively un-invaded, 'pristine' site that was also treated identically to W plots in 2008 and had been measured using the same experimental design. This 'pristine' site was located on the southern edge of the Little San Bernardino Mountains adjacent to Coachella Valley. For the full site description and floristic summary of the 'pristine' site please *see* 'Native' site from Steers (dissertation – Chp. 4). In the PCA, cover of invasive grass, invasive forb, and native annuals, and native annual species richness were used as variables. Two analyses were run separately for interspace and understory annual assemblages using PC-ORD© 4.27 (MjM Software, Gleneden Beach, Oregon). Plot scores from meaningful axes from each PCA were then analyzed using ANOVA with an LSD test to compare the three annual assemblages for each microhabitat.

RESULTS

During the experiment, four invasive annual and 46 native annual species were recorded (Table 1). The year 2008 had greater interspace and understory native species richness in terms of average number of species per unit area (Figure 2) and total number of unique species recorded (Table 1). Native species richness in control plots did not differ between interspace and understory microhabitats for both 2006 and 2008 based on Student's t-tests (data not shown). These results were maintained when analyses were replicated with data from H and W treatments (data not shown), which had the greatest native species richness of all treatments in both years for both microhabitats (Figure 2). While there were no differences between understory and interspace native richness within the same year, some species were recorded exclusively in one of the microhabitats and not the other. For example, *Amsinckia tesselata*, *Cryptantha maritima*, *Emmenanthe pendulifora*, *Stephanomeria virgata*, and *Uroppapus lindleyi* were only documented from understory microhabitat. Likewise, some species were only documented from interspaces. Also, some species documented in 2006 were absent in 2008, and visa versa (Table 1). However, increased sample number and/or area sampled would have shown that while many of these species were much more abundant in one microhabitat or year, none were actually exclusive (Steers personal observation). Perennial herbs and woody shrubs were also recorded, totaling 18 species, but most had very low frequency and cover (Table 2). The most common perennial encountered was *Lotus scoparius*.

Vegetation at Treatment Application Time

When the R treatment was implemented in the first post-fire season on November 3, 2005, invasive grasses were abundant at 18.8% cover and invasive forbs and native annuals had very low absolute cover, at 0.3% and 0.2%, respectively (data not shown). By January 13, 2006, when H and W plots were sprayed with Fusilade II, invasive grass cover had increased greatly, reaching 48.7%, or 74% of what the maximum cover would be in control plots measured at peak season (Figure 3). Invasive and native annuals had also increased by this time. Invasive forb cover was 3.4%, or 74% of peak season cover, while native annual cover was 4.7%, only 37% of what it would reach at peak season in control plots. At the time of herbicide spraying, 61% of *Schismus* spp. and 35% of *E. cicutarium* individuals were already in flowering stage.

When R plots were raked again on December 14, 2007 in the third and final season, invasive grasses were less abundant than in 2006, at 9.1% absolute cover, while invasive forb and native annual cover was greater than in 2006, at 2 and 0.8 %, respectively. When H and W plots were sprayed with herbicide in January 7, 2008, cover of invasive grass, invasive forb, and native annuals in control plots was only 5.5, 3.8, and 2.4%, respectively (Figure 3), or 14%, 34%, and 11%, respectively, of what maximum peak season cover would be later in the year for control plots. This revealed that these plots were treated at a much earlier growth stage than in 2006. Just as importantly, no

Schismus spp. or *E. cicutarium* individuals had reached fruiting and/or flower stage at herbicide application time in 2008.

In 2008 at herbicide application time, absolute cover values in control plots were similar to those found in H plots, likely reflecting the failure of Fusilade II to kill invasive grasses and forbs in 2006. When W plots were weeded a week later, invasive grass and native forb cover was much higher than control in these plots, likely due to an increase in these two groups caused by the *E. cicutarium* removal in 2006 (Figure 3).

Treatment Effects on Annual Vegetation

Interspace

In 2006, treatments R, H, and W reduced alien annual grass cover by about half (Figure 4). In 2008, H and W treatments reduced alien grass cover to almost zero percent while the raking treatment had no effect. In 2006, treatment W reduced invasive forb cover but in 2008, when precipitation was more favorable and Fusilade II was sprayed at an earlier phenological stage, both H and W treatments were equally effective at reducing invasive forb (*E. cicutarium*) cover. While all treatments were effective at reducing invasive grass in 2006, native annuals had no positive response in this year and did not differ from the control. However, in 2008 the H and W treatments had greater native annual cover than control and raking treatments. In fact, the raking treatment actually reduced native annual cover in 2008 (Figure 4). Native species richness of annual plants responded similarly to native cover measures, although reduced native richness in the R treatment was already evident by 2006 (Figure 2).

All treatments reduced invasive grass density in 2006 (Figure 5), with the lowest densities occurring in the R treatment. By 2008, alien grass density in the R treatment was equal to the control while the densities in H and W plots were very low, implying excellent herbicide effectiveness. Invasive annual forb density was reduced by the three treatments, especially for H and W plots in 2006 and 2008 (Figure 5). Raking severely reduced native annual density in both years. However, due to high variance in 2008 there was no decrease compared to control (Figure 5). In 2008, treatments H and W increased native annual density.

Schismus spp. biomass was reduced by treatments H and W in 2006, and then by all three treatments in 2008 (Table 3). *Erodium cicutarium* biomass had a similar response as the *Schismus* spp. except only treatment W was effective in reducing biomass in 2006. *Chaenactis fremontii* biomass increased in the R treatment in 2006, but had an opposite response in 2008. Only the H and W treatments in 2008 increased *C. fremontii* biomass (Table 3).

Understory

In 2006, understory annual plant cover exhibited similar responses as in the interspace microhabitat except that understory treatment effects were magnified (Figure 4). Especially for native annual cover, treatments induced positive responses compared to control plots in 2006, unlike the interspace microhabitat. These patterns were also seen in 2008. Differences in understory native annual richness between treatments were similar to those observed for understory native annual plant cover, both in 2006 and 2008

(Figures 2 and 4). Treatments utilizing Fusilade II clearly reduced invasive grass and forb cover the most while increasing native annual cover and richness the most (Figures 2 and 4).

Density of invasive grasses and forbs was reduced by all treatments in 2006 and 2008, except the raking treatment had no effect on invasive grasses in 2008 (Figure 5). In 2006, treatments had little effect on native annual density but in 2008, the R treatment reduced native annual density while the W treatment increased native annual density.

Erodium cicutarium biomass was not measured in understory microhabitat since it was uncommon in this microhabitat in 2006 when biomass sampling was first initiated (Figures 4 and 5). However, *Schismus spp*. and *C. fremontii* biomass were sampled in the understory (Table 3). Treatments W and H were equally effective at reducing invasive grass biomass in 2006 and 2008, but only treatment W increased *C. fremontii* biomass in both years. The R treatment decreased understory *C. fremontii* biomass in 2008.

Principle Components Analyses

The interspace annual community of the burned W treatment showed high similarity with the unburned 'pristine' W treated community on the PCA (Figure 6). Axis 1 explained 71% of the variance and was positively correlated with invasive grass and forb cover and negatively correlated with native annual forb and native annual richness. Axis 2 only represented 16% of the variance, had a broken-stick eigenvalue greater than the model eigenvalue, and was therefore not meaningful (McCune and Mefford 1999). The ANOVA, based on plot scores from all three communities on axis 1, showed differences (F (2, 33) = 50.7305, $p < 0.0001$). The LSD test indicated that there was no difference between the burned W treatment plots and the unburned ‘pristine’ W plots ($p = 0.8695$), but the burned control plots were different from both burned W plots ($p < 0.0001$) and unburned ‘pristine’ W plots ($p < 0.0001$).

Axis 1 for the understory data explained 62% of the variance and was correlated similarly with the same variables as interspace axis 1, while understory axis 2 was also not meaningful. Again, the ANOVA, based on understory scores from axis 1, showed differences among all three communities (F (2, 33) = 49.5629, $p < 0.0001$). However, this time the LSD test revealed that each of the three annual communities differed from each other. The LSD test indicated that there was a difference between the burned W treatment plots and burned control plots ($p < 0.0001$), and between burned W plots and the unburned ‘pristine’ W plots ($p = 0.0012$). The unburned ‘pristine’ W plots were also different from the burned control plots ($p < 0.0001$). The W treatment at the burned site produced a more native dominated and species rich community than the W treatment at the unburned ‘pristine’ site (Figure 6). The statistical difference that separated these communities was likely driven by 65% higher native cover and 52% greater species richness found in the burned W treatment plots compared to the unburned ‘pristine’ W plots (data not shown). Finally, both burned and unburned W treated plots were characterized by much greater native cover and species richness than burned control plots regardless of microhabitat. When the same analyses were performed for interspace and understories using control data from the unburned ‘pristine’ site instead of data from W treated plots, similar results as those reported above were also found for both microhabitats (data not shown).

Treatment Effects on Perennial Vegetation

Interspace perennial plant cover in control plots went from 0.2% in 2006 to 0.1% in 2008 and from 2.5% to 3.7% in understory microhabitat. Perennial cover was usually greater in treated plots compared to control, but no treatment effects were found based on Kruskal-Wallis tests when all treatments were compared at once. However, when comparing perennial plant cover or density in treatment plots to control plots on an individual basis, some treatments did actually produce greater native perennial cover or density values compared to the control using this non-parametric test. Treatment R had greater perennial plant cover than the control for interspace microhabitat in 2008 ($\chi^2 = 4.8093$, $p = 0.0283$). Treatment W also had greater cover than control for interspace microhabitat in 2008 ($\chi^2 = 5.4996$, $p = 0.0190$), and greater perennial density than control in both 2006 ($\chi^2 = 5.4679$, $p = 0.0194$) and in 2008 ($\chi^2 = 4.9647$, $p = 0.0259$).

DISCUSSION

The small, unburned patch of creosote bush scrub opposite the fuel break at the study site was too small in area to compare it with the burned vegetation using a similar sampling design, but some general impacts of the fire can still be determined qualitatively. First, the most obvious effect of the fire was the dramatic reduction in abundance of desert shrubs. While some shrub individuals were able to resprout after the fire, shrub cover remained very low throughout the experiment (Steers personal observation). Some shrubs, such as *Lotus scoparius*, benefited from the fire, which was not surprising considering *L. scoparius* seeds have increased germination in response to fire in cis-montane California shrublands (Keeley 1991). Second, *Bromus madritensis* abundance was dramatically reduced by the fire, and *Schismus* spp. and *Erodium cicutarium* seemed to benefit from the fire, similar to other studies (Minnich and Dezzani 1998, Brooks 2002).

The W plots experienced reduced invasive grasses and no invasive forbs in 2006, and almost complete removal of both these groups in 2008. Consequently, perennial cover and density was the highest in this treatment over all years. Statistically greater cover and density of perennial plants in interspace W plots compared to the control lends evidence for the competitive suppression of desert shrub seedlings by invasive annuals and may contribute to understanding why, for many desert shrubs, recruitment can be virtually non-existent after invasive plant fed fires (Steers dissertation – Chp. 1). Although invasive grass competition with mature shrubs has been documented in CBS (DeFalco et al. 2007), competition at the seedling stage has not. However, it is generally assumed to occur since shrub and tree seedlings from other western vegetation types are competitively suppressed by similar invasive annual grasses (Schultz et al. 1955, Davis and Mooney 1985, Gordon et al. 1989, Eliason and Allen 1997, Pendelton et al. 2007). Use of Fusilade has also been successful in establishing shrub seedlings in coastal sage scrub impacted by frequent fire and invasive annual grasses (Cione et al. 2002).

For burned understory microhabitat, treatments had no effect on perennial plant cover and density possibly due to propagule limitation. Like many CBS desert shrubs that are sensitive to fire when fully grown (Brooks and Minnich 2006), desert shrub seeds may also be highly sensitive to fire. This may explain why invasive plant removal from understories did not result in increased perennial plant density or cover despite this microhabitat likely having greater propagules density than the interspace (Nelson and Chew 1977). Furthermore, Brooks (2002) has found that *L. tridentata* understory temperatures during fire can reduce species richness while interspace fire intensities are not severe enough to result in any changes.

Vegetation at Treatment Application Time

Success of the raking treatment was highly dependant on the annual plant species group (invasive grass, invasive forb, or native annual) composition at treatment time. In 2006, when precipitation was early in the season, the majority of emerged annuals were invasive grasses, and the raking treatment disproportionately impacted this species group. In 2008, precipitation came later in the growing season and invasive grasses were not as abundant as in 2006, but invasive and native forbs were more abundant. Consequently, the R treatment had a greater negative impact on invasive and native forbs than invasive grasses in 2008 compared to 2006. The timing of treatment implementation relative to the phenological stage of plant species during application can largely affect success, especially for treatments that are non-species specific (*reviewed in* DiTomaso 2000).

According to label specifications, Fusilade II works best when alien annual grasses are young and haven't reached flowering stage. The ability of Fusilade II to kill *E. cicutarium* was also dependant on spraying individuals at an early stage before they had reached flowering. Fusilade II was effective at killing invasive grasses and forbs in 2008 because *Schismus* spp. and *E. cicutarium* were much less phenologically advanced, in terms of size and flowering/fruiting stage than in 2006. This same outcome has also been observed when controlling these species with Fusilade II in unburned creosote bush scrub (Steers dissertation – Chp. 4).

Treatment Effects on Annual Vegetation

Although mechanical control techniques like scuttle hoe application have produced successful results for controlling invasive plants in rangelands (*reviewed in* DiTomaso 2000), when compared to treatments utilizing Fusilade II in this study, invasive plant removal with a scuttle hoe was not as effective, or was counter-productive. Treatments like R, which cause mortality with a non-species-specific mode of action, could be useful in certain instances when invasive plants are vulnerable and desired plants are not, such as when early season precipitation disproportionately induces invasives to germinate while native seedbanks remain relatively dormant (Steers, personal observation). However, this particular treatment also resulted in major soil disturbance, which can promote invasive plants (*reviewed in* Hobbs and Huenneke 1992). The use of fire to control invasive annual grasses in more temperate ecosystems can also be problematic for similar reasons (*reviewed in* Rice 2005). Use of a general herbicide, such as glyphosate, could have achieved similar plant mortality rates as the scuttle hoe application but with no soil disturbance, which would have better tested this phenological-based approach.

Fusilade II was a very effective product for controlling alien annual grasses and *E. cicutarium*. This product has successfully reduced invasive grass abundance in many instances (Pavlick et al. 1993, Arnold et al. 1998, Cione et al. 2002, Allen et al. 2005, Cox and Allen 2008, Marushia and Allen *in press*). While the phenological stage of target plants is critical to the success of Fusilade II, mid-season droughts and consequent plant stress can also have a great effect. In 2006, precipitation was below average and irregular in distribution. The drought that occurred after the first storm of the season, when herbicide application would normally have been ideal based on phenology, caused mortality or stress to the annual plants. Stress limits product effectiveness according to label specifications. In 2008, precipitation was greater and rainfall events occurred closer together, preventing any periods early in the growing season where drought stress could have affected herbicide response by the invasive grasses and forbs. Had invasive species mortality in 2006 been similar to that in 2008, it is very likely that native annuals would have responded more positively despite lower precipitation.

No evidence of negative effects from Fusialde II on native species were observed at this study site. *Vulpia octoflora*, a native annual grass that did occur occasionally in plots treated with Fusilade II, did not appear to be damaged in any way. This may be due to general herbicide resistance by this genus or due to phenological differences in germination or flowering time that allowed this plant to avoid vulnerability during application. Had *Brassica tournefortii*, a common desert invasive forb, been present at the site, treatment H may not have been as effective as W since *Brassica* spp. are not susceptible to Fusilade II (Steers dissertation – Chp. 4).

Principle Components Analyses

PCA was used to ordinate the W treatment and control plot scores against plots located in a nearby unburned, relatively uninvaded stand of creosote bush scrub that was also treated identically to W plots. While this unburned site may not be a perfect reference stand due to its off-site location and possible environmental dissimilarities, it was chosen because it contained some of the highest native abundance and richness in the region (Steers dissertation – Chp. 4). These ordinations were used to illustrate how burned native annual communities differ from 'pristine' sites when invasive annuals are present or removed.

The results for both interspace and understory burned W treatment plots clearly showed that the removal of invasive grasses and forbs results in native annual assemblages that are similar to those of the relatively pristine, unburned site. Interestingly, understory burned W treatment plots from BMCP were ordinated farther to the left on Axis 1 than the unburned W treatment plots from the 'pristine' site, which was partly due to greater native species richness found in the burned understory of W plots. In unburned creosote bush scrub, species richness is usually lower in understory microhabitat compared to the interspace (Fowler and Whitford 1996, Brooks 2002, Steers dissertation – Chp. 4) even when invasive plants are removed from both microhabitats

(Steers dissertation – Chp. 4). However, this phenomenon was not observed at the burned site in the presence or in the absence of invasive annual plants despite potentially lethal fire intensities in the understory as opposed to the interspace (*sensu* Brooks 2002). The high species richness found in burned understories is possibly due to light no longer limiting native annuals in this microhabitat following the removal of the shrub canopies by the fire. Decreased understory species richness in other ecosystems has also been attributed to light limitation by the canopy (Maranon and Bartolome 1993). Alternatively, relatively high species richness in burned *L. tridentata* understories in the absence of invasive plants could also be a result of fire disturbance itself, in accord with the intermediate disturbance hypothesis (Connell 1978, Kondoh 2001, Roxburgh et al. 2004).

Finally, although the interspace and understory microhabitats were not sampled before the fire, and only adjacent unburned microhabitats suggest that native richness was already very low due to high invasive plant abundance in both microhabitats, results from these PCA ordinations indicate that fire itself had a minimal direct negative effect on native annual plant structure and species composition. Rather, the biggest threat to native annual species abundance and richness appears to be competitive exclusion by invasive annual plants, which unfortunately are promoted by fire disturbance in CBS (Cave and Patten 1984, Brooks 2002, Steers dissertation – Chp. 2). Results from the ordinations suggest that in the absence of invasive annuals, native annuals can be resilient to fire disturbance. Interestingly, their perennial associates in CBS, especially cacti and long-lived shrubs, can take decades to centuries to reestablish after fire (O'Leary and Minnich

1981, McLaughlin and Bowers 1982, Cave and Patten 1984, Brown and Minnich 1986, Alford et al 2005, Brooks and Minnich 2006, Steers dissertation – Chp. 1).

Resiliency of Desert Annuals to Fire

The resistance of creosote bush scrub vegetation to invasion by plant species appears low. For example, over one hundred plants are currently listed by Brooks and Esque (2002) as threats to desert vegetation in California. Mensing and Byrne (1998) reported a rapid, pre-mission invasion by *E. cicutarium* throughout southern California, implicating the invasion through the deserts was rapid as well. Minnich (2008) has also documented rapid invasion by annual grasses and *Brassica tournefortii* in CBS of southern California in the 20th century. While desert areas with low soil nutrients (Brooks 1999b, Steers dissertation – Chp. 2) may be more resistant to invasion, and while droughts in the American Southwest may periodically limit certain invasive annuals, like *B. madritensis* (Salo 2004, Minnich 2008), the deserts of southern California remain highly susceptible to invasion by exotic plant species. Furthermore, this study also shows that a competitive hierarchy of invasive annuals allows for invaders to persist and continue competitive exclusion of native plants if the abundance of the dominant invasive species is decreased after fire, as have other studies (Minnich and Dezani 1998, Brooks 2002). For example, reduction of *B. madritensis* abundance after fire resulted in the increase of other invasive annuals like *Schismus spp*. and *E. cicutarium*, which suppress native species (Brooks 2000, Schutzenhofer and Valone 2006). Overall, these examples clearly show that the native annual plant community of CBS has low resistance to invasive species that are pre-adapted to the arid environment of southern California.

If defining resiliency as the degree and rate at which a community returns to its previous state once a perturbation (disturbance/invader) is removed (*sensu* Pimm 1991, Knapp 2001), then treatment W (removal of all invasive species) demonstrated that burned CBS annual communities are indeed resilient. The degree of resiliency measured in this study is high considering that W treated annual communities at BMCP had similar or greater cover and species richness compared to an unburned, virtually uninvaded site that was chosen for its high native cover and richness. Although, direct comparison to this site must be taken with caution since it is only a surrogate and we do not know what the unburned, pre-invaded annual community resembled at BMCP.

Even though the W treated burned understory community at BMCP had higher native annual plant cover and richness than the unburned, uninvaded 'pristine' understory, we know that the W treatment understory at BMCP did not fully return to its unburned, uninvaded state. While species typical of the understory were still present, their cover was likely not as great as what would be indicative of the uninvaded, pre-fire condition. This is based on measures from paired burned vs. unburned CBS stands 4.5 km to the southwest that show large post-fire reductions in the coverage of annuals typical of understory microhabitat (Steers dissertation – Chp. 2). If invasive annuals are controlled indefinitely at BMCP, the understory annual community might not achieve pre-perturbation abundance levels until shrub structure is restored.

The rate at which the annual community resembled unburned, uninvaded CBS was rapid for interspace annual assemblages, occurring in two seasons (spring of 2007 had no annual plant germination so it is not counted). This rate may have increased had Fusilade II been totally effective in the first season. Other communities in harsh environments with short-lived species can also show high resiliency rates once invasives are removed (Knapp et al. 2001). Because native desert annuals are known to have long-lived seedbanks (Freas and Kemp 1983), and exhibit density-dependent inhibition of germination if other germinated annuals already occupy space (Inouye 1980), the potential for the positive response of native annual plants once invasive plant are removed should be high. The resiliency of some of these annual plant species after fire can also be explained, in part, based on their current distributions, which extend into cis-montane vegetation types that experience greater fire frequency than CBS shrublands (Steers dissertation – Chp. 2).

CONCLUSION

Most restoration efforts in creosote bush scrub have focused on cases of severe physical disturbances (e.g. roads, mining, and farming) (Grantz et al. 1998; Lovich and Bainbridge, 1999; Walker and Powell, 2001) or on riparian ecosystems that have been invaded by *Tamarix ramosissima* (Tamarisk) (Fleishman et al. 2003). Examples of restoration of creosote bush scrub impacted by invasive grasses and fire are lacking. However, removal of invasive grasses and forbs seems to be a logical first step in the restoration of burned creosote bush scrub.

The control of invasive annuals in exotic/native species mixtures without non-target effects is challenging. The success of non-species specific plant removals, such as treatment R, will be highly dependant on initial species composition at treatment application time. Therefore, treatments such as these can easily be counterproductive when a large proportion of early germinated plants are native, as occurred in early December of 2007. In this study, treatments utilizing Fusilade II, especially when applied before invasives reached flowering stage and in years with adequate rainfall and distribution, worked best for reducing invasive plant abundance and promoting the native plant community.

I have shown that if invasive annuals can be controlled after fire, then native annuals can form rich assemblages that are similar in average native species richness and cover to unburned, relatively uninvaded sites with high regional species richness. However, the resiliency of the native annual community will likely depend on fire intensity (Brooks 2002), which was not measured. In the case of native annuals primarily restricted to understory microhabitat, resiliency may also depend on the return of shrub structural complexity, which can take decades to centuries (Brown and Minnich 1986, Lovich and Bainbridge 1999, Steers dissertation – Chp. 1). Finally, invasive plant control can increase the ability of perennials to reestablish passively, which is critical for reinstating the spatial complexity for which these shrublands are known for (Bolling and Walker 2002).

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FIGURES AND TABLES

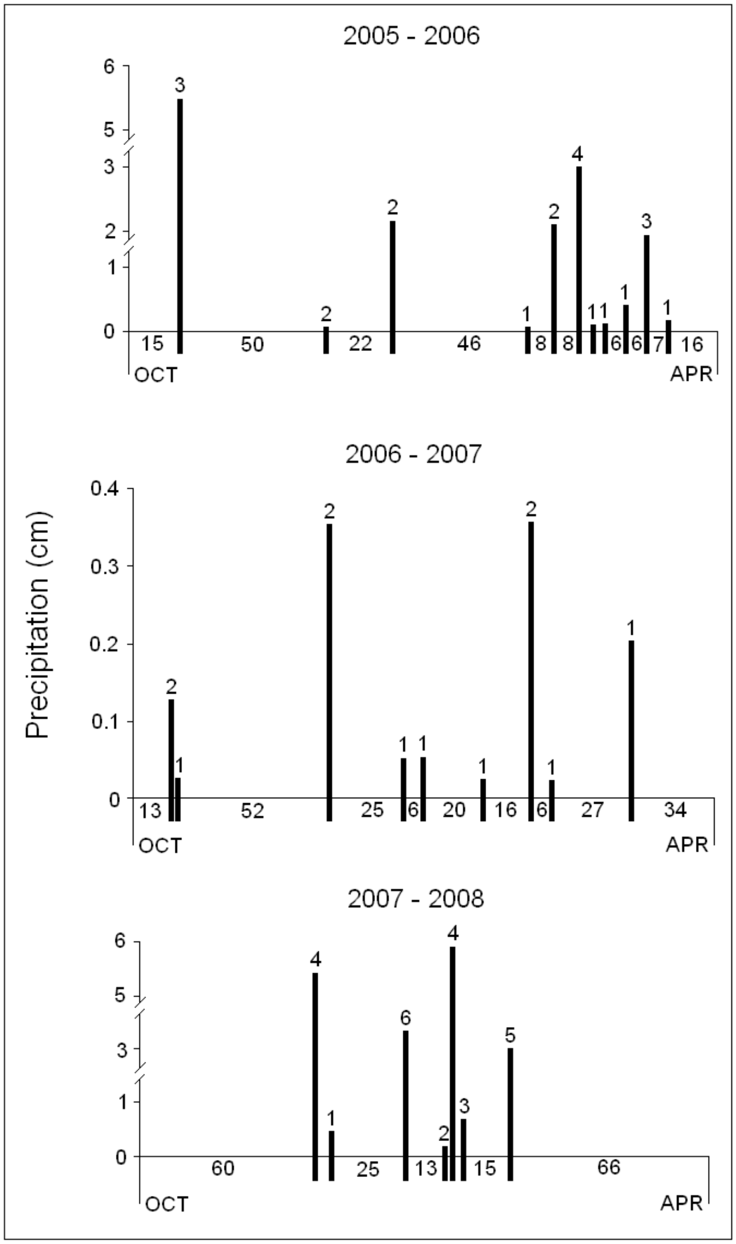


Figure 3.1 Wet season precipitation for 2005-2006, 2006-2007, and 2007-2008. Numbers above bars indicate consecutive days of precipitation while number below x-axis and in between bars indicate the number of consecutive days without rain (consecutive days without rain that were five or less are not shown). Note difference in precipitation scale between rainy seasons. X-axis starts on October 1st and Ends on April 30th.

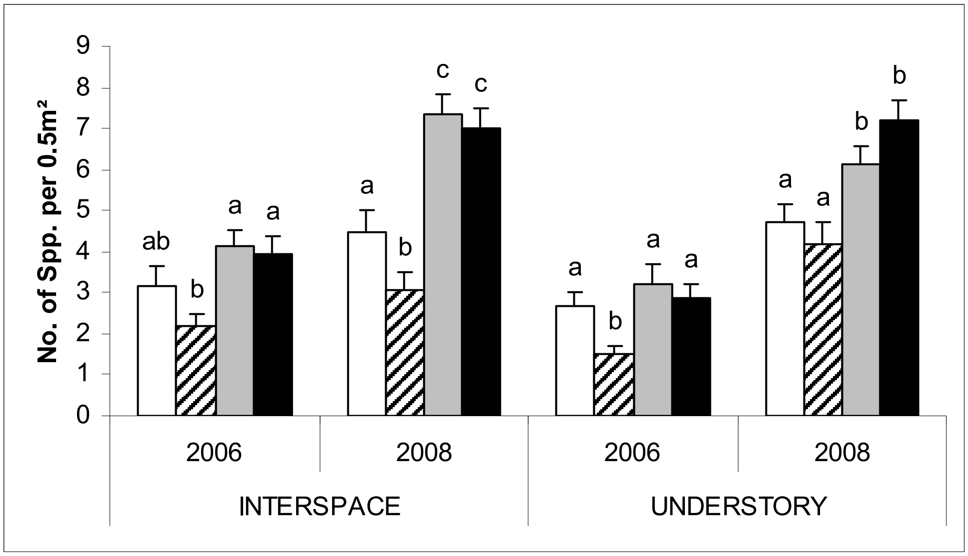


Figure 3.2 Native annual species richness at peak spring season by treatment, year, and microhabitat. Treatments C, R, H, and W are represented by white, dashed, grey, and black bars, respectively. Different letters between bars indicate differences between treatments within the same year and microhabitat only, based on ANOVA and LSD tests.

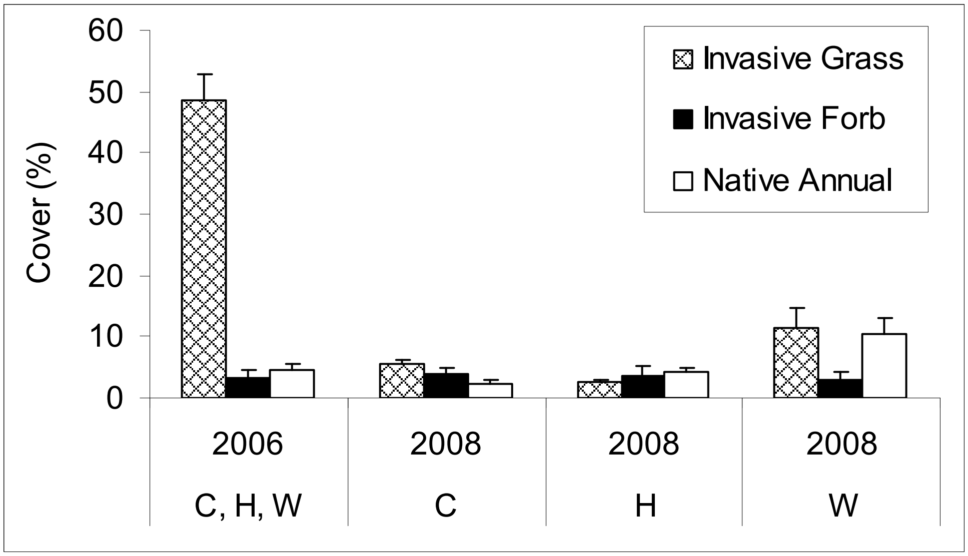


Figure 3.3 Percent cover of invasive grass, invasive forb, and native annuals at treatment application time when treatments H and W were implemented in 2006 and 2008. No treatments had been applied yet when 2006 data was taken so cover was pooled across plots.

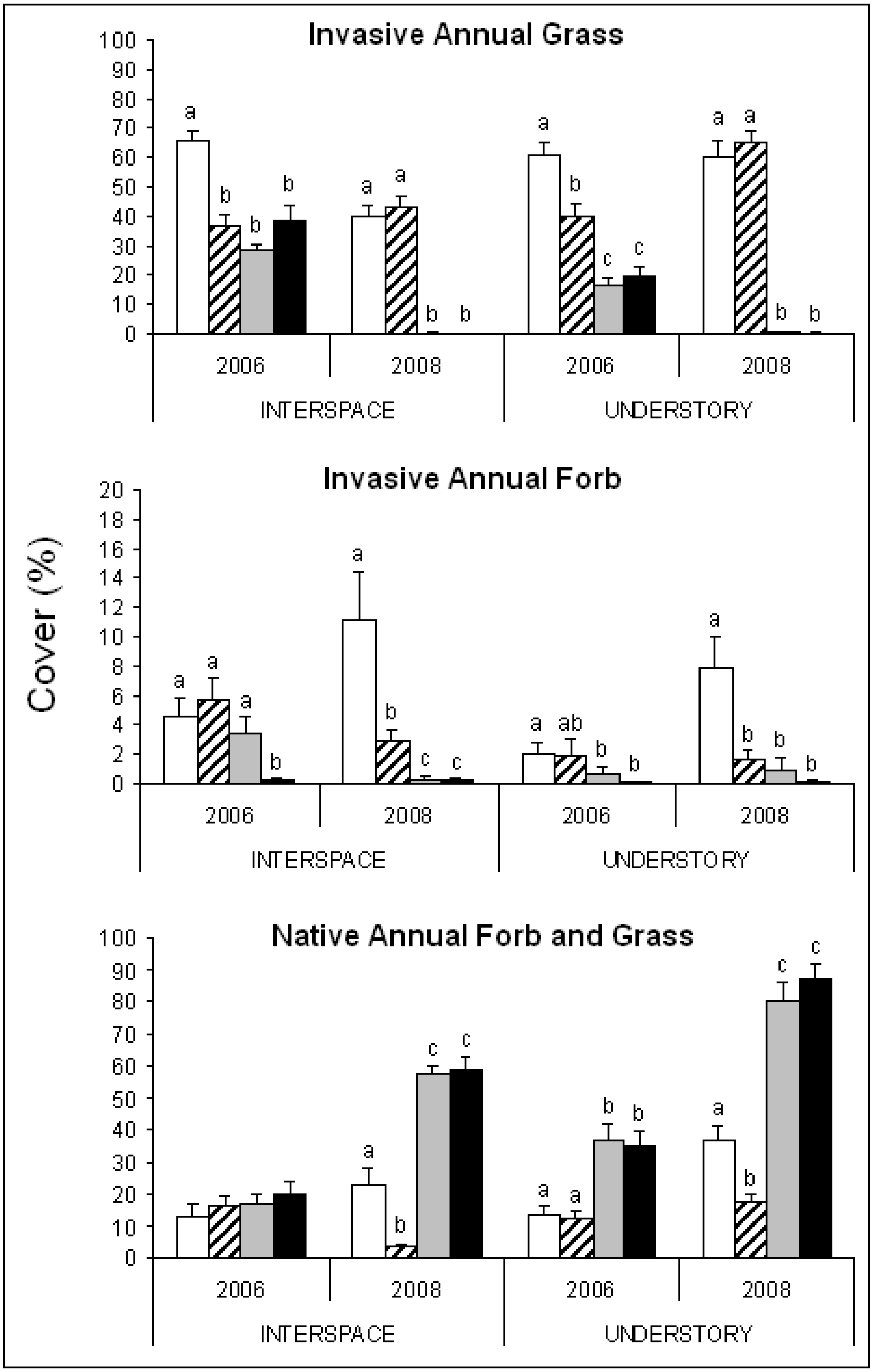
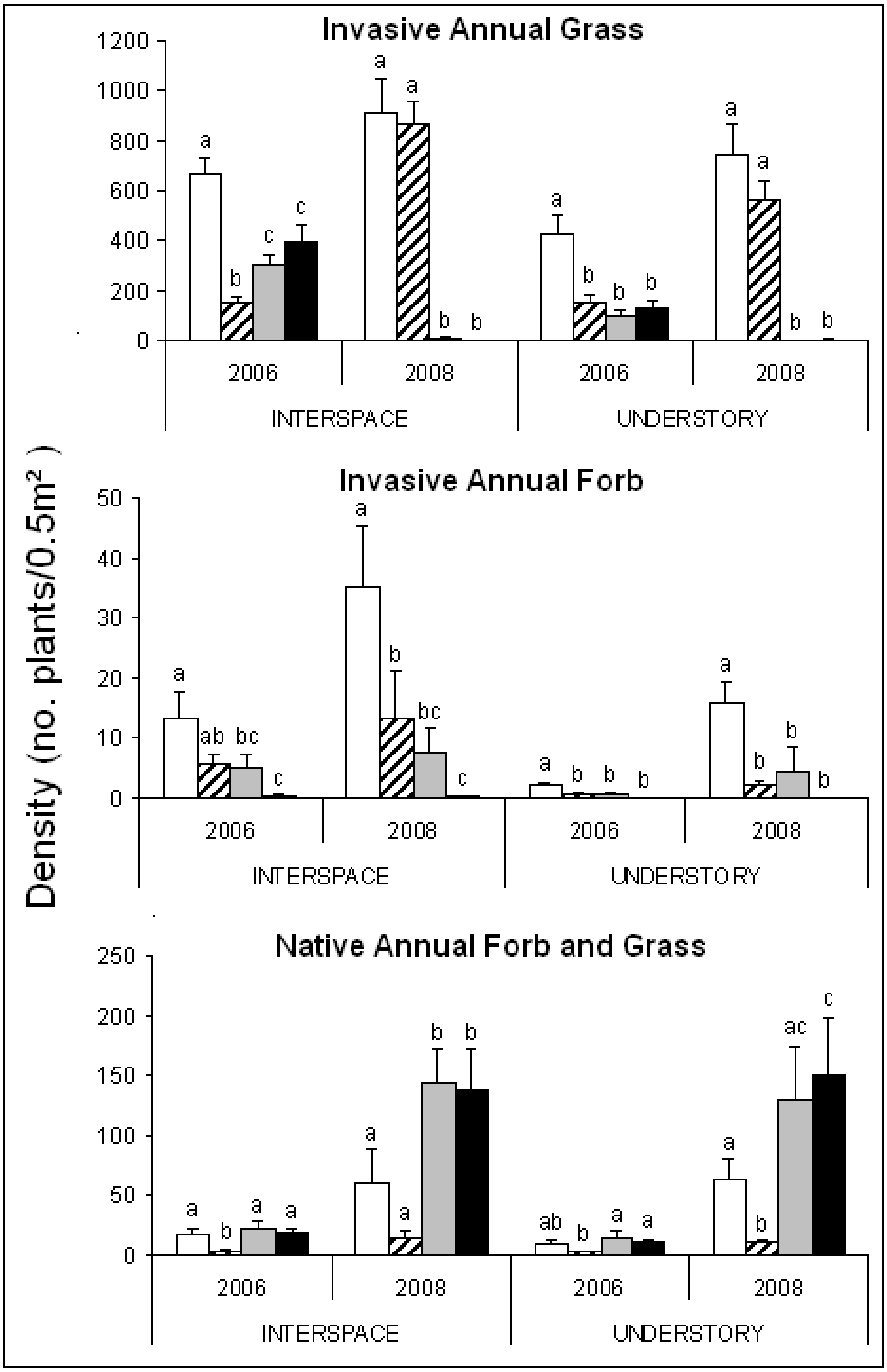


Figure 3.4 Cover of invasive grass, invasive forb, and native annuals at peak spring season. See Figure1 for treatment descriptions and statistical properties.


Invasive Annual Grass

Invasive Annual Forb

Native Annual Forb and Grass

Figure 3.5 Density per 0.5m² of invasive grass, invasive forb, and native annuals at peak spring season. See Figure1 for treatment descriptions and statistical properties.

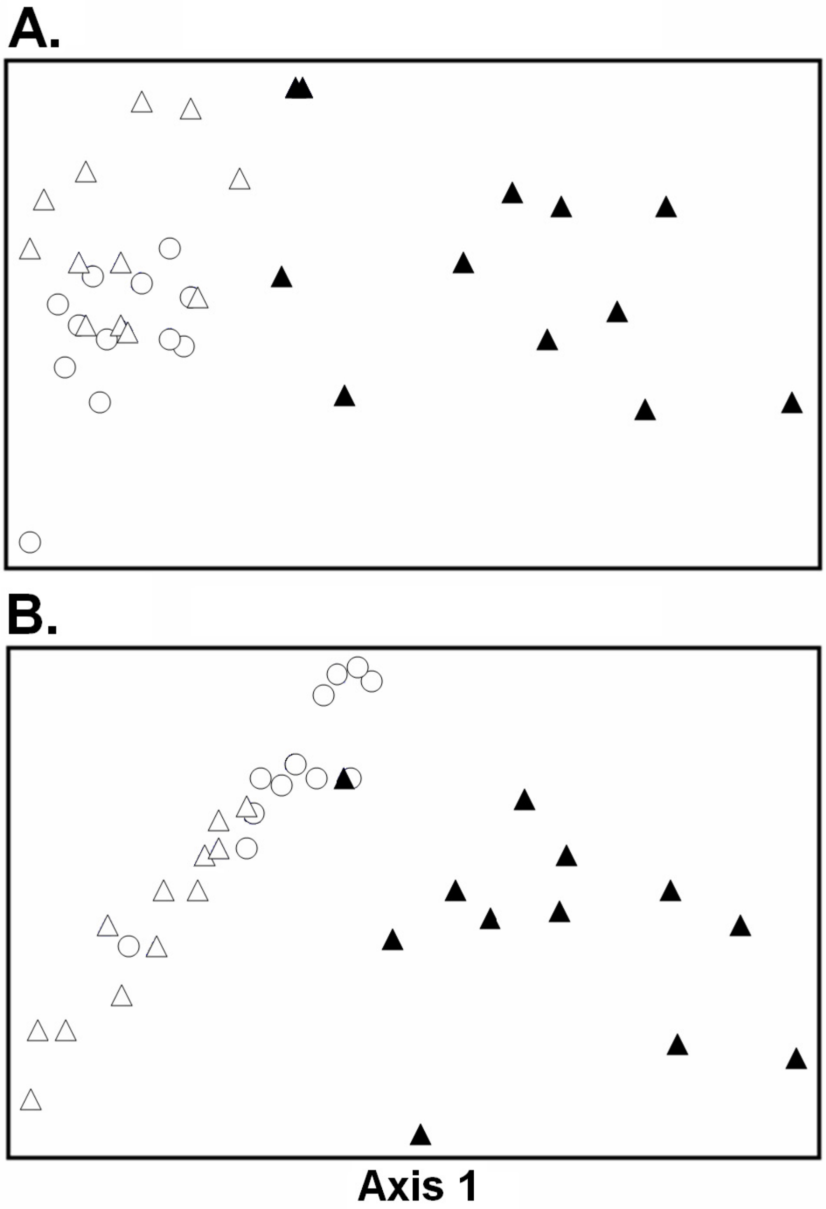


Figure 3.6 **A**. Interspace treatment plot ordination based on environmental space using PCA. White triangles, black triangles, and white circles represent burned treatment W at BMCP, burned control at BMCP, and treatment W at the unburned, uninvaded reference site, respectively. Axis 1 was positively correlated with native annual plant cover and species richness to the left and positively correlated with invasive grass and invasive forb cover to the right. Axis 2 was not meaningful and is not labeled. **B**. Understory treatment plot ordination using PCA. Same symbology for treatment and sites, and same relationship of environmental variables with Axis 1 as the graph above.

Table 3.1 Cover of annual species found in treatment plots (C, R, H, and W) in 2008. Native species exhibiting less than 0.1% in all treatments were left out, including *Centrostegia thurberi*, *Chorizanthe watsonii*, *Crassula connata*, *Cryptantha angustifolia**, *Cryptantha maritima**, *Filago californica*, *Gilia stellata**, *Linanthus bigelovii**, *Loeseliastrum schottii**, *Plantago patagonica*, *Thysanocarpus laciniatus*, *Tropidocarpum gracile**, and *Uropappus lindleyi**. Asterisked species were only found in 2008. Species recorded only in 2006 were *Lupinus concinnus, Stephanomeria virgata*, and *Stylocline gnaphaloides*.

		INTERSPACE				**UNDERSTORY**			
Family	Species	**C**	**R**	**H**	**W**	**C**	**R**	**H**	**W**
INVASIVE ANNUAL FORB									
Geraniaceae	*Erodium cicutarium*	11.2	2.9	0.3	0.2	7.9	1.6	0.9	0.1
INVASIVE ANNUAL GRASSES									
Poaceae	*Bromus madritensis*	0.5	2	< 0.1		3.7	6.6	0.3	< 0.1
	Bromus tectorum		< 0.1						
	Schismus spp.	39.6	40.9	0.1	< 0.1	56.4	58.5	0.2	0.2
NATIVE ANNUALS									
Asteraceae	*Calycoseris parryi*	0.7	< 0.1	2.9	2.5	1.4	1.1	3.4	2.2
	Chaenactis fremontii	16.8	2.2	38.5	33.3	26.5	9.1	39.8	57.4
	Coreopsis californica		< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	0.3
	Filago depressa			< 0.1	< 0.1				0.1
	Malacothrix glabrata	0.5		< 0.1	0.6	0.3	0.6	< 0.1	2.3
	*Rafinesquia neomexicana**				0.4				
	*Stephanomeria exigua**	< 0.1			0.5				
Boraginaceae	*Amsinckia tessellata**					0.3			
	Cryptantha barbigera	0.4	< 0.1	3.9	3.5	3.2	2.9	10.5	7.9
	Pectocarya heterocarpa	0.1	< 0.1	0.8	0.9				
	Pectocarya linearis	0.9	0.1	1.2	7.3	0.8	0.2	3.5	6.4
	Pectocarya penicillata	< 0.1	< 0.1	< 0.1	1.1	0.2	< 0.1	1.2	3.2
	Pectocarya recurvata	< 0.1		0.7	1.2	< 0.1		0.3	1.5
Brassicaceae	*Descurainia pinnata**			< 0.1			< 0.1	< 0.1	0.2
	Guillenia lasiophylla	< 0.1	< 0.1		0.2	0.2	< 0.1	0.4	
	Lepidium lasiocarpum	0.1	0.2	0.5	0.4	0.3	0.1	0.2	0.5
Fabaceae	*Lotus strigosus*	< 0.1	< 0.1	0.2	0.1	< 0.1	< 0.1	< 0.1	0.2
	Lupinus bicolor	0.4	< 0.1	0.6	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
	Lupinus sparsiflorus					< 0.1	0.1	< 0.1	< 0.1
Hydrophyllaceae	*Emmenanthe penduliflora*					< 0.1	0.5	0.8	< 0.1
	Phacelia distans		0.2	< 0.1	< 0.1	1.1	0.8	8.1	0.3
Lamiaceae	*Salvia columbariae*	0.3	0.3	3.4	1.5	1.1	0.5	6.1	1
Loasaceae	*Mentzelia sp.*		< 0.1	< 0.1			< 0.1	0.7	0.2
Onagraceae	*Camissonia bistorta*		< 0.1	0.7	< 0.1				
	Camissonia californica	0.4	< 0.1	0.9	0.6	0.4	1.2	4	1
	Camissonia pallida	< 0.1	< 0.1	0.4	0.8		0.2	0.2	0.5
Poaceae	*Vulpia octoflora*	< 0.1	< 0.1	< 0.1	0.1	< 0.1	< 0.1	0.2	0.8
Polemoniaceae	*Eriastrum diffusum*	< 0.1	< 0.1	0.1	0.2		< 0.1	< 0.1	< 0.1
Polygonaceae	*Chorizanthe brevicornu*	1.7	< 0.1	1.5	0.4	< 0.1		0.4	0.2
	Eriogonum maculatum				0.7				< 0.1
Portulacaceae	*Calyptridium monandrum*	0.2	< 0.1	0.8	1.7	< 0.1	< 0.1	< 0.1	0.3

Table 3.2 Native perennial cover in 2008 for all treatments (C, R, H, and W). Species exhibiting less than 0.1% in all treatments were left out, including *Larrea tridentata**, *Salazaria mexicana**, *Stephanomeria pauciflora*, and *Stillingia linearifolia*. Species marked with an asterisk were only found in 2008. Species occurring in 2006 but not in 2008 were *Chamaesyce albomarginata*, *Selaginella bigelovii*, and *Yucca schidigera*, all individuals of which appeared to have died, at least in experimental plots, during the drought in the second year (2007).

		INTERSPACE				**UNDERSTORY**			
Family	Species	**C**	**R**	**H**	**W**	**C**	**R**	**H**	**W**
Asteraceae	*Encelia actoni*					0.2			0.2
	Ambrosia dumosa		0.8	< 0.1					
	Viguiera parishii					0.5			
Fabaceae	*Acacia greggii*		0.2					< 0.1	
	*Psorothamnus arborescens**		0.5						
	Lotus scoparius	< 0.1	0.3	1	0.3	0	< 0.1	< 0.1	< 0.1
Krameriaceae	*Krameria grayi*					< 0.1	< 0.1	0.1	
Liliaceae	*Dichelostemma capitatum*	< 0.1	< 0.1	0.3	0.3	< 0.1		< 0.1	< 0.1
Malvaceae	*Sphaeralcea ambigua*				0.2		1.8	0.2	
Nyctaginaceae	*Mirabilis bigelovii*		< 0.1	< 0.1		2.9	< 0.1	1.6	1.5
Poaceae	*Pleuraphis rigida*		< 0.1			0.1			

Table 3.3 Biomass (g/0.5m^2), including standard errors, for *Schismus* spp, *E. cicutarium*, and *C. fremontii*. Different letters indicate differences between treatments within year, species, and microhabitat only, based on ANOVA and LSD tests.

	INTERSPACE			UNDERSTORY	
	Schismus	*Erodium*	*Chaenactis*	*Schismus*	*Chaenactis*
2006					
C	^{A} 61.9 ± 4	^{A} 7.8 ± 2	^{A} 12.7 ± 4.5	^{A} 63.2 ± 4.3	^{A} 17.9 ± 5.5
R	^{A} 50.9 ± 5.7	^{A} 7.1 ± 1.9	^{B} 28.3 ± 6.6	^{A} 66.1 ± 10.2	^{AB} 22.2 ± 6.7
H	^{B} 22 ± 1.7	^{A} 4.5 ± 1.6	^{AB} 13.7 ± 2.3	^{B} 14.1 ± 2.2	^{AB} 34.4 ± 7.8
W	^{B} 29.1 ± 4.1	^{B} 0.4 ± 0.2	^{AB} 14.4 ± 3.4	^{B} 16 ± 2.4	^{B} 41.7 ± 8.7
2008					
C	^{A} 153.9 ± 14	^{A} 11.1 ± 3.2	^{A} 29.8 ± 7.8	^{A} 53.2 ± 6.9	^{A} 35.9 ± 6.2
R	^{B} 9.5 ± 1	^{B} 2.9 ± 0.9	^{B} 2.5 ± 1	^{B} 81.9 ± 7.2	^{B} 8.2 ± 1.4
H	^{C} 0.1 ± 0.1	^{C} 0.3 ± 0.2	^{C} 68.5 ± 6.8	^{C} 0.1 ± 0.1	^{AC} 56.8 ± 9.8
W	^{C} 0 ± 0	^{C} 0.2 ± 0.1	^{C} 59.2 ± 7.8	^{C} 0.1 ± 0.1	^{C} 77.8 ± 8.4

CHAPTER 4. Native plant response to invasive plant removal in a winter-rainfall, annual community: what is the role of resource heterogeneity?

ABSTRACT

In terms of competition, invasive annual grasses and forbs hierarchically rank above native annuals in winter-rainfall, annual plant assemblages of the western United States. Therefore, removal of both invasive grasses and forbs results in maximum competitive release of native annual plants. Because invasive plants are typically more abundant in areas with relatively higher resources, the greatest response by natives to invasive removal should also be where resources are relatively high. The purpose of this study was to evaluate the response of native annual plants to the simultaneous removal of invasive annual grasses and forbs in two contrasting microhabitats, resource poor shrub interspaces and relatively resource rich fertile island understories. Four sites were used in this study that contained varying amounts of invasive annual grasses, *Erodium cicutarium*, and *Brassica tournefortii*. I found that invasive plants were more abundant in understory than interspace microhabitats, that competition importance did not differ between microhabitats, that competition intensity was only greater in understory microhabitats at one of the four sites, and that native species richness was greater in interspace microhabitats but had the greatest relative increase in response to invasive plant removal in the understory. I then compared the removal of all invasive plants to a treatment utilizing Fusilade II, a grass specific herbicide that is also lethal to species in the genus *Erodium*. At sites where the invasive species composition was mostly grasses and *E. cicutarium*, Fusilade II worked as effectively as removal of all invasive plants, but

in sites where invasive plants had low abundance or where the invasive mustard was dominant, both treatments had no effect or the Fusilade II treatment was not as effective as total invasive plant removal, respectively. Finally, these results suggest prioritizing resource rich microenvironments for invasive species control. However, this may not always be optimal, and site-specific factors and various ecosystem processes must be considered.

INTRODUCTION

Many western North American vegetation types have been invaded by exotic annual grasses and forbs since European contact. These invasive annuals are highly competitive with native perennial and annual species (Eliason and Allen 1997, Dyer and Rice 1999, DeFalco et al 2003, Vila and Weiner 2004, Cox and Allen *in press*, although see Seabloom et al. 2003). They also alter ecosystem processes (Ehrenfeld 2003) and the fire cycle to the detriment of the native vegetation, especially in the context of grass invasions (reviewed in Brooks et al 2004). Their impact on native ecosystems is very apparent and dramatic (Mack et al. 2000, Mooney and Cleland 2001, Henderson et al, 2006). Three groups of exotic annuals that have been especially successful in western North America are grasses (Beatley 1966, Seabloom et al. 2003), filarees (*Erodium* spp.) (Bartolome 1979, Mensing and Byrne 1998, Brooks 2003) and mustards, especially species in the genus *Brassica* (Bell and Muller 1972, Trader et al, 2006).

Invasive annual grasses, filarees, and mustards are ubiquitous in low elevation vegetation of the semi- and arid west where precipitation primarily occurs in the winter.

When one of these three invasive groups is removed from invasive and native species mixtures, there is often an increase in the remaining invasive annual groups (Brooks 2000, Allen et al. 2005, Barrows et al, 2008, Cox and Allen 2008, Cox and Allen *in press*). For example, when invasive grasses are removed, filaree abundance increases (Brooks 2000, Cox and Allen *in press*). These studies imply a strong competitive interaction between the exotic invasive species groups. Some studies also show that native abundance can increase when just one of the invasive groups are removed (Brooks 2000, Schutzenhofer and Valone 2006, Barrows et al. 2008) but the greatest increase in native annuals occurs when all invasive species groups are removed (Cox and Allen *in press*). Therefore, competition among multiple plant species components appears to be an important ecosystem characteristic of these annual communities with an apparent competitive hierarchy placing these three invasive groups above native annuals. Simultaneous removal of all invasive annuals is therefore necessary for maximum 'release' of native components. However, the degree to which native annual communities respond to complete invasive species removal may depend on several factors, one of which is resource availability.

Interspecific competition is a critical factor for determining plant community composition (Grubb 1977, Grace and Tilman 1990, Aerts 1999) and is thought to be of a greater intensity in areas with higher resources and consequently, more productivity (Grime 1979, Belcher et al. 1995, Aerts 1999). Within a habitat, the degree of competition can vary as resources are spatially patchy and/or characterized by pulsed temporal availability (Chesson 2000, Davis et al. 2000, Pugnaire et al. 2004, Snyder

2008). The spatial and temporal heterogeneity of these resources should produce certain places and times where competition is more intense than otherwise (Grime 1979, Goldberg and Novoplansky 1997, Daehler 2003, James et al. 2006, DeFalco et al. 2007). A competing hypothesis is that competition intensity does not vary along productivity gradients (Grace and Tilman 1990). Attempts to reconcile these two opposing hypotheses ('Grime-Tilman' debate) regarding the relationship between competition and productivity have been proposed (Weldon and Slauson 1986, Grace 1993, Brooker et al. 2005). Specifically, Brooker et al. 2005 argue that Grime's hypothesis is actually in regard to competition importance while competition intensity is the critical measure for testing Tilman's hypothesis, and that these two measures (importance and intensity) need not be correlated (Weldon and Slauson 1986, Zhang et al. 2008). Therefore, under this modified framework, the hypotheses can be stated as: competition importance should increase with increasing productivity, while competition intensity should not vary (Brooker et al. 2005).

Fertile islands associated with the understories of shrubs in arid vegetation create extremes in resource heterogeneity across the landscape. Increased soil nutrients, organic matter, and water availability, ameliorated temperatures, and decreased solar radiation have been characterized as important factors differentiating relatively resource rich fertile islands compared to shrub interspaces (Romney et al. 1980, De Soyza et al. 1997, Schlesinger and Pilmanis 1998, Brooks 1999, Titus et al. 2002, Pugnaire et al. 2004, Thompson et al. 2005). Since water and then nitrogen are considered the two most limiting resources to annual plant growth in arid shrublands of North American

(Gutierrez and Whitford 1987) it is not surprising that annual plant productivity is typically higher under shrubs than in interspaces (Fowler and Whitford 1996, Guo 1998, Guo and Berry 1998). Considering these spatial differences, interspecific competition among the annual plant assemblages should be more important in the understory than in resource poor, interspace microhabitats, while competition intensity should not vary between these microhabitats. Furthermore, species richness may also be greater in resource poor interspaces due to decreased competition (Huston 1979). Lastly, current theory also predicts a positive correlation between resource availability and invasive species abundance (Davis et al 2000, Bashkin et al. 2003, Deahler 2003, Foster and Dickson 2004, Colautti et al. 2006), which would suggest that invasive annuals are more abundant in understories than in the interspace.

This study evaluates the differences in competition between relatively resource rich shrub understories and resource poor interspace microhabitats based on the response of native annual plants to complete invasive species removal. I hypothesize that (1) resource rich understory microhabitats will have greater invasive species abundance, (2) competition importance will be greater in understories than relatively resource poor interspaces, but competition intensity will not vary between microhabitats, and (3) native richness will be greater in interspace microhabitats but will increase proportionately more in the understory once invasives are removed.

I am testing these hypotheses on the western edge of the Colorado Desert of southeast California, one of the most relatively resource limited regions where invasive annual grasses, filaree, and mustards occur. This location is important since higher resource-rich areas (i.e. cis-montane California) in the region have a longer history of invasion and widespread disturbance (i.e. grazing, higher fire frequency, nitrogen deposition). Consequently, they may be more native plant propagule limited (Seabloom et al. 2003, Cox and Allen 2007), which could introduce difficulties in interpreting the effect of invasive plant removal on native plant responses (*sensu* Foster and Dickson 2004).

Finally, I compare the results from the invasive plant removals with a treatment utilizing fluazifop-P-butyl, a grass specific herbicide in the same herbicide family (Aryloxyphenoxy-propionate) as haloxyfop. In a greenhouse experiment, haloxyfop was shown to cause mortality to plants in the genera *Erodium* and *Pelargonium* at the same rates used to kill grasses (Christopher and Holtum, 2000). I wanted to test the ability of Fusilade II to kill both invasive grasses and invasive *E. cicutarium* in the field. Control of exotic dicots when mixed with native dicots in natural assemblages is extremely difficult without non-target effects. A tool that reduces both invasive grasses and forbs without negative consequences to native annual forbs would be very useful alone or as part of an integrated approach to restoring invaded annual communities.

METHODS

STUDY SITES

The study area was in western Coachella Valley, Riverside County, California. This area is part of the extreme northwest Colorado Desert, a subregion of the Sonoran Desert that lies in the rain shadow of the Transverse and Peninsular Ranges. The vegetation of this area is mostly creosote bush scrub, dominated by *Larrea tridentata*. *Ambrosia dumosa* is also common. High coverage of bareground (interspace) between shrubs is indicative of this area and of creosote bush scrub in general (Holland and Keil 1995). Soil nutrient analyses from under *L. tridentata* and interspace microhabitats within the study area revealed greater carbon (C), nitrogen (N), NH_4^+, NO_3^-, Olsen-P, and K^+ in the understory compared to the interspace, as predicted (Romney et al. 1980, De Soyza et al. 1997, Brooks 1999, Schlesinger and Pilmanis 1998, Titus et al. 2002) (data not shown).

Four study sites located in Coachella Valley, California that contained differing ratios of native annual forbs, exotic annual grasses (*Bromus madritensis* and *Schismus* spp.), redstem filaree (*Erodium cicutarium*), and Sahara mustard (*Brassica tournefortii*), but no other detected exotic species, were used for this study. The four sites, ‘Grass,’ ‘Filaree,’ ‘Mustard,’ and ‘Native,’ were named based on dominant annual species at the time of treatment implementation. Two of the sites, ‘Grass’ and ‘Filaree’ occurred less than 0.5km apart but were implemented in different years with different dominant annual species when treated. All sites were in creosote bush scrub vegetation. Among all study sites, no native annual grass species were encountered. All native annual plants were forbs, representing 16 plant families and 44 species (Table 1). Species nomenclature follows Hickman (1996).

The Grass and Filaree sites (33º52’50.54’’N, 116º28’42.38’’W and 33º52’55.20’’N, 116º28’50.86’’W, respectively) were located on the western slopes of Flat Top Mountain, part of the western Indio Hills, approximately 7km NE of the city of

Palm Springs. These sites were about 250m apart from each other on the same hillside at an elevation of about 200m and slope of about 2–5%. Soils were well-drained, calcareous granitics, with a gravelly sand texture (Knecht 1980). Treatments were first implemented at the Grass site in 2005 when *Schismus* spp. dominated. In 2008, treatments were implemented at the Filaree site when the entire hillside was dominated by *E. cicutarium. Bromus madritensis* and *Brassica tournefortii* were rare in the interspace and uncommon in the understory of both the Grass and Filaree sites.

The Mustard site (33º53'29.43''N, 116º27'38.23''W) was located in a stabilized sand field about 1km NE of the Grass and Filaree sites. Elevation was 225m and the slope was 0-1 degree with fine sandy soils (Knecht 1980). *Brassica tournefortii* dominated interspace and understory microhabitats. *Schismus* spp. were common while *E. cicutarium* was occasional.

The Native site (33º54'36.04''N, 116º19'47.79''W) was on a granitic alluvial fan in East Deception Canyon, a major north to south drainage of the Little San Bernardino Mountains on the northern edge of Coachella Valley, about 19km ENE of Palm Springs. The elevation was at 460m, slopes ranged from 1 to 3 degrees, and soil was a calcareous, gravelly sand mixed with cobbles and stones on the surface and in the profile (Knecht 1980). Annual vegetation was dominated by native annuals in both the interspace and understory. The Native site contained about 80% of all native species encountered in the study and had the greatest number of unique species (Table 1). *Schismus* spp, *E. cicutarium*, and *B. tournefortii* were rare.

PRECIPITATION

Unlike much of the Sonoran Desert, the study area primarily has unimodal precipitation that occurs in winter months. Average annual precipitation is 138.9mm, with 115.1mm average precipitation occurring in the cool season, from October through April, based on 80yr records from Palm Springs (WRCC 2008). Summer rainfall is infrequent and the summer annual flora is depauperate (Ludwig et al. 1988, Andrew Sanders *personal communication*). Within the four years of the study, cool-season precipitation varied greatly, from one of the wettest on record (2004-05) to one of the driest (2006-07). In the first year, 2005, precipitation from October through April was extremely high (282.5mm). In the following year there was below average precipitation (79.5mm). In the third year, there was almost no precipitation (3.8mm), and finally in the forth year of study, 2008, there was average precipitation (115.2mm). Precipitation in the preceding warm seasons (May through September) was low, at 2.3mm, 5.3mm, 10.4mm, and 3.1mm for the years 2004 through 2007, respectively.

EXPERIMENTAL DESIGN

Two treatments were utilized in this experiment, (1) the removal of all invasive annual grasses with the use of Fusilade II, a grass-specific herbicide, combined with the removal by hand of all invasive forbs (R), and (2) the use of Fusilade II alone (F). The two treatments and a control (C) were implemented in a randomized, complete block design composed of twelve blocks. Plots were 8x8m and centered on a mature *Larrea tridentata* individual (Figure 1). Control plots were left un-manipulated. The entire surface area of the R and F plots was sprayed with Fusilade II, at a rate of 20ml/64m², taking care to avoid spraying over the top of *L. tridentata*. Herbicide Helper® (Monterey Lawn and Garden Products, Inc, Fresno, CA) was used as a surfactant at the rate of 16ml/64 m². At all sites and in all years when treatments were implemented, which was on January 19th, 2005 at the Grass site, and on January16th, 17th, and 19th for the Native, Filaree, and Mustard sites, respectively, plots were sprayed before grasses had reached flowering stage, as recommended by the manufacturer. In R plots, *E. cicutarium* and *B. tournefortii* were also weeded to complement the grass-specific herbicide in removing all invasive annuals. Invasive forbs in R plots were weeded by hand to minimize damage to native forbs. Most of the tap root was usually removed during the weeding of each exotic forb (*see* Schutzenhofer and Valone 2006). Weeding was done within a week of herbicide spraying, coinciding with the estimated time of grass mortality based on label specifications. *Erodium cicutarium* was weeded out to a 30cm buffer around where the sampling frame was placed while *B. tournefortii* was weeded out to a 70cm buffer since it can become much larger at maturity. Treatments were implemented once in January 2005 at the Grass site. In January 2008 the experiment was replicated at the Filaree, Mustard, and Native sites.

VEGETATION SAMPLING

Peak Season Annual Vegetation Sampling

Percent cover by species and species richness were measured in grided, rectangular 0.5m² (1mx0.5m) sampling frames. For interspace measures, two sampling frames were placed in the two corners of the plot least influenced by standing shrubs, fertile islands, ant mounds or small mammal disturbances (Figure 1), consistent with the 'open areas' microhabitat used by Guo (1998). At the mustard dominated site, three interspace plot frames were used instead of two to maintain similar statistic power across sites since interspace annual plant abundance was thought to be low in the sandy substrate, *a priori*. Sampling frames were also placed in the understory of the plot-central *L. tridentata* individual, on the north and south understories, and areas under shrubs with disturbances or apparent resource heterogeneity were avoided. Annual plants were measured in both the interspace and understory microhabitats. Sampling frame locations within each plot were demarcated with wooden stakes so that the same locations could be resampled. After the R and F treatments were applied once to the Grass site in January 2005, the annual vegetation was sampled the following four spring seasons (March 9, 2005, January 1, 2006, and March 1, 2008) at peak annual flowering in the permanently marked sampling frame quadrats. At the Grass site in 2006, an early season drought and above average temperatures resulted in drought stress, mortality, and a consequent early peak flowering. As mentioned previously, scarce rain the following season resulted in no germination of annual plants so sampling did not take place. In 2008, vegetation was also sampled at peak spring in the three other study sites on February 28th, and March 4th and 8th, for the Native, Mustard, and Filaree sites, respectively.

Baseline Parameters for F Effectiveness

In order to better understand Fusilade II effectiveness on both invasive grasses and *E. cicutarium*, biomass and phenological measures were taken at treatment application time. In 2005 at the Grass site and in 2008 at the Filaree site, the biomass of *Schismus spp*. and *E. cicutarium* were measured adjacent to control plots in twelve randomly placed interspace samples using a 0.125m^2 (50cm x 25cm) quadrat. Twelve 0.5m^2 sampling frames were also used to measure *Schismus* spp. and *E. cicutarium* cover in one of the permanent interspace sampling frame locations in the control plots. Then regressions of cover to biomass from the small sampling frames (0.125m^2) were used to calculate biomass in the larger sampling frames (0.5m^2) for interspace *Schismus* spp. and *E. cicutarium* biomass. Phenology of *E. cicutarium* was measured as the number of individual plants in flowering and/or fruiting condition divided by total *E. cicutarium* density in the 0.125 m^2 frames in 2005 at the Grass site and in all three new sites in 2008. *Schismus* spp. phenology was not recorded in sampling frames but observations were made at each study site when Fusilade-II was applied since this was an important factor for herbicide effectiveness according to label specifications. In the following springs, 2005 and 2008 respectively, the same method was used to sample peak *Schismus* and *Erodium* biomass, but phenology was not recorded since all plants were already in flower or fruiting stage. *Brassica tournefortii* was never measured for baseline or peak season parameters since it was uncommon at two of the four sites and is not thought to be affected by Fusilade II.

DATA ANALYSES

First, data from control (C) plots was used to determine which microhabitat (interspace or understory) was more invaded. Student t-tests were used to test for statistically significant differences between microhabitats x site x year at $\alpha = 0.05$. Then, C and R plots were utilized to measure competition importance and intensity in the two microhabitats using appropriate indexes (Brooker et al. 2005). Competition importance for both microhabitats was calculated using the index, C_{imp} (Brooker et al. 2005):

$$C_{imp} = (X_{control} - X_{removal})/(\mathrm{Max}X_{removal} - y)$$

where $X_{control}$ and $X_{removal}$ are total native annual plant cover values in the presence ($X_{control}$) and absence ($X_{removal}$) of invasive annual plants, and where $\mathrm{Max}X_{removal}$ is the maximum $X_{removal}$ value recorded among all interspace or understory plots per site, and y is the smaller total native annual plant cover found in either $X_{control}$ (C plots) or $X_{removal}$ (R plots) per block. Competition intensity was calculated with the index, RCI (Goldberg et al. 1999):

$$\mathrm{RCI} = (X_{removal} - X_{control})/X_{removal}.$$

For both indexes, total native cover from R plots was used as $X_{removal}$ and total native cover from paired C plots was used for $X_{control}$. All invasive species were lumped together as were all native species to form two functional groups, invasive annuals and native annuals, so that the results reflect the native annual community response to the removal of all invasive annuals. Student t-tests were used to test for significant differences at $\alpha = 0.05$.

Using C_{imp} to measure competition importance results in values ranging from 1 to -1, since C_{imp} represents the impact of competition as a proportion of the total environment (Brooker et al. 2005). Therefore, positive values indicate facilitation, a value of zero is neutral, and negative values represent competition importance. The closer a C_{imp} value is to -1, the greater the competition importance. Competition intensity scores derived from the index RCI eliminate confounding due to the environment (Goldberg 1999) and represent a simple ratio based on, in this case, native annual cover in the absence of invasive annuals relative to native annual cover in the presence of invasive plants. Therefore, while many studies show RCI scores between zero and one (reviewed in Goldberg 1999), values can range well beyond 1, with a greater positive score indicating greater competition intensity.

The indices (RCI and C_{imp}) used in this study are for “single-taxon” competitive measures. Community based indices and methods to test community scale competition have been proposed (reviewed by Weigelt and Jolliffe 2003, and Zimdahl 2004) but they require growing monocultures of several species and/or manipulating densities of multiple species, and are not easily implemented in field studies (Goldberg et al. 1999). I measured community level competition by lumping annual species into two ‘functional’ groups that were clearly distinct on the critical attribute of being native or invasive. I feel the use of these functional groupings did not violate the usefulness of these single-taxon indexes. Furthermore, I feel this approach would capture the overall trend in the native annual community and would buffer against the variability one could encounter if using multiple single species due to their individualistic responses (Guo 1998).

Relative increase in native species richness was calculated from paired C and R treatments in each block to determine which microhabitat had the greatest relative increase in species richness, based on the equation:

$$\mathrm{RIR} = (\mathrm{R}_{\mathrm{richness}} - \mathrm{C}_{\mathrm{richness}}) / \mathrm{R}_{\mathrm{richness}}$$

where $\mathrm{R}_{\mathrm{richness}}$ represents the native richness found in R plots and $\mathrm{C}_{\mathrm{richness}}$ represents the native richness found in paired C plots. RIR and absolute native richness for each microhabitat x site x year were statistically compared using student's t-test at $\alpha = 0.05$.

Finally, native richness and invasive and native cover were compared statistically among C, R, and F treatments, using ANOVA with an LSD test for multiple comparisons at $\alpha = 0.05$, to evaluate the effectiveness of Fusilade II alone (F), as a potential restoration tool to reduce both invasive annual grass and invasive *Erodium* in annual plant assemblages. JMP® 7.0.2 (SAS Institute, Inc. Cary, NC) was used for all statistical analyses.

RESULTS

Invasive Plant Abundance

As predicted, I found greater cover of invasive annual species in understory vs. interspace microhabitats (Table 2). Greater invasive plant cover in the understory was maintained at all sites and in all years except at the native forb dominated site, which had very low presence and cover of invasives and too many missing data points to meet assumptions of the student's t-test or non-parametric analyses.

Microhabitat Differences in Competition

Values obtained from C_{imp} and RCI showed that competition by invasive annuals on native annuals is important and intense at all sites and in all years. However, competition importance (C_{imp}) did not vary between microhabitats within sites (Table 2). Competition intensity (RCI) values for native annual forb cover response to invasive annual removal between understory and interspace microhabitats were only different at one site, the invasive mustard dominated site in 2008 (Table 2), where intensity was greater in understory microhabitats compared to interspace ($\alpha < 0.05$). At all other sites and in all other years there were no differences.

Species Richness Under vs. Inter Shrub

Native annual plant richness was greater in interspace than understory habitats at all sites and in all measurable years (Table 2). Native richness responded more to invasive plant removal in understory than in interspace microhabitats at only two sites, the Filaree and Mustard sites in 2008 (Table 2). While interspace microhabitats may have greater native richness, once invasive annuals are removed from both microhabitats a relatively greater increase in native richness occurs in the understory.

Comparisons between C, R, and F Treatments

Grass Site

Interspace Habitat

At the beginning of the study in 2005, both R and F treatments equally reduced exotic annual grass cover, while only the R treatment was effective at reducing invasive annual forb cover (Figure 2). Native annual forbs responded positively to both R and F treatments, but greater native cover and richness were observed only in R plots, implicating the importance of exotic forb competition with native annuals. In the second year, 2006, neither invasive grass nor invasive forb cover was different among treatments. However, native forb cover and richness were greater than control only in the R treatment. Because precipitation in the 2006 season (Oct. through April) was below average and only 28% of the previous year, invasive grass, invasive forb, and native forb cover were much lower in the second year. In 2007 there was insufficient rain to trigger germination of any annual plants and no live plants were recorded.

In 2008, average precipitation resulted in a high proportion of both invasive and native forbs and invasive grasses were no longer dominant. Increased native forb cover and reduced invasive forb cover were measured in 2008 in both R and F treatments, four years after they were implemented. However, there were no differences in native forb richness this year. Treatment F was as effective as R by the forth spring season (2008) in all measured variables. Both treatments had equally positive effects on native annuals by year four, but in previous years (2005 and 2006) only treatment R (full removal of both invasive grasses and forbs) showed positive responses for both native cover and richness (Figure 2).

Understory Habitat

Similar to what occurred in interspace habitat, both understory R and F treatments reduced invasive grass cover in the first growing season, 2005 (Figure 3). Unlike the interspace, differences remained into the following season, but by the last year, 2008, there were no differences. In 2005, invasive forb cover was relatively low in understory microhabitats compared to the interspace and there were no differences in invasive forb cover between treatments this year. Invasive forb cover showed no differences between treatments in 2006 as well, but in 2008, invasive forb cover was less in R and F treatments compared to control. Invasive forbs were the dominant plant functional group in 2008, unlike all other years where invasive grass was dominant. 2008 was the only year where both R and F treatments had greater native forb richness. In preceding years, only R had greater species richness. However, native forb cover was greater than control in both R and F treatments for 2005, 2006, and 2008 regardless of whether invasive grasses or forbs were dominant (Figure 3).

Filaree, Mustard, and Native Sites

Interspace

Treatments R and F reduced invasive grass cover at all three sites treated in 2008 (Figure 2). Only treatment R was able to reduce invasive forb cover at the Mustard site while invasive forb cover was too low and infrequent to be tested at the Native site. The R and F treatments both reduced invasive forb cover at the Filaree site compared to control. There was no difference in invasive forb cover between the F treatment and control at the Mustard site since the primary invasive forb was Brassica tournefortii, which is not susceptible to Fusilade II like species of Erodium. Native forb cover was greater in F and R treatments at the Filaree and Mustard sites, but not in any treatments at the Native site since invasive annuals were such a small proportion of the total annual community. Native forb richness was greater in the F treatment at the Mustard site, and showed no differences between treatments and control at the Filaree and Native site. Invasive species abundance and composition had a strong influence on treatment effectiveness. Where invasive species were less common, such as the Native site, native responses to treatments were less pronounced.

Understory

Treatments R and F were equally effective at reducing invasive grass and forb cover at the Filaree site (Figure 3). At the Mustard site, R and F were equally effective at reducing invasive grass cover but differed in reducing invasive forb cover. Invasive forb cover was only lower in R plots while F had similar invasive forb cover as C. Consequently, the native responses to the R and F treatments at both Filaree and Mustard sites reflected the amount of invasives still present at peak season. Native forb cover and richness were both greater than control in R and F plots at the Filaree site, and only greater in R plots at the Mustard site. Treatments had no effect on invasive plant abundance or measured native annual parameters at the Native site.

Baseline Parameters for F Effectiveness

At the Grass site in 2005, initial biomass of *E. cicutarium* at treatment application time was no different than at peak season. However, initial *Schismus* spp. biomass was less than peak season biomass (Figure 4). At treatment application time, 70% ± 9.7%SE of *E. cicutarium* was flowering and/or fruiting. When treatments were applied in 2008, no *E. cicutarium* were in flowering and/or fruiting stage at any of the three new sites. Also, the biomass of both *E. cicutarium* and *Schismus* spp. were both less at treatment application time than at peak season (Figure 4) in 2008. Because the first significant precipitation event in 2008 came 41 days later than in 2005, both *E. cicutarium* and *Schismus* spp. were in a much earlier phenological stage at the time of treatment application.

DISCUSSION

Microhabitat Differences in Invasive Plant Abundance

The greater invasive plant cover documented in understory versus relatively resource poor interspaces is consistent with current theory that predicts greater invasive abundance in more resource rich environments (Davis et al 2000, Bashkin et al. 2003, Deahler 2003, Foster and Dickson 2004, Colautti et al. 2006), and with the findings of

Brooks (1999) who confirmed this relationship in the Mojave Desert based on biomass measures. It follows that shrub understories may act as refugia for invasive species and may allow for their spread throughout the resource poor desert matrix. If interspace resources eventually become high enough to promote invasive annual dominance, fertile islands may then act as an invasive plant colonization source. Fertilization experiments in the Mojave Desert have shown that adding N to interspace and understory microhabitats increases invasive annual grass abundance (Brooks 2003, Allen et al. 2009). Since deserts are low in soil N, eutrophication from anthropogenic nitrogen deposition could have profound impacts, leading to invasive grass colonization into the interspace from understory microhabitats. At the study sites, interspace invasive plant abundance was high everywhere except the Native site (Table 2). Atmospheric N deposition is elevated in this area since it is down-wind of the Los Angeles Basin. Measures of N deposition across the region show that the Native site receives less N deposition than the other study sites (Rao 2008, Allen et al. 2009), which might explain in part why invasive annuals were relatively uncommon here.

Microhabitat Differences in Competition

As expected, I found that competition is both important and intense between invasive annual plants and native annuals in understory and interspace microhabitats at all the study sites except the Native site, since invasive plants were rare there. Contrary to my predictions, there were no differences in competition importance between interspace and understory microhabitats at any of the sites. Similarly, competition intensity was not different between microhabitats except at the Mustard site, which had greater competition intensity in the understory compared to the interspace. A similar study conducted in the Negev Desert, Israel, that examined competition among native species showed no difference in intensity between understory and interspaces, and led the authors to reject Grime's (1979) hypothesis that competition increases as resources/productivity increase (Tielbörger and Kadmon 2000a). However, Grime's hypothesis can not be tested using competition intensity, rather indices that measure competition importance must be used (Brooker et al. 2005). While Tielbörger and Kadmon's (2000a) conclusion would be invalid because of their choice of competition index, the results from this study using the appropriate C_{imp} index (Brooker et al. 2005) support their conclusion.

Tielbörger and Kadmon (2000a) utilized one site during one growing season, while this study utilized four study sites. At only the Mustard site was competition intensity greater in the understory versus the interspace, which suggest that differences in competition intensity between microhabitats will be site specific. Maestre et al. (2005) has shown that the outcome of interference and facilitation studies are largely influenced by the measures of plant performance being considered, so these results could have been different had I measured another variable, such as fecundity. The one site that did show greater competition intensity in the understory had very high native cover in the interspace to begin with. Also, species identity can make a difference in the outcome of competition intensity measures along productivity gradients and the Mustard site had dominant invasive and native annual plants that were different compared to the other two invaded sites (Grass and Filaree sites).

Microhabitat Differences in Species Richness

The results strongly affirmed that species richness was greatest in resource poor interspaces rather than relatively resource rich understories. Pugnaire et al. (1996) stated four major reasons to explain why species richness declines with increased fertility in the context of shrub understories: (1) lack of spatial heterogeneity, (2) adverse effects of litter accumulation on the establishment of new species, (3) lower light availability, and (4) increased competition. The first reason is related to Tilman's (1982) hypothesis that increased heterogeneity of resource combinations allows for increased stable coexistence among various species. This study purposefully utilized homogenous, undisturbed, and similar locations within both microhabitats at every site to minimize this effect of spatial variability. Thus, I can only conclude that when resource heterogeneity within microhabitats is held constant, species richness is less in interspaces than understories.

I also do not think that increased litter accumulation in understories had a strong impact on the pattern. Although litter was greater in understories at all sites and in all years ($p < 0.001$, data not shown), total annual cover was also always greater in the understory microhabitat, suggesting that litter levels were not high enough to impact species richness. I do however, have reason to believe that reasons three and four could, in part, explain the observed pattern in this study system.

Although the majority of the study sites x years showed no differences between native and invasive annual competition intensity between understory and interspace, one site did show an increase in the understory (Table 2), and, albeit not always significant, every site in all years showed a relatively greater increase in native richness in the understory compared to the interspace once all invasive annuals were removed. Examples of competitive exclusion are not unknown from desert annual communities (Goldberg and Estabrook 1998) and this phenomenon could be heightened where invasive species are more abundant, such as shrub understories. Other studies at local or small scales similar to this experiment have shown greater species richness in relatively resource poor environments, especially where the resource rich matrix is invasive dominated (Harrison 1999, Gea-Izquierdo et al. 2007). Experimental additions of N have decreased species richness in the context of invasive species (Brooks 2003, Allen at al. 2009) and have increased native species richness where little or no invasive grasses or forbs are present (Gutierrez and Whitford 1987, Allen et al. 2009). Besides increased competition between invasive and native annuals being important, competition among native annual species could have also been heightened in the understory, but this was not tested.

Considering that similar results have been reported from creosote bush scrub and other vegetation types elsewhere (implied by Westman 1981, Schmida and Whittaker 1981, Jackson et al. 1990, Gutiérrez et al. 1993, Fowler and Whitford 1996, Tewksbury and Lloyd 2001, López-Pintor et al. 2006; but see Pugnaire et al. 1996), we are not surprised to see less species richness in the understories. However, we are not simply comparing resource rich versus resource poor microhabitats, but microsites that also differ dramatically in PAR (Pugnaire et al. 2004). Since we know light levels are important for the germination and/or seedling survival of certain species (Maranon and Bartolome 1993, Eliason and Allen 1997), the negative effects of decreased PAR in understories may explain these results. Among interspace desert microhabitats where light was not limiting, increased richness was found in the microsite with the greatest soil resources (Brooks 1999, Guo and Berry 1998) and where soil N was experimentally increased in open areas (Gutierrez and Whitford 1987). Where PAR was limiting in both resource-poor and -rich understories, there was overall, no difference in annual plant richness (De Soyza et al. 1997). These studies suggest that decreased species richness in understory microhabitats could be the consequence of PAR being too limiting for the requirements of certain native annuals components (*sensu* Maranon and Bartolome 1993) and/or exclusion due to heightened competition for light among the annuals (*sensu* Goldberg and Miller 1990).

Finally, the relationship between resources and species richness is hump-shaped (Guo and Berry 1998, Mittelbach et al. 2001), so annual species richness should not always be greater in interspaces. Species richness between understories and interspaces will vary based on site fertility and the degree of difference in resources between the understory and interspace within a site (Tewksburry and Lloyd 2001). Pugnaire et al. (1996) found a humped-shape response of understory annual richness with shrub age; as shrubs aged and continuously accumulated resources beneath, annual richness increased up to a point and then eventually decreased as competitive displacement became more important. It appears that facilitative effects of shrubs can outweigh competitive interference among understory annuals where local/site-scale soil resources are most limiting, but as local scale resources increase or the ratio of understory to interspace resources increases, any benefits of understory microhabitats will eventually be overshadowed by other factors, such as competitive interactions among understory annuals. Of note in desert shrublands, independent of local scale resource levels or the resource differences between microsites, when rainfall events are relatively low, rainfall interception by shrubs can be significant, causing annual richness and abundance to be lower due to less soil moisture in understories compared to interspaces (Tielbörger and Kadmon 2000b). I do not think this was ever a factor at the study sites since the first rainstorms of each season when annuals germinated were large events, at no time did I ever notice decreased plant abundance in understories compared to interspaces, and peak season annual cover was always greatest in the understories.

Comparisons between C, R, and F Treatments

Previous work in Mediterranean climates with invasive grass, invasive forb, and native annual mixtures have shown that a competitive hierarchy places the invasives above the natives, and the removal of just one invasive group, such as invasive grasses, leads to an increase in the other remaining invasive groups, such as invasive forbs (Brooks 2000, Allen et al. 2005, Barrows et al, 2008, Cox and Allen 2008, Cox and Allen *in press*). Competitive release of natives is fully realized only when all invasives are removed. The increased native cover and species richness that I observed once all invasives were removed was significant and long lasting (up to four years) so the impact of these invasive annuals is great.

Plant invasions into the desert are considered recent compared to other parts of North America such as cis-montane California (Kemp and Brooks 1998, Mensing and Byrne 1998). Likewise, the history of disturbances such as grazing and short-interval fire regimes that would promote invasives and decrease native propagules were absent within the study sites. Native annual seedbanks might also be more long-lived in the desert because of increased precipitation variability (Freas and Kemp 1983). All of these factors suggest that native propagules are not limiting in this study area, which may explain why such a large native response was stimulated by invasive species removals. In cis-montane California, where similar invasive plant removal studies have taken place, there is greater annual productivity and less resource limitation but greater native propagule limitation (Seabloom et al. 2003, Cox and Allen 2007, Cox and Allen *in press*). Therefore, it is likely that additional seeding would be necessary to see similar native responses to what I found in the desert.

The F (Fusilade II) treatment worked as effectively as R (total invasive removal) at sites where invasive grasses and *E. cicutarium* were the primary invasive components, which makes sense considering Fusilade II is considered lethal to species in the genus *Erodium*. At sites where *B. tournefortii* was the most important invasive plant, the F treatment was not as effective as R. New methods are needed to target mustards and invasive annual forbs other than *Erodium* spp, without damage to native annuals. Also, where invasive annuals are uncommon, such as the Native site, removal of invasives has no immediate effect. However, invasive control at early stages of invasion is much more efficient and effective than at later stages of invasion (Hobbs and Humphries 1995, Simberloff 2003).

Fusilade II Effectiveness and Management Implications

Fusilade II and its predecessor, Fusilade, have been used successfully in restoration studies to control invasive annual grasses (Pavlick et al. 1993, Arnold et al. 1998, Cione et al. 2002, Allen et al. 2005, Cox and Allen 2008, Marushia and Allen *in press*). Besides corroborating anecdotal evidence that reported *Erodium* death from Fusilade II (Kelly 2007), this is the first study to my knowledge that utilized this product to induce mortality on a species of *Erodium* in the field. Invasive annual grasses and *E. cicutarium* form a large proportion of the annual community throughout the extent of creosote bush scrub in North America. They are also abundant components of cis-montane grasslands, shrublands and woodlands in California, and are major co-occuring invasive annuals elsewhere in the world such as Australia (Westbrooke et al. 1998) and Chile (Figueroa et al. 2004). This study has shown that Fusilade II can be used to remove both of these invasive species groups, a finding that has great implications for invasive plant control and restoration.

Applying Fusilade II before grasses begin inflorescence development is critical to this herbicide's effectiveness based on label specifications, and this study also draws attention to the importance of the phenological stage of *E. cicutarium* at herbicide application time. Based on this study, it is clear that *E. cicutarium*, like grass species, is more responsive to Fusilade-II before inflorescence initiation. Because *Erodium* spp. germinate quickly with the first substantial rains and have a rapid phenology compared to most native annuals in California (Jennings 2001, Bartolome 1979), and because targeting both invasive grasses and invasive *Erodium* spp. is of importance, herbicide application should be implemented early in the growing season.

Great care must be especially taken when treating sites with susceptible native plants, such as grasses and certain forbs. No native annual grasses were found but a native filaree (*E. texanum*) was present at one of our study sites that showed symptoms of herbicide damage such as burned leaves, and mortality. Where susceptible native species occur, great consideration must be taken about whether or not to use this product. Pretreatment seed collection of vulnerable species should also be considered. Furthermore, additional study is needed to determine/fine-tune specific application rates and timing of spraying that will maximize invasive grass and *Erodium* spp. mortality and minimize damage to sensitive native plants.

CONCLUSIONS

The results of this study indicate that resource rich understory microhabitats are more invaded and have, in general, a greater response to invasive removal than relatively resource poor inter-shrub microhabitats. Prioritizing resource rich microenvironments for management efforts could thus be a logical conclusion from this study. Targeting understory microenvironments could allow certain marginalized plants to recolonize this microhabitat once invasives are removed. However, species- and site-specific factors and multiple ecosystem processes must be taken into consideration when prioritizing invasive species management. For example, in some parts of the desert, invasive annual grasses invade into shrub interspaces and connect widely spaced shrubs with their persistent, dried-out biomass, leading to devastating wildfires that would not otherwise occur. In areas where interspace grass invasions are taking place and promoting fire, control efforts would also be especially important in the interspaces since fires cause significant, long-term losses of native plant diversity in these desert shrublands (Steers dissertation – Chapters 3 and 4).

Regions of California with a Mediterranean climate or surrounding deserts with a Mediterranean-like precipitation pattern such as the western Mojave and Colorado Deserts (Warner 2004) share similarities among the native flora, with some native annuals showing affinity to both the California and Desert Floristic provinces (Keeler-Wolf 2007). It is not a surprise then that similar exotic annual grasses (*Bromus* and *Schismus* spp.) and forbs (*Brassica* and *Erodium* spp.) are invasive in both regions. Therefore, the results obtained in this study should also have direct implications to cis-montane California and other regions with a Mediterranean climate such as Australia and Chile that are also invaded by similar alien annual grasses and forbs.

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FIGURES AND TABLES

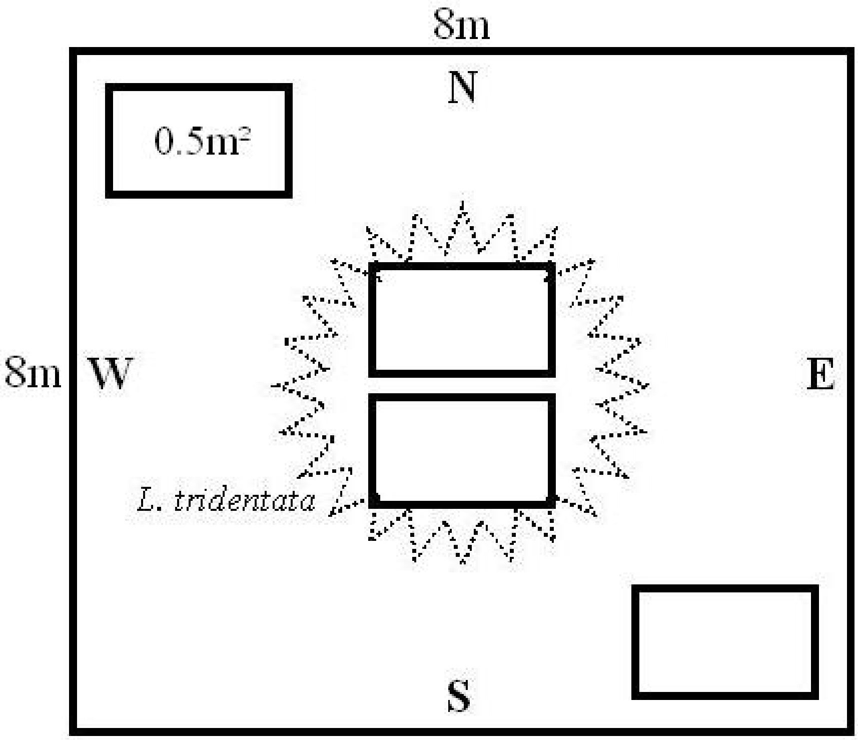

Figure 4.1 Plot dimensions and typical sampling frame locations. Figure not drawn to scale.

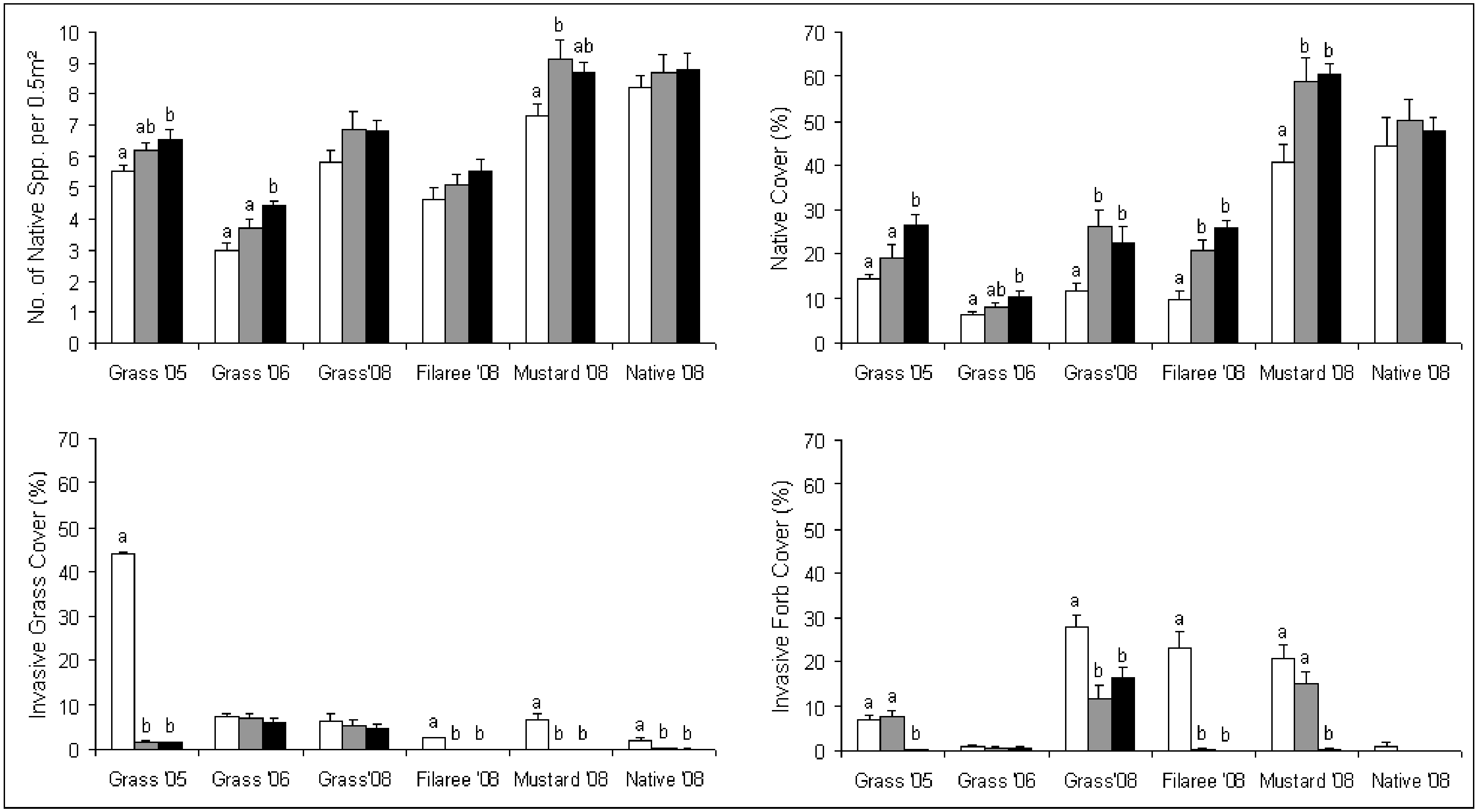

Figure 4.2 Interspace annual vegetation parameters of the three treatments, C, F, and R, at all sites and in all measurable years. White bars correspond to treatment C, grey bars to F, and black bars to R. If letters are present, they indicate significant differences between the treatments only within the site and year that are displayed, and not between other sites or years within the same graph.

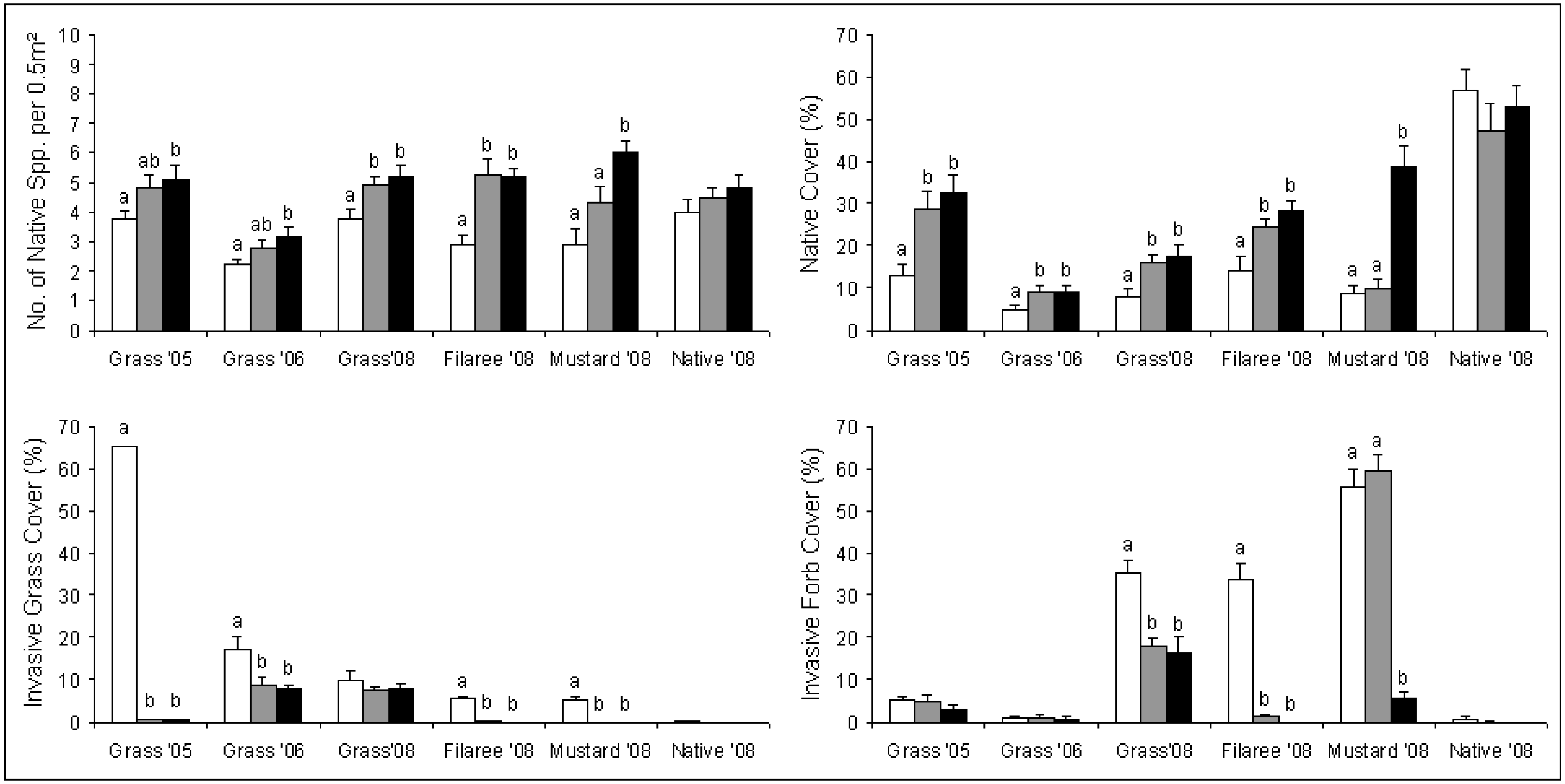

Figure 4.3 Understory annual vegetation parameters of the three treatments, C, F, and R, for all measurable years. See Figure 2 for description of graph attributes.

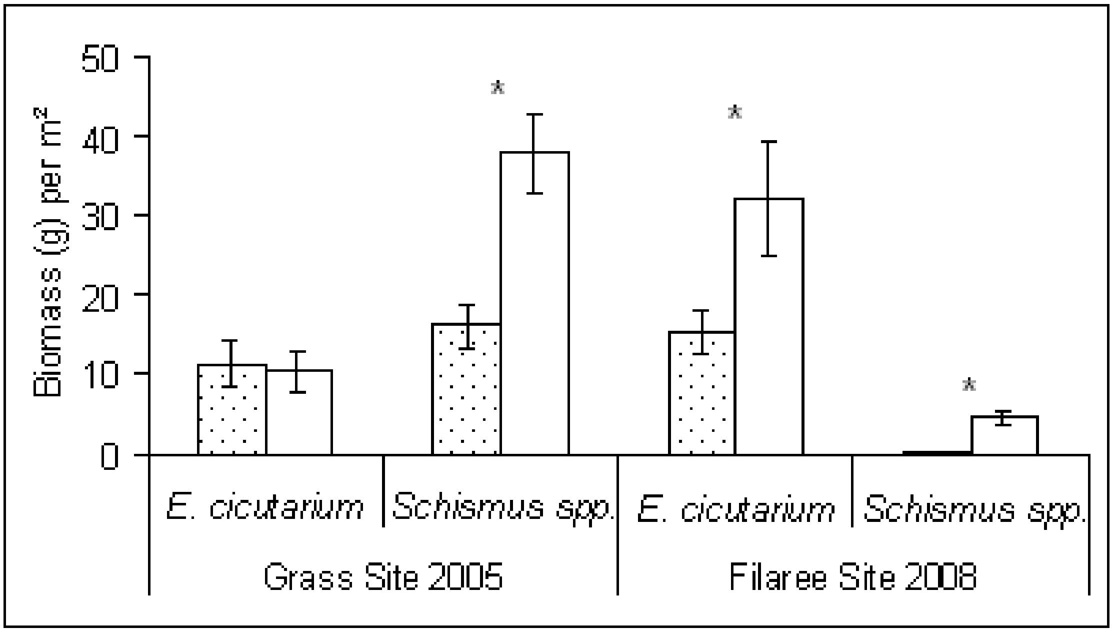

Figure 4.4 Initial (stippled bars) and peak (white bars) biomass for *Erodium cicutarium* and *Schismus* spp. at the Grass site in 2005, when treatments were implemented, and at the Filaree site in 2008, when it was treated. Data are from untreated control plots. Asterisks above paired bars indicate significant differences between initial and peak biomass. Differences were significant at alpha = 0.001, alpha = 0.05, and alpha = 0.0001, for the *Schismus* spp. 2005, *E. cicutarium* 2008, and *Schismus* spp. 2008, respectively.

Table 4.1 Annual species found at each site by year sampled, based on data from all treatments (C, R, and F). X shown without superscript indicates that species were present in both interspace and understory microhabitats. An 'I' or 'U' superscript indicates that a species was only found in the interspace or understory, respectively.

Family	**Species**	**Study Sites and Years Sampled**					
		Grass 2005	Grass 2006	Grass 2008	Filaree 2008	Mustard 2008	Native 2008
INVASIVE ANNUAL FORBS							
Brassicaceae	*Brassica tournefortii*	X	X^U	X	X	X	X
Geraniaceae	*Erodium cicutarium*	X	X	X	X	X	X
INVASIVE ANNUAL GRASSES							
Poaceae	*Bromus madritensis*			X^U			
	Schismus spp.	X	X	X	X	X	X
NATIVE ANNUAL FORBS							
Asteraceae	*Chaenactis fremontii*	X	X	X	X	X	X
	Conyza canadensis				X^U		
	Filago depressa	X	X	X	X	X	X
	Malacothrix glabrata	X^U	X^U	X	X	X	X
	Monoptilon bellioides						X^I
	Rafinesquia neomexicana				X^U	X	X
	Stephanomeria exigua						X
Boraginaceae	*Cryptantha angustifolia*	X	X	X	X	X	X
	C. barbigera						X
	C. maritima	X^U	X^U		X^U	X^I	X
	C. micrantha			X^I		X^I	X
	C. nevadensis						X^U
	C. pterocarya						X^U
	Pectocarya heterocarpa	X	X^I	X	X	X	X
	P. linearis	X^U	X^I	X	X^I	X	
	P. platycarpa	X^U	X	X	X	X	
	P. recurvata	X	X	X	X	X	X
Brassicaceae	*Lepidium lasiocarpum*	X		X	X^U		
Campanulaceae	*Nemacladus glanduliferus*						X^I
	N. rubescens						X^I
Caryophyllaceae	*Achyronychia cooperi*	X	X	X^I	X^I	X	X^I
	Loeflingia squarrosa	X		X^I		X	X^I
Crassulaceae	*Crassula connata*	X		X	X^U	X	X
Fabaceae	*Astragalus didymocarpus*	X^I			X^U	X^U	
	Lotus strigosus					X^I	
	Lupinus arizonicus						X
	L. shockleyi					X^I	
Geraniaceae	*Erodium texanum*						X
Hydrophyllaceae	*Emmenanthe penduliflora*						X
	Nama demissum						X^I
	Phacelia crenulata				X		X
	P. distans	X^U					X^U
Malvaceae	*Eremalche exilis*					X	
Onagraceae	*Camissonia californica*						X
	C. claviformis	X	X	X	X	X	X
	C. pallida	X	X	X	X	X	X
Plantaginaceae	*Plantago ovata*				X^I	X	
Polemoniaceae	*Eriastrum sp.*	X^I	X^I			X	X
	Linanthus jonesii					X^I	X^I
	Loeseliastrum schottii			X	X	X	X^I
Polygonaceae	*Chorizanthe brevicornu*	X	X	X	X	X	X
	Eriogonum thomasii	X^I	X^I	X^I	X		X^I
Portulacaceae	*Calyptridium monandrum*	X		X^I	X	X	X

Table 4.2 Difference in annual plant parameters between interspace and understory microhabitat per study site and year. Bold values with the following symbols, * = 0.05; ‡ = 0.01; † = 0.001, ^ = 0.0001, correspond to the alpha level where significant differences were found.

	Grass Site						**Filaree Site**		**Mustard Site**		**Native Site**	
	2005		2006		2008		2008		2008		2008	
	Inter	Under	Inter	Under	Inter	Under	Inter	Under	Inter	Under	Inter	Under
Total Annual Cover	65.6	**83.7‡**	15.1	22.8	46.1	53	35.5	**53.1‡**	68.7	69.7	47.7	57.3
Total Invasive Cover	51.2	**70.7†**	6.4	**13.6***	34.4	**44.9‡**	25.8	**39.2***	27.9	**60.8^**	3.1	0.8
Invasive Grass Cover	44.3	**65.6^**	5.2	**12.3***	6.6	9.7	2.6	**5.5‡**	6.8	5.3	**2.1‡**	0.1
Invasive Forb Cover	7	5.1	1.2	1	27.7	35.2	23.2	33.7	21.1	**55.5^**	1	0.6
Native Annual Cover	14.4	13	6.2	4.7	11.8	8.1	9.7	13.9	**40.9^**	8.9	44.6	56.6
Native Annual Richness	**5.5^**	3.8	**3***	2.2	**5.8†**	3.8	**4.6‡**	2.9	**7.3^**	2.9	**8.2^**	4
C_{imp} Scores	-0.35	-0.51	-0.21	-0.2	-0.28	-0.22	-0.43	-0.33	-0.61	-0.49	0.01	0.07
RCI Scores	0.41	0.4	0.18	0.28	0.4	0.38	0.6	0.43	0.33	**0.69***	-0.04	-0.15
RIR Native Richness	0.13	0.16	0.31	0.24	0.09	0.26	0.13	**0.41***	0.14	**0.5‡**	0.04	0.11

CONCLUSION

This dissertation demonstrated that both fire and invasive species decrease native plant abundance and species richness in creosote bush scrub (CBS). With regard to the perennial components of CBS, typical fires in the study area removed almost all individuals since most desert shrubs are poorly adapted to this type of disturbance (Brooks and Minnich 2006). Evidence of invasive annual plant suppression of native shrub seedlings after fire was also documented (Chapter 3). However, the short-lived shrub, *Encelia farinosa*, may be unaffected by invasive annuals at the seedling stage relative to other shrub species (Chapter 1). *Encelia farinosa* eventually became dominant through seedling recruitment (Chapter 1), which confirmed predictions made in previous surveys within the study area from 5 year old burned stands (Brown and Minnich 1986). The high abundance of *E. farinosa* was also consistent with a successional model for desert vegetation put forth by Vasek (1983), who stated that relatively small, short-lived shrubs are the primary sere during the initial stages of secondary succession in CBS.

Two separate multiple linear regressions correlating the dependent variables, invasive annual plant cover (%) and native annual plant richness (m^{-2}), with soil variables, such as texture and nutrients, were performed utilizing data captured from the unburned stands (Chapter 2). These analyses showed that invasive plant abundance was positively correlated with soil fertility, and native annual plant richness was negatively correlated with soil fertility and positively correlated with bare ground cover (%). These results suggest that low fertility conditions with high bare ground may act as refugia in highly invaded communities such as this study area, similar to findings in other ecosystems (Harrison 1999, Gea-Izquierdo et al. 2007).

Due to recent droughts, *B. madritensis*, an important fire promoting grass in the desert (Brooks 1999), exhibited relatively lower abundance than other invasive annuals (Minnich 2008, Chapter 2). The cover of this species was also decreased in recently burned stands, similar to what other studies have reported (Cave and Patten 1984, Brooks 2002). Fire increased invasive annual grass abundance due to a positive response by *Schismus* spp, but this increase did not last more than several years (Chapter 2). Since the study area was so highly invaded to begin with, increases in invasive plant abundance after fire resulted in detrimental impacts to native annual plants even though they were already suppressed before fire (Chapter 2 and 4). The high abundance of invasive annual plants in this region also suggests that the potential for fire occurrence is elevated here due to persistent and high amounts of horizontal fuel connectivity between shrubs. Brooks and Esque (2002) have documented that this area is indeed impacted by larger and more frequent fires relative to other parts of California's desert ecosystems.

Although fires did not convert CBS to annual grassland following the invasive grass-fire cycle (D'Antonio and Vitousek 1992), the post-fire combination of high invasive annual grass abundance (Chapter 2) and increased shrub density (Chapter 1) resulted in a vegetation type (highly invaded *Encelia* shrublands) with structural and fuel characteristics that will likely make it more vulnerable to fire than unburned CBS. Therefore, under current conditions, an invasive plant – fire regime (Brooks et al. 2004) appears to be in place within this landscape.

Fire clearly resulted in species depauperate plant communities, especially for stands that burned more than once (Chapters 1 and 2). Invasive plant removal treatments in unburned CBS stands also demonstrated that invasive grasses and forbs have negative impacts on native annual plants. Fire and invasive species are double threats to the CBS of the study area. Since invasive annual plants are critical for promoting the majority of fire in this region (Brooks and Esque 2002), restoration methods that remove alien grasses would be especially useful. Chapters 3 and 4 demonstrated that Fusilade II, a grass-specific herbicide, can be very effective in reducing both invasive annual grasses and *Erodium cicutarium*, which are the most abundant invasive species in the region (Chapter 2). Removal of invasive annuals in both burned and unburned contexts resulted in native annual assemblages that were more species rich and native dominated than annual communities left invaded in both contexts. These findings may have important applications to other desert locales impacted by invasive plants and fire, and other ecosystems invaded by similar annual plants.

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APPENDIX A. GPS coordinates identifying the start and end of each 100m line transect per stand per site utilized for Chapter 1. GPS data was recorded using NAD27 CONUS (UTM) coordinate system.

SITE	STAND	LINE	START		END	
			Easting	Northing	Easting	Northing
2a	UNBURN	1	11S 0529858	3753743	11S 0529766	3753785
		2	11S 0529862	3753758	11S 0529772	3753800
		3	11S 0529867	3753767	11S 0529780	3753815
		4	11S 0529875	3753783	11S 0529786	3753829
		5	11S 0529882	3753797	11S 0529800	3753850
		6	11S 0529893	3753808	11S 0529810	3753862
2a	BURN	1	11S 0529995	3753543	11S 0529895	3753545
		2	11S 0529990	3753556	11S 0529890	3753563
		3	11S 0529897	3753604	11S 0529797	3753616
		4	11S 0529900	3753619	11S 0529801	3753632
		5	11S 0529793	3753612	11S 0529694	3753624
		6	11S 0529783	3753635	11S 0529684	3753643
2b	UNBURN	1	11S 0538962	3762040	11S 0538866	3762071
		2	11S 0538963	3762052	11S 0538867	3762080
		3	11S 0538967	3762063	11S 0538868	3762090
		4	11S 0538971	3762068	11S 0538872	3762099
		5	11S 0538967	3762085	11S 0538871	3762110
		6	11S 0538972	3762096	11S 0538876	3762119
2b	BURN	1	11S 0539186	3761978	11S 0539093	3762018
		2	11S 0539183	3761995	11S 0539091	3762036
		3	11S 0539194	3762003	11S 0539102	3762043
		4	11S 0539198	3762011	11S 0539108	3762054
		5	11S 0539206	3762020	11S 0539115	3762062
		6	11S 0539183	3762037	11S 0539121	3762117
19&2	UNBURN	1	11S 0539123	3757528	11S 0539060	3757606
		2	11S 0539133	3757535	11S 0539070	3757613
		3	11S 0539160	3757553	11S 0539086	3757626
		4	11S 0539169	3757563	11S 0539104	3757639
		5	11S 0539198	3757573	11S 0539138	3757654
		6	11S 0539214	3757575	11S 0539152	3757655
19&2	BURN X 2	1	11S 0538483	3758303	11S 0538403	3758362
		2	11S 0538479	3758292	11S 0538398	3758350
		3	11S 0538471	3758276	11S 0538387	3758328
		4	11S 0538465	3758264	11S 0538380	3758318
		5	11S 0538450	3758242	11S 0538365	3758297
		6	11S 0538440	3758217	11S 0538350	3758261

9	UNBURN	1	11S 0533054	3753096	11S 0533069	3753187
		2	11S 0533105	3753175	11S 0533053	3753187
		3	11S 0533089	3753179	11S 0533090	3753280
		4	11S 0533075	3753178	11S 0533073	3753280
		5	11S 0533056	3753174	11S 0533059	3753274
		6	11S 0533033	3753170	11S 0533038	3753270
9	BURN	1	11S 0533106	3753031	11S 0533100	3753129
		2	11S 0533091	3753029	11S 0533085	3753129
		3	11S 0533079	3753026	11S 0533068	3753126
		4	11S 0533063	3753022	11S 0533052	3753125
		5	11S 0533048	3753026	11S 0533041	3753126
		6	11S 0533033	3753023	11S 0533026	3753123
12	UNBURN	1	11S 0537608	3757789	11S 0537509	3757787
		2	11S 0537613	3757795	11S 0537513	3757800
		3	11S 0537613	3757805	11S 0537514	3757809
		4	11S 0537619	3757818	11S 0537519	3757824
		5	11S 0537623	3757832	11S 0537523	3757839
		6	11S 0537623	3757844	11S 0537525	3757853
12	BURN	1	11S 0537690	3758064	11S 0537608	3758124
		2	11S 0537695	3758077	11S 0537611	3758131
		3	11S 0537725	3758116	11S 0537667	3758195
		4	11S 0537739	3758124	11S 0537684	3758207
		5	11S 0537751	3758144	11S 0537690	3758222
		6	11S 0537763	3758153	11S 0537714	3758238
20	UNBURN	1	11S 0532688	3756223	11S 0532789	3756216
		2	11S 0532689	3756232	11S 0532789	3756223
		3	11S 0532798	3756228	11S 0532698	3756238
		4	11S 0532811	3756235	11S 0532710	3756246
		5	11S 0532842	3756239	11S 0532744	3756248
		6	11S 0532858	3756246	11S 0532760	3756255
20	BURN	1	11S 0532819	3756399	11S 0532754	3756469
		2	11S 0532820	3756388	11S 0532750	3756460
		3	11S 0532811	3756383	11S 0532742	3756449
		4	11S 0532816	3756375	11S 0532739	3756440
		5	11S 0532806	3756365	11S 0532734	3756432
		6	11S 0532803	3756358	11S 0532728	3756425
20	BURN X 2	1	11S 0532862	3756431	11S 0532778	3756483
		2	11S 0532867	3756440	11S 0532784	3756488
		3	11S 0532873	3756447	11S 0532786	3756500
		4	11S 0532874	3756458	11S 0532788	3756512
		5	11S 0532879	3756466	11S 0532796	3756516
		6	11S 0532884	3756472	11S 0532801	3756522

24	UNBURN	1	11S 0535137	3749459	11S 0535108	3749365
		2	11S 0535128	3749476	11S 0535089	3749384
		3	11S 0535130	3749496	11S 0535092	3749405
		4	11S 0535138	3749521	11S 0535093	3749431
		5	11S 0535129	3749551	11S 0535079	3749461
		6	11S 0535120	3749567	11S 0535071	3749482
24	BURN	1	11S 0534960	3749343	11S 0534943	3799240
		2	11S 0534976	3749344	11S 0534978	3749245
		3	11S 0535016	3749412	11S 0535004	3749312
		4	11S 0535027	3749380	11S 0535020	3749279
		5	11S 0535059	3749321	11S 0535027	3749226
		6	11S 0535069	3749307	11S 0535038	3749213
28	UNBURN	1	11S 0532097	3753662	11S 0532140	3753764
		2	11S 0532091	3753668	11S 0532130	3753763
		3	11S 0532081	3753666	11S 0532113	3753756
		4	11S 0532069	3753670	11S 0532115	3753759
		5	11S 0532056	3753667	11S 0532094	3753758
		6	11S 0532047	3753670	11S 0532082	3753763
28	BURN	1	11S 0532347	3753848	11S 0532337	3753946
		2	11S 0532335	3753855	11S 0532324	3753949
		3	11S 0532316	3753945	11S 0532326	3753851
		4	11S 0532313	3753838	11S 0532310	3753936
		5	11S 0532300	3753838	11S 0532297	3753934
		6	11S 0532313	3753953	11S 0532313	3753953

APPENDIX B. GPS coordinates identifying the mid-point of every modified NAWMA plot utilized for Chapter 2. GPS data was recorded using NAD27 CONUS (UTM) coordinate system.

Site	Stand	Point	Easting	Northing
3a	UNBURN	1	11S 0529841	3753751
		2	11S 0529801	3753788
		3	11S 0529833	3753787
		4	11S 0529795	3753825
		5	11S 0529880	3753799
		6	11S 0529847	3753837
3a	BURN	1	11S 0529976	3753540
		2	11S 0529930	3753561
		3	11S 0529873	3753608
		4	11S 0529821	3753629
		5	11S 0529758	3753615
		6	11S 0529734	3753639
3b	UNBURN	1	11S 0538935	3762049
		2	11S 0538872	3762079
		3	11S 0538956	3762067
		4	11S 0538904	3762092
		5	11S 0538967	3762085
		6	11S 0538915	3762111
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		5	11S 0539137	3762059
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10	UNBURN	1	11S 0533108	3753198
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10	BURN	1	11S 0533106	3753051
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		3	11S 0533074	3753073
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13	UNBURN	1	11S 0537594	3757788
		2	11S 0537513	3757800
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		6	11S 0537537	3757851
13	BURN	1	11S 0537678	3758074
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		3	11S 0537702	3758147
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21	UNBURN	1	11S 0532705	3756220
		2	11S 0532756	3756227
		3	11S 0532787	3756231
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		5	11S 0532783	3756246
		6	11S 0532835	3756247
21	BURN	1	11S 0532810	3756410
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		4	11S 0532761	3756420
		5	11S 0532789	3756381
		6	11S 0532735	3756419
21	BURN X 2	1	11S 0532850	3756438
		2	11S 0532817	3756472
		3	11S 0532829	3756467
		4	11S 0532791	3756502
		5	11S 0532875	3756469
		6	11S 0532825	3756508
29	UNBURN	1	11S 0532112	3753696
		2	11S 0532121	3753741
		3	11S 0532083	3753672
		4	11S 0532094	3753725
		5	11S 0532092	3753754
		6	11S 0532063	3753710
29	BURN	1	11S 0532344	3753869
		2	11S 0532325	3753927
		3	11S 0532323	3753871
		4	11S 0532312	3753920
		5	11S 0532299	3753870
		6	11S 0532333	3754051