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Invasive and native plant responses to shrubland fuel reduction: comparing prescribed fire, mastication, and treatment season

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ABSTRACT

Fuel reduction in the wildland–urban interface is a widely used international strategy for assisting human communities regarding wildfire threats, but very little research has examined whether certain fuel reduction methods and their seasonal timing promote nonnative invasion. To address this issue, we evaluated nonnative and native plant response to five of the most commonly-practiced shrubland fuel reduction methods in Mediterranean climates, including (a) fall prescribed fire, (b) winter prescribed fire, (c) spring prescribed fire, (d) fall mastication (slashing) and (e) spring mastication. Treatments were replicated four times in mature northern California chaparral and surveyed for three years after treatment; treatment type was randomly assigned. We found that the effects of treatment type (fire/mastication) were more apparent than the effects of treatment season (fall/winter/spring), but there were some differences among seasons of prescribed fire. Mastication treatments had the highest number of nonnative invasive species. Mastication treatments also had 34% higher nonnative annual grass abundance than the fire treatments. Winter and spring prescribed fire treatments were most resistant to nonnative invasion since these areas had the fewest nonnative species, lowest nonnative species abundances, and highest relative proportions of native plants. In shrublands where controlling nonnative annual grass is an important objective, managers should consider cool season prescribed fire as a viable fuel reduction treatment. In cases where prescribed fire is not feasible, mastication provides an alternative that can exacerbate nonnative grass production in the short term but may maintain native plant seedbanks over the long term if the site remains undisturbed for several decades. Results from this study could be applicable to other areas of Mediterranean shrublands.

1. Introduction

Fuels management has become a top priority in the wildland–urban interface in the United States (Stephens et al., 2009a), south-east Australia (Cary et al., 2003), and southern Europe (Camia et al., 2003) due to an increasing loss of homes to wildfire and the escalating costs of fire suppression. Strategic removal of flammable fuels can be part of an effective approach to help protect homes and communities from fire, but it can also facilitate nonnative species invasion (Briese, 1996; Keeley, 2001, 2006; Rossiter et al., 2003; Merriam et al., 2006).

Nonnative species invasion is considered one of the greatest threats to conserving native ecosystems because of its potential to alter species diversity (Di Castri et al., 1990; Vitousek et al., 1996; Chapin et al., 2000; Abbott and Burrows, 2003; Paynter and Flanagan, 2004; Franklin et al., 2008), change fire regimes (Mack and D'Antonio, 1998; Brooks et al., 2004), and convert shrublands to grasslands (Zedler et al., 1983; D'Antonio and Vitousek, 1992). Consequently, fire managers are caught in the middle of a difficult dilemma: how to preserve natural shrubland ecology while simultaneously protecting humans from wildfire (Burrows et al., 2008). Very little research has addressed this conflict, and managers need more information to determine whether certain fuel reduction strategies promote nonnative species invasion. To address research needs, our study compares native and nonnative plant response to two common shrubland fuel reduction practices (prescribed fire and mechanical mastication (slashing)) performed in three seasons (fall, winter and spring).

California chaparral has some of the highest native plant diversity and rare or endangered species of any Mediterranean ecosystem (Cowling et al., 1996; Keeley, 2005). In California, chaparral occupies only 6% of the state's land area but contains one-quarter of the state's native vascular plant species (Keeley and Davis, 2007). Periodic disturbance, historically in the form of summer or fall wildfire, is considered necessary to maintain a full suite of native chaparral plants because many species depend on fire cues (heat, smoke and charate) for germination. But recent anthropogenic disturbance, such as fuel reduction, is shifting the ecological

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balance from native fire-stimulated species to invasive nonnative annuals that invade from the nearby urban areas (Sauvajot, 1995; Eliason and Allen, 1997; Rundel, 2000; Keeley, 2006; Keeley et al., 2008).

Nonnative annual grass invasion along the wildland–urban interface has serious implications not only for native shrubland conservation but also for human safety and wildfire risk. Annual grasses have flammable fuel characteristics that can increase the probability of ignition near homes, expand fuel continuity between structures, increase rates of fire spread, and lengthen the fire season by curing earlier and persisting later than native species (Regelbrugge, 2000; Keeley, 2001; Brooks et al., 2004). In addition to presenting fire control challenges, annual grass invasion can magnify the risk of erosion and flooding since grass roots are much shallower and uptake less water than native chaparral vegetation (Mooney and Parsons, 1973; Spittler, 1995; Keeley, 2002).

Managers face tremendous pressure to control nonnative species invasion after fuel reduction (Keeley, 2006), but often select fuel reduction methods for their logistical ease rather than biological outcome partly due to a lack of research. Prescribed fire, for instance, is a frequently-favored fuel treatment because it can be applied to large areas of steep, complex terrain at a relatively low cost. Unfortunately, prescribed fire is often deemed unfeasible because of air quality regulations, public disapproval, weather constraints, or the risk of fire escape (Stephens and Ruth, 2005). Mechanical methods have become an increasingly popular fuel reduction alternative (Cary et al., 2003; Western Governors Association, 2006), but very little science has examined their ecological effects.

Seasonal timing of fuel reduction is another key management decision that is frequently swayed by operational considerations rather than conservation impact. Shrubland prescribed fire treatments are often performed in the winter or spring because escape risk is lower, air quality constraints are minimized, and personnel/equipment are more available outside of the wildfire season. But these wet season treatments can have detrimental effects on native obligate seeding species if fire intensity is too low to break physical dormancy or if seeds have imbibed water and become more sensitive to heat (Sweeney, 1956; Williams and Lame, 1999; Odion and Davis, 2000; LeFer and Parker, 2005). Dry season prescribed fires, on the other hand, may actually favor native obligate seeders by destroying the seedbanks of heat-sensitive nonnative annuals (Keeley, 1987; Moreno and Oechel, 1991; Beyers and Wakeman, 2000). Post-treatment plant germination, growth, and survival are strongly influenced by the timing of precipitation and temperature relative to treatment (Fig. 1) and should also be considered in fuel management decisions. In addition, natural seasonal fluctuations in resource availability, competition and seed dispersal can have pivotal influences on post-treatment plant recovery patterns (Horton and Kraebel, 1955; Florence and Florence, 1988; Meyer and Schiffman, 1999; Williams et al., 2003).

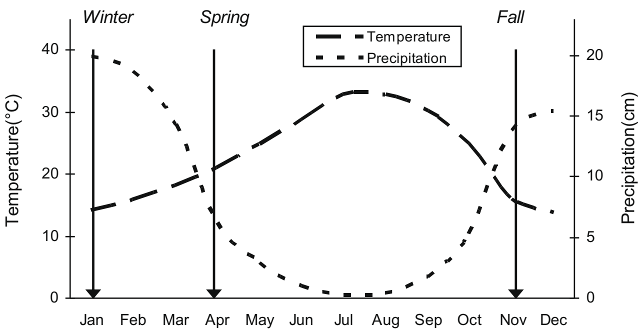

Fig. 1. Monthly temperature and precipitation averages for the study area. Arrows indicate the three different seasons of treatment implementation.

Early studies provide an important foundation for understanding plant community succession after disturbance (Sampson, 1944; Horton and Kraebel, 1955; Sweeney, 1956; Hanes, 1971; Mooney and Parsons, 1973; Biswell, 1974), but these studies often lack applicability to contemporary fuel management issues, particularly regarding mechanical methods and nonnative species invasion. Recent literature addresses nonnative species response to wildfire (Briese, 1996; Harrison et al., 2003; Keeley et al., 2005; Keeley, 2006), one or two seasons of prescribed fire (Dunne et al., 1991; LeFer and Parker, 2005) or fuel break construction (Keeley, 2001; Merriam et al., 2006), but the literature lacks a replicated comparison among prescribed fire, mastication, and season of treatment.

To address this research gap, we designed our experiment to compare nonnative plant response to five common fuel reduction treatments used in Mediterranean shrublands, including fall prescribed fire, winter prescribed fire, spring prescribed fire, fall mastication, and spring mastication. Winter mastication was not included because of limited road access and undesirable machinery impacts in wet soil conditions. In our study, we focus on three conservation questions: (1) which shrubland fuel reduction technique minimizes nonnative species richness and abundance (i.e. extent of invasion), (2) which technique minimizes the abundance of nonnative annual grasses (i.e. site flammability), and (3) which technique maximizes native species richness and abundance.

2. Methods

2.1. Study region

We conducted our study in chamise (*Adenostoma fasciculatum*) dominated chaparral of northern California's Coast Range, approximately 50 km inland from the Pacific coast and 175 km north of San Francisco, CA (39 N, 123 W). The research area experiences a typical Mediterranean climate with hot, dry summers and cool, wet winters (Fig. 1). Maximum mean temperatures vary widely throughout the year, averaging 34 °C in summer and 7 °C in winter. The 30-year rainfall average is 100 cm, with nearly all precipitation occurring between October–May. Annual rainfall during our 2001–2005 study averaged 99.0 cm and ranged from 90.7–124.5 cm. Treatment areas were located 700–1000 m above sea level on south and west aspects with slopes of 25–55%. Soils are derived from weathered sandstone and shale and are classified as shallow, rocky and moderately acidic. Fire and other major disturbances were absent from the study area for at least 40 years prior to treatment.

Our study sites are representative of California chamise chaparral, with chamise comprising >65% of the overstory vegetation, and buckbrush (*Ceanothus cuneatus*) and manzanita (*Arctostaphylos spp.*) occupying more minor overstory components. Pre-treatment vegetation averaged 1.5–2 m in height and nearly 100% shrub cover. Understory native herbaceous plants were uncommon in pre-treatment conditions, and nonnative annual grasses were rare, occasionally occurring in gaps or along roadsides.

2.2. Study design

Each of the five fuel reduction treatments is replicated four times, for a total of 20 experimental units. Each unit is approximately two hectares in size and are distributed across a <2 km distance. Treatment type (prescribed fire/mastication) and season (fall/winter/spring) were randomly assigned to the experimental units, although mastication was restricted to sites with slightly more gradual slopes (25–40% versus 35–55% for burn units) because of limited equipment maneuverability in steep topography. Treatment seasons were defined as: fall (3–20 November), winter (8–18 January), and spring (31 March–3 April for prescribed fire, and 23 April–2 June for spring mastication). Spring mastication treatments were conducted slightly later than spring fire treatments because access roads were not dry enough for masticator travel until later spring months. We do not expect this discrepancy in spring treatment timing to significantly affect our findings since our analysis demonstrated that treatment type (fire or mastication) overshadowed the effect of treatment season.

We performed fuel reduction treatments between 2001 and 2003 at the University of California Hopland Research and Extension Center and adjacent Bureau of Land Management Cow Mountain area. Our initial goal was to complete all four replicates of each treatment within a few consecutive days in the same year, but unfavorable weather conditions and equipment availability forced us to split replicates over two years.

2.3. Treatment implementation and vegetation monitoring

Prescribed fires were ignited with driptorches to produce upslope headfires (Stephens et al., 2008). We attempted to create uniform flame lengths and rates of spread within experimental units, but fire behavior is inherently variable. To account for heterogeneity associated with complex fire behavior patterns (Moreno and Oechel, 1991; Odion and Davis, 2000), we collected multiple vegetation samples in each replicate (see Vegetation Monitoring section).

Mastication was performed by a steel-track tractor with a front-mounted rotating toothed drum which shredded above-ground biomass into a patchy <5 cm layer of small diameter woody debris that remained on the soil surface. Subsurface soil and root systems were not disturbed. Treatment heterogeneity was minimal in mastication treatments since the equipment operator performed systematic passes through the vegetation. Vegetation removal was 95–100% in both fire and mastication treatments.

Each experimental unit contained 10 permanent sampling plots that were 2.5 m^2 in size (total sampled area was 25 m^2 for each experimental unit) and randomly dispersed throughout the unit. We measured species richness and abundance by identifying and counting all plant individuals found within the sampling plots between May–July, both before treatment and again three years after treatment. Data from the 10 sampling plots were pooled to produce a single value for each experimental unit.

2.4. Data analysis

We present data from the third post-treatment year because nonnative species diversity and abundance, particularly for nonnative annual grasses, was highest in this time period (see also Horton and Kraebel, 1955; Sweeney, 1956; Keeley et al., 2003). By focusing on third year results, we are able to eliminate ephemeral species from the analysis and focus on longer term management implications.

We used one-way analysis of variance (ANOVA) to determine if significant differences ($p < 0.05$) existed among treatments for species richness and abundance. If a significant difference was detected, we used Tukey–Kramer HSD tests to determine which fuel treatments were statistically different. Non-normal data were log-transformed (for absolute values) or arcsine square root transformed (for relative percentage values) to meet assumptions of normal distribution and equal variance when necessary.

Species diversity was estimated for all treatments using the Shannon–Wiener Index. The Shannon–Wiener Index accounts for both species richness and evenness, and was calculated as $H' = -\sum \mathrm{p}_i \ln p_i$, where p_i is the proportion of individuals found in the ith species. We also determined similarities in species composition using Jaccard's Index, calculated as $J = A/(A + B + C)$, where A is the number of species shared between the two treatment types, B is the number of species found exclusively in fire units, and C is the number of species found exclusively in mastication units.

We measured fire intensity and severity using the proxy variables of pre-burn fuel moisture and soil moisture. We selected these moisture variables because they are relatively simple to measure in the field and have a direct influence fire behavior and soil heating, which in turn affect seed survival and dormancy release (Keeley, 1987; Parker and Kelly, 1989; Williams et al., 2003). In each experimental unit immediately prior to burning, we collected six soil samples (at depths of 0–3 cm and 3–6 cm, in three random locations) and 18 fuel samples (one live and one dead sample of chamise, buckbrush and manzanita species, in three random locations). We oven-dried the samples for 24 h at 105 °C and calculated the percent dry weight of each sample.

3. Results

3.1. Plant community response

We identified 146 plant species in the third post-treatment year, of which 23% were nonnative and 77% were native. Species belonged to 47 plant families, with *Asteraceae* and *Poaceae* families representing 18% and 13% of all species, respectively. We recorded 193,190 plant individuals and identified 99% to the species level.

Species richness (the combined number of species found within all four treatment replicates) ranged from 54 to 100 (Table 1). Fall and spring mastication treatments had the highest average species richness (56.1 ± 4.4 [mean ± SD] and 50.9 ± 4.6, respectively), while spring fire treatments had the lowest (26.5 ± 8.6) [ANOVA, $N = 20$, $F_{4,19} = 11.49$, $p < 0.0002$]. Overall, masticated treatments had 19.9 ± 3.6 more species than prescribed fire treatments ($t_{2,18} = 5.57$, $p < 0.0001$). Total plant abundance was also substantially higher in mastication units, with an average of 19,477 individuals per replicate, compared to 3694 individuals in the fire replicates.

We estimated community diversity (Shannon–Wiener Index), and found that treatments produced relatively diverse floras (range, 2.1–2.4), but diversity was not statistically different among treatments (ANOVA, $N = 20$, $F_{4,19} = 0.81$, $p = 0.54$). We also calculated community similarity (Jaccard's Index) and found that 25–28% of species were shared among all treatments. Overall, fall treatments had the greatest diversity of life forms (Table 1).

Nineteen species were found exclusively in mastication units. These species include five nonnatives and 14 natives, and together comprised <4% of the total mastication abundance. Eight species were found exclusively in prescribed fire units; these species were all native and comprised 2.1% of the total prescribed fire abundance. Three of the prescribed fire-only species were found in all seasons of fire treatment and included the annual whispering bells (*Emmenanthe pendiflora*), subshrub yerba santa (*Eriodictyon californicum*), and herb California everlasting (*Gnaphalium californicum*). Five species were present in two of the three seasons of fire treatment and included hairy sun cup (*Camissonia hirtella*), intermediate sun cup (*Camissonia intermedia*), prickly cryptantha (*Cryptantha muricata*), sticky monkey flower (*Mimulus aurantiacus*) and California chicory (*Rafinesquia californica*).

We expected fuel and soil moisture to differ between each season of prescribed burning, but soil moisture (dry weight basis, %) showed no significant differences among seasons (ANOVA, $F_{4,11} = 1.28$, $p = 0.32$). Live fuel moisture (dry weight basis, %) was statistically higher in the spring but was not different between the fall and winter (Kruskal–Wallis test).

Table 1
Species richness, by origin and life form. Data represent the number of species found in the four replicates of each treatment (mean ± standard error).

Origin	Life form	Fall fire	Winter fire	Spring fire	Fall mastication	Spring mastication
Nonnative	Annual grass	6 ± 1	3 ± 1	3 ± 1	8 ± 0	8 ± 1
	Annual/biennial herb	6 ± 1	2 ± 0	3 ± 0	10 ± 1	7 ± 0
	Perennial grass	1 ± 0	0	0	1 ± 0	0
Subtotal		24	8	12	28	23
Native	Annual grass	2 ± 0	1 ± 0	1 ± 0	2 ± 0	2 ± 0
	Annual/biennial herb	18 ± 1	14 ± 3	14 ± 2	21 ± 2	20 ± 3
	Annual parasite	0	0	0	1 ± 0	0
	Perennial fern	1 ± 0	0	0	1 ± 0	0
	Perennial geophyte	1 ± 0	1 ± 0	1 ± 0	3 ± 1	3 ± 1
	Perennial grass	1 ± 0	1 ± 0	0	1 ± 0	1 ± 0
	Perennial herb	4 ± 1	3 ± 0	2 ± 1	7 ± 1	6 ± 1
	Perennial shrub	4 ± 0	6 ± 0	3 ± 0	4 ± 1	5 ± 0
	Perennial subshrub	2 ± 0	2 ± 0	1 ± 0	2 ± 0	1 ± 0
Subtotal		60	54	42	72	71
Species total		84	62	54	100	94

3.2. Fuel reduction treatment that minimizes nonnative species richness and abundance

Winter and spring prescribed fire had the lowest number of nonnative species (5 ± 1.4 and 5.5 ± 1.7, respectively) while fall and spring mastication had the highest (19 ± 3.5 and 14 ± 1.3, respectively) (Fig. 2). On average, fire treatments had 9 ± 1.8 fewer nonnative species than the mastication treatments ($t_{2,18} = 5.23$, $p < 0.0001$). Since the total number of species varies widely among treatments, it is also important to consider relative species richness (percentage of species that are nonnative). Winter prescribed fire had the lowest percentage of nonnative species (16.3% ± 4.6) and fall mastication had the highest (33.6% ± 3.9) [ANOVA, $N = 20$, $F_{4,19} = 7.8775$, $p < 0.0013$].

Nonnative species abundance showed a wide range of variation among treatments, with mean abundances ranging from 441 to 15 719 individuals among replicates. Winter prescribed fire had the lowest percentage of nonnative individuals (12.7% ± 5.6) compared to spring and fall mastication with the highest (61.9% ± 16.8 and 60.1% ± 13.4, respectively) (Fig. 3). On average, 23% of the total prescribed fire abundance was nonnative compared to 61% in the mastication treatments ($t_{2,18} = 4.02$, $p < 0.0008$).

3.3. Fuel treatment that minimizes nonnative annual grass abundance

Nonnative annual grass abundance was notably different among treatments, with winter prescribed fire having the lowest abundance (382) and fall mastication having the highest (11,116) (Fig. 4). Nonnative annual grasses were found in nearly every 2.5 m^2 sampling plot in the mastication treatments. On average, nonnative annual grasses composed 13.8% of the total abundance in fire treatments and 47.5% in mastication treatments ($t_{2,17} = 4.56$, $p < 0.0003$). Although many of these annual grasses are small in size and may seem to pose a minor change to the ecosystem, the between-treatment contrast in nonnative annual grasses can be seen visually on the landscape (Supplementary material).

The overwhelming majority of the nonnative grass abundance in this study was contributed by four species, including European hairgrass (*Aira caryophylla*), nitgrass (*Gastridium ventricosum*), brome fescue (*Vulpia bromoides*) and rat-tail fescue (*Vulpia myuros*) (Appendix A). These species comprised 93% and 98% of the nonnative grass abundance in the mastication and prescribed fire treatments, respectively.

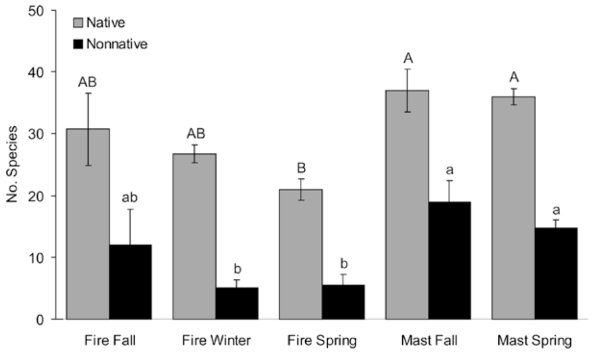

Fig. 2. Average number of native and nonnative species by treatment. Upper-case letters indicate significantly different means for native species as determined by Tukey HSD tests (ANOVA, $N = 20$, $F_{4,19} = 5.82$, $p = 0.005$). Lower-case letters indicate significantly different means for nonnative species (ANOVA, $N = 20$, $F_{4,19} = 13.6$, $p < 0.0001$). Whiskers represent one standard deviation from the mean.

3.4. Fuel treatment that maximizes native species richness

Fall and spring mastication had the highest number of native species (37 ± 1 and 36 ± 5, respectively) and spring prescribed fire had the lowest (21 ± 7) (Fig. 2) [ANOVA, $N = 20$, $F_{4,19} = 5.82$, $p = 0.005$]. While the total number of native species is important, the relative percentage of native species may be a better indicator for native plant conservation. For example, fall mastication had the greatest number of native species but showed the lowest percentage of native species (67%). Winter prescribed fire had the fewest

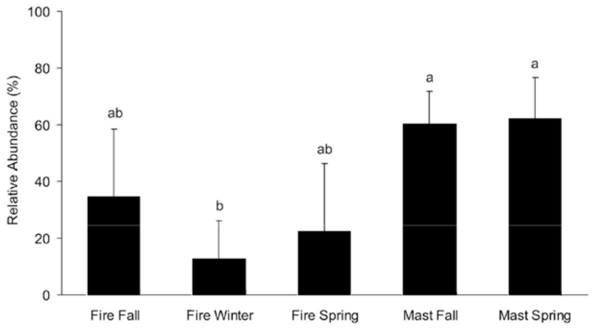

Fig. 3. Percentage of individuals that are nonnative (ANOVA, $N = 20$, $F_{4,19} = 4.506$, $p = 0.0143$). Letters indicate significantly different means as determined by Tukey HSD tests. Whiskers represent one standard deviation from the mean.

native species overall but showed the highest percentage of natives (84%).

Similar to nonnative species abundance, native plant abundance showed significant differences among fuel treatments (ANOVA log-transformed data, $N = 20$, $F_{4,19} = 3.56$, $p = 0.03$). Fall mastication had the highest native abundance (11,990) and spring prescribed fire had the lowest (1222). Again, relative values present a very different picture from the absolute values. Spring mastication had the greatest number of native individuals, but showed the lowest relative percentage of native plants (36%). Winter prescribed fire, on the other hand, had one of the fewest native individuals but the highest relative native plant abundances (84%).

Nitrogen-fixing species are an important component of plant composition because they improve soil conditions and allow sites to support higher diversity and productivity in early post-disturbance chaparral (Dunn and DeBano, 1977; Nilsen and Schlesinger, 1981; Westman, 1981; Guo, 2001). In our sampling, we identified 16 nitrogen-fixing species, all native, which were primarily members of the *Ceanothus*, *Lotus* and *Trifolium* genera. The average number of nitrogen-fixing species in the experimental units was 4.5 ± 1.7, and the abundance of nitrogen-fixing plants was significantly different among fuel treatments [ANOVA, log-transformed data, $N = 20$, $F_{4,19} = 6.82$, $p = 0.025$]. Fall and spring mastication treatments had the highest number of nitrogen-fixing individuals (4032 and 1677, respectively), and spring prescribed fire had the lowest (220). On average, mastication treatments had two more nitrogen-fixing species ($t_{2,18} = 3.10$, $p < 0.0031$) and 2540 more nitrogen-fixing individuals than prescribed fire treatments ($t_{2,18} = 2.64$, $p < 0.033$).

4. Discussion

4.1. Summary of treatment effects

Our research demonstrates that fuel reduction treatments can produce significantly different nonnative and native plant responses. Overwhelmingly, fall and spring mastication had the highest values for every nonnative variable we measured. Not only did both mastication treatments have consistently higher nonnative values than any of the fire treatments, but these numbers were exceptionally higher. For example, nonnative annual grass abundance was 29 times higher after fall mastication and 15 times higher after spring mastication treatment when compared to the spring prescribed fire treatment (lowest nonnative grass abundance). Although nonnative grasses comprise a relatively low percentage of total biomass in the treatment areas, the prevalence of these species can affect native plant success as well as site flammability.

In addition to having the most nonnative species, mastication treatments had an average of 10 more native species and 70% more native individuals than the prescribed fire treatments, including several fire-following species. We did not expect this strong native recovery after mastication since many chaparral species are considered dependent on fire for germination (Halse, 1993; Baskin and Baskin, 1998; Keeley and Davis, 2007). Furthermore, we were surprised to find 14 native species located exclusively in mastication treatments compared to only eight native species located exclusively in prescribed fire treatments. Upon closer examination however, we noted that the 14 mastication-only species are generally common to open, grassy disturbed sites but the eight species missing from mastication are all relatively fire-dependent. The risk of losing a small number of fire-dependent species may not have immediate conservation consequences, but could have cumulative effects after recurring disturbance events (Zammit and Zedler, 1994; Hobbs et al., 1995).

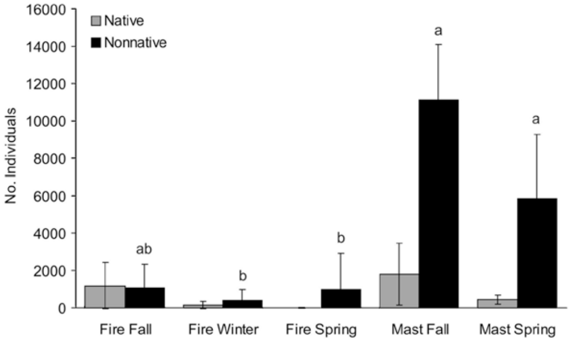

Fig. 4. Annual grass abundance by native and nonnative status. Letters indicate significantly different means for nonnative abundance as determined by Tukey HSD tests (ANOVA, log-transformed data, $N = 20$, $F_{4,19} = 7.124$, $p = 0.002$). Whiskers represent one standard deviation from the mean.

We found several species in the mastication treatments that can be classified as 'fire-followers' because of their dependency on fire-related germination triggers. Examples include *Helianthemum scoparium* (peak rush-rose), *Agoseris heterophylla* (annual agoseris) and *Gilia capitata* (globe gilia). These species were also present in the prescribed fire treatments. The presence of fire-following species in masticated areas may be attributed to polymorphic seed banks (Sweeney, 1956; Keeley, 1991; Zammit and Zedler, 1994) and/or sufficiently high solar heating that overcomes physical seed dormancy (Baskin and Baskin, 1998).

Several unique site characteristics may explain the high native and nonnative species assemblages found in mastication treatments. First, masticated areas may have higher seedbank recruitment than burned areas because the soil was not exposed to potentially damaging heat (Zammit and Zedler, 1994). Second, the mulch-like material that remains on the soil surface after mastication may improve germination and survival conditions by retaining moisture and nutrients (Horton and Kraebel, 1955; Meyer and Schiffman, 1999). This mulch layer may also trap seeds and prevent them from being transported offsite by wind or water. Third, shrub regrowth was severely reduced by deer browsing in masticated areas, most likely due to the absence of movement-impeding plant skeletons (J. Potts, unpublished data, 2008), and this low shrub cover may have increased the availability of light, water, nutrients, and colonization space for herbaceous species (Sampson, 1944; Keeley et al., 2003; Keeley, 2005). In addition, the reduced shrub cover in masticated areas may result in lower small mammal seed herbivory since rodents often avoid areas with sparse cover because of increased predator pressure (Mills, 1986). Lastly, the high number of nitrogen-fixing species in mastication treatments may improve soil conditions where masticated sites are able to support higher diversity and plant numbers, particularly from invasive nonnative species that have higher nitrogen requirements than native species (Guo, 2001).

Pre-treatment vegetation characteristics, including seed bank size and composition, can play a role in determining post-treatment vegetation composition. Our pretreatment data revealed that treatment replicates were statistically similar (ANOVA) with regards to above-ground species richness, abundance, native/nonnative species composition and shrub cover. We did not test seed bank characteristics. The above-ground community similarities suggest that post-treatment vegetation differences are a direct result of the treatment itself rather than a reflection of pre-treatment conditions. We also tested whether replicates with high pre-treatment species richness values had high post-treatment values (Pearson pairwise correlations), but we did not find any significant correlations between pre- and post- treatment values for any replicate.

4.2. Seasonal timing of treatments

Seasonal timing of treatments did not produce trends as consistent or pronounced as among treatment types, but we did notice some patterns among treatment seasons. Small changes in species composition relative to seasonal timing of fire were also found in experiments in Northern Australia (Bowman et al., 1988; Williams et al., 2003) and South Africa (Scholes and Walker, 1993). Fall and spring mastication treatments behaved very similarly in all tests and rarely showed statistical seasonal differences. Prescribed fire treatments exhibited a greater degree of seasonal variation but lacked any true significant differences. The absence of strong botanical distinction among the post-fire treatments may be partially explained by the similar soil moistures at the time of treatment.

The seasonal timing of precipitation and climate variables relative to treatment (Fig. 1) is likely responsible for the vegetation recovery patterns that were observed. For example, fall fire treatments showed higher native and nonnative species richness/abundance than the winter and spring fire treatments. The large number of nonnative species after fall fire treatments can be attributed to post-treatment precipitation timing since many nonnative species germinate immediately after the first fall rains (nearly 2–3 months earlier than natives), and quickly dominate the new niche space before native plants have a chance to establish. The relatively low native and nonnative richness/abundance after spring treatments was also expected because new plants have a very short time to develop adequate root systems prior to the hot, dry Mediterranean summer.

Overall, winter and spring prescribed fire treatments may have the least impact on nonnative species spread because of their notably low nonnative species numbers. Winter and spring treatments also seem to provide a native species advantage since the native: nonnative plant ratio is very high. Despite these favorable characteristics, it is important to consider that winter and spring fire treatments had the lowest native richness and abundance relative to other treatments. This low native plant diversity may affect community function in the long term.

We have focused on native and nonnative herbaceous plants in the preceding pages, but shrub recovery also deserves attention in order to understand the response of the entire vegetation community. Our unpublished data show that masticated areas have an average shrub cover of 44% after the third post-treatment year compared to 71% shrub cover in the prescribed fire areas. Although the slower shrub recovery may be ideal because it requires less frequent re-treatment, the interspaces among shrubs are filled with flammable nonnative grasses that can carry fire throughout the shrub matrix, allowing an area to burn under moderate conditions when it would not likely burn otherwise. An increasing number of anthropogenic ignitions at the wildland-urban interface enhances the risk of short interval burning, which can facilitate a shift in plant community types from shrublands to grasslands (Zedler et al., 1983; D'Antonio and Vitousek, 1992; Haidinger and Keeley, 1993), and exacerbate erosion and flooding associated with type conversion (Keeley and Fotheringham, 2003).

5. Conclusion

Fire managers face a challenging task to simultaneously safeguard human communities, preserve native shrublands, and minimize nonnative species invasion. As our research demonstrates, it is important to carefully select fuel reduction treatments since unique post-treatment plant patterns can influence future fire regimes and plant succession dynamics.

In our study, mastication showed much higher plant richness and abundance for both native and nonnative species, including the highest proportion of nonnative plants. Based on our single treatment results, mastication may be a desirable fuel reduction strategy because native diversity is high and ensures seed bank renewal, assuming that these plants reach reproductive maturity and accumulate sufficiently large seed banks before the next disturbance. As the shrub canopy recovers, nonnative herbaceous species will be shaded out and confined to small openings in the mature overstory. An added benefit of a mastication treatment is that shrub regeneration is much slower than in prescribed burned areas (J. Potts, unpublished data), resulting in less frequent re-treatment. The primary drawback of the slow shrub recovery in masticated areas is that the shrub interspaces are occupied by flammable nonnative grasses which can increase the area's ignition potential and accelerate vegetation type conversion to a more permanent annual grassland state.

An alternative fuel treatment scenario could involve winter or spring prescribed fire in the interest of reducing nonnative species spread and minimizing site flammability. Cooler season burns are also ideal because fire control is easier and smoke management concerns can be slightly less due to greater atmospheric mixing. The drawback to winter or spring fire treatments is that native diversity is lower and this could have long-term implications to ecosystem integrity and function.

One key remaining question is how native and nonnative species will fare after repeated fuel reduction treatments (Bowman et al., 1988; Bond and Archibald, 2003; Williams et al., 2003; Burrows et al., 2008), since most areas will need to be re-treated to maintain lower fuel hazards (Stephens et al., 2009b) in the urban–wildland interface. Our study only examines plant response after a single treatment application, but it is likely that nonnative annuals will gain greater advantage after multiple treatments if treatment frequency is shorter than the time needed for native species to reach reproductive maturity and/or accumulate adequate seedbanks. Furthermore, it is important to consider the potential for a stronger nonnative annual response under increasing atmospheric nitrogen deposition (Padgett et al., 1999). Future chaparral management will greatly benefit from further studies of seed bank dynamics, treatment frequency, and treatment scale.

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Appendix A

List of nonnative species, including frequency and abundance data by treatment type. Frequency is the number of sampling plots in which the species was found, out of a possible 200. Abundance is the number of plant individuals found in the sampling plots within each treatment type (mean ± standard error).

Species	Life form	Frequency	Total	Abundance				
				Fall fire	Winter fire	Spring fire	Fall mast	Spring mast
Filago gallica	Annual herb	152	21,301	830 ± 370	40 ± 15	287 ± 245	3436 ± 1903	734 ± 376
Aira caryophyllea	Annual grass	128	38,887	399 ± 198	57 ± 28	718 ± 713	5017 ± 529	3532 ± 560
Gastridium ventricosum	Annual grass	98	13,659	336 ± 202	316 ± 298	245 ± 237	2001 ± 1055	517 ± 246
Hypochaeris glabra	Annual herb	80	3418	3 ± 2	1 ± 1		403 ± 301	449 ± 259
Vulpia bromoides	Annual grass	74	12,845	7 ± 3	5 ± 5	20 ± 20	1908 ± 745	1272 ± 963
Vulpia myuros	Annual grass	74	7445	292 ± 216	4 ± 1	4 ± 3	1076 ± 682	486 ± 337
Bromus madritensis	Annual grass	37	1545	43 ± 29		2 ± 2	329 ± 170	13 ± 8
Torilis arvensis	Annual herb	36	370	12 ± 11		1 ± 1	53 ± 36	27 ± 19
Lactuca serriola	Annual herb	33	135	1 ± 0		1 ± 0	5 ± 2	28 ± 15
Galium parisiense	Annual herb	29	1108	37 ± 36	20 ± 20	2 ± 2	216 ± 155	2 ± 2
Bromus hordeaceus	Annual grass	20	541	1 ± 1			111 ± 63	23 ± 19
Lactuca saligna	Annual herb	20	69			1 ± 1	5 ± 5	12 ± 7
Senecio vulgaris	Annual herb	19	43	2 ± 1	1 ± 1		1 ± 0	8 ± 5
Centaurea melitensis	Annual herb	16	276	60 ± 56		1 ± 1	7 ± 6	2 ± 2
Anagallis arvensis	Annual herb	14	234	41 ± 25			15 ± 9	3 ± 3
Cynosurus echinatus	Annual grass	10	33	1 ± 1			3 ± 2	5 ± 2
Sonchus asper	Annual herb	6	13	1 ± 1			1 ± 1	2 ± 2
Taeniatherum caput-medusae	Annual grass	6	22	2 ± 2			3 ± 3	1 ± 0
Cerastium glomeratum	Annual herb	4	359	1 ± 1			1 ± 1	89 ± 89
Avena fatua	Annual grass	2	5				1 ± 1	1 ± 1
Briza minor	Annual grass	2	8				2 ± 2	1 ± 1
Erodium cicutarium	Annual herb	2	2	1 ± 1				1 ± 1
Erodium sp.	Annual herb	2	4			1 ± 1	1 ± 1	
Holcus lanatus	Perennial grass	2	2				1 ± 0	
Tolpis barbata	Annual herb	2	5	1 ± 1				
Trifolium hirtum	Annual herb	2	22	1 ± 1			5 ± 5	
Brachypodium distachyon	Annual grass	1	2	1 ± 1				
Briza maxima	Annual grass	1	5				1 ± 1	
Carduus pycnocephalus	Ann/bien herb	1	1				1 ± 1	
Centaurea solstitialis	Annual herb	1	11				3 ± 3	
Piptatherum miliaceum	Perennial grass	1	6	2 ± 2				
Polypogon monspeliensis	Annual grass	1	39	10 ± 10				
Verbascum thapsus	Biennial herb	1	1					1 ± 1

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.03.001.

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