Hydroseeding increases ecosystem nitrogen retention but inhibits natural vegetation regeneration after two years of chaparral post-fire recovery

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Abstract

Fire is a natural disturbance in many ecosystems such as semi-arid chaparral shrublands, but rates of vegetation regeneration may be slow after intense fires. Thus, land managers may resort to practices such as mulching or seeding in areas that are prone to soil erosion and nutrient loss. These practices, in particular seeding with annual grasses, are controversial because they may inhibit rates of natural vegetation regeneration, introduce exotic species, and be ineffective at soil and/or nutrient retention. We assessed how hydroseeding affected rates of chaparral vegetation regrowth and ecosystem nitrogen (N) storage during the first 2 years of post-fire recovery. We selected 3 north-facing slopes that were within 500 m of each other: one slope was unburned while the other slopes burned during the “Cocos” fire in May 2014 and were either hydroseeded with a mix of native grasses and suffrutescent shrubs (seeded) or left to naturally regenerate

(control). We hypothesized that seeding would reduce native woody shrub cover and production but that ecosystem N storage would be higher in the seeded stand. Seeding significantly reduced woody shrub cover, aboveground biomass, shrub and total species richness, and rates of shrub growth. However, herbaceous biomass, dominated by grasses that were absent on the naturally regenerating slope, was significantly higher in the seeded areas, causing significantly higher total vegetation cover in the seeded area. The higher herbaceous cover led to an increase in plant N storage and a reduction in soil extractable NO_3 . Hydroseeding also caused a reduction in potential N mineralization, and during the growing season, an increase in soil microbial biomass. Our results suggest that seeding recently burned chaparral slopes reduces nutrient loss but at the expense of native plant abundance and diversity. While the long-term effects of seeding on vegetation composition are unknown, changes in vegetation from a shrub- to a grass-dominated system may fundamentally alter future fire regimes.

Key words: Disturbance, nitrogen cycling, Mediterranean-type shrublands, plant species richness, secondary succession, wildfire.

1. Introduction

Fire has important impacts on the biotic and abiotic properties of semi-arid shrublands such as chaparral, and can alter nutrient and water availability (Rundel 1983; Riggan et al., 1994; Meixner et al., 2006), rates of primary production (Black 1987; Kaye et al., 2010; Vourlitis and Hentz 2016), soil microbial activity and composition (Neary et al. 1999; Knicker 2007; Fonturbel et al., 2012), and plant species composition (Keeley and Keeley 1986; Gou 2001). These impacts are strongly affected by fire severity, which in turn affects rates of vegetation and

microbial recovery (Neary et al. 1999; Knicker 2007). Nutrient losses are positively related to fire intensity (DeBano and Conrad 1978); however, nutrient availability may exhibit an increase immediately after fire due to the rapid decomposition and mineralization of ash (Fenn et al. 1993; Carreira et al. 1994; Vourlitis and Pasquini 2008; Vourlitis and Hentz 2016). This nutrient pulse may lead to high rates of nutrient loss from leaching (Riggan et al. 1994; Meixner et al. 2006), but leaching losses typically decline over time as plants recover (Vourlitis and Hentz 2016). Similarly, microbial populations typically decline after fire (Hanan et al. 2016), but low intensity fires may have a small effect on microbial populations while moderate-high intensity fires significantly reduce microbial population size (Neary et al. 1999; Knicker 2007; Fonturbel et al., 2012). This relationship may be due to how fire intensity affects the biochemical quality of the remaining ash, as relatively more labile C fractions are progressively lost as fire intensity increases (Knicker 2007). Post-fire microbial populations generally increase over time as litter produced by recovering shrubs increases; however, inhibitory effects of fire can persist for several years (Neary et al. 1999; Knicker 2007; Fonturbel et al., 2012).

Slow rates of vegetation recovery that may associated with large and intense fires are often a concern to land managers because of the potential for erosion, prolonged nutrient loss, and declines in stream water quality (Keeler-Wolf 1995; Beyers 2004). As a result, post-fire seeding, often in the form of hydroseeding where a mixture of seeds, water, nutrients, and organic matter are applied to the burned area, has been used to hasten the development of vegetation and reduce soil and nutrient losses (Asche and Barton 1995; Keeler-Wolf 1995; Beyers 2004). However, post-fire seeding treatments can cause a decline plant community diversity by delaying native plant emergence and/or introducing non-native plant species (Asche and Barton 1995; Keeler-Wolf 1995; Beyers 2004). This may be especially true when burned

70 areas are seeded with non-native grasses and forbs that can persist and compete with
71 regenerating native plants for available resources (Elliot and White 1987; Beyers 2004; Keeley
72 2004) and/or change future fire frequency (Zedler et al., 1983; Keeler-Wolf 1995).

73 Despite potential drawbacks, hydroseeding was recently used on the campus of California
74 State University, San Marcos (CSUSM) to help rehabilitate a chaparral stand that burned the
75 May 2014 “Cocos” wildfire. This slope was almost completely denuded by the fire, leaving only
76 charred skeletons of the burned shrubs, and while fire intensity was not quantified, the
77 consumption of the tall, dense chaparral vegetation suggests that the fire was intense.
78 Furthermore, the fire occurred on a relatively steep slope that was above the campus and
79 neighboring residential area. Thus, concern for possible erosion prompted university officials to
80 hydroseed a portion of the slope in December 2014, providing an opportunity to assess the
81 effects of post-fire management on vegetation recovery and nitrogen (N) storage and cycling.
82 Given observation that post-fire seeding can reduce native plant recovery (Asche and Barton
83 1995; Keeler-Wolf 1995; Beyers 2004), we hypothesized that native woody shrub cover and
84 production would be lower in hydroseeded areas. However, because herbaceous plants, which
85 were part of a hydroseed mix, have faster rates of growth and N uptake than woody shrubs (Aerts
86 and Chapin 2000), we hypothesized that ecosystem N retention would be higher in the areas
87 treated with hydroseed. Finally, while little is known about how post-fire management affects
88 microbial biomass and/or activity (Fontúrbel et al. 2012; Hanan et al. 2016), we hypothesize that
89 higher herbaceous biomass in hydroseeded areas would increase microbial biomass and N
90 immobilization because microbial N activity in chaparral soils is C limited (Jenerette and
91 Chatterjee 2012; Vourlitis and Fernandez 2015).

92 **2. Materials and methods**

2.1. Site description

Research was conducted between September 2015 and April 2016 in three chaparral stands located on the campus of California State San Marcos (CSUSM). Two of the stands burned during the May 2014 “Cocos” fire (Fig. 1), while the third was not affected by the fire or fire-fighting activities. The burned stands were located on a north-facing slope, with a portion that was hydroseeded in December 2014 (hereafter referred to as the “seeded” stand) and another portion approximately 100 m from the hydroseeded stand that was left to recover naturally (hereafter referred to as the “control” stand) (Fig. 1). The unburned stand was located on an adjacent N-facing slope approximately 500 m north of the burned areas.

All of the stands had similar elevation (approximately 220 m above sea level), slope angle (ca. 20-30°), and soil type. Soil consisted of a coarse sandy-loam of the Cieneba series, which is a Typic Xerorthents (Inceptisol) with an average bulk density of 1.34 g/cm³ (Bowman et al. 1973; Vourlitis et al. 2015). Vegetation consisted of a Chamise-Black Sage series chaparral (Sawyer and Keeler-Wolf 1995), with *Adenostoma fasciculatum* Hook & Arn., *Salvia mellifera* Green, *Eriogonum fasciculatum* Benth., *Rhus integrifolia* (Nutt.) Brewer & S. Watson and *Malosma laurina* (Nutt.) Abrams as the dominant woody shrub species. Vegetation abundance was not measured in the unburned stand; however, plant cover exceeded 100% and was similar in structure and species composition to the burned stands prior to the May 2014 fire.

The hydroseed mix was not amended with fertilizer and consisted of native chaparral and coastal sage scrub species, including *Artemisia californica* Less. (2.2 kg/ha), *E. fasciculatum* (5.6 kg/ha), *Acmispon glaber* (Vogel) Brouilet (6.7 kg/ha), *Mimulus aurantiacus* var. *puniceus* (Nutt.) D.M. Thomps. (2.2 kg/ha), *Isocoma menziesii* (Hook & Arn.) G. Nesom (2.2 kg/ha), *Lupinus succulentus* Koch (3.4 kg/ha), *Festuca microstachys* (Nutt.) Benth. (6.7 kg/ha), and *Bromus*

carinatus Hook & Arn (11.2 kg/ha). It is unknown whether the seeds used in the hydroseed mix were from local sources.

2.2. Field sampling

Field sampling was conducted over four dates, 15 April and 28 September, 2015 and 1 February and 18 April, 2016; however, not all sites and/or response variables were measured on the same dates, causing an unbalanced sampling design. All plant and soil samples were obtained within permanent 2 m radius (12.56 m²) circular plots (n = 10 plots/site) that were randomly located within a ca. 0.5 ha area at each site.

Soil samples were obtained from the unburned stand on 28 September, 2015 and the burned stands on 28 September, 2015 and 1 February, 2016. Soil samples were randomly obtained from the upper 0-10 cm soil layer of each plot using a 4.7 cm diameter bucket auger (September 2015) or a 5.2 cm diameter polyvinyl-chloride (PVC) tube (February 2016). Soil samples were analyzed for extractable N (NH₄ and NO₃), soil water content, and microbial C (described in section 2.3.).

Vegetation sampling was conducted in the burned stands on all dates except 28 September, 2015. On 15 April, 2015 the cover of all plants within each plot was measured; thereafter, the cover of all woody shrubs within each plot was measured. Estimates of cover were derived from measurements of projected plant area (A_p), where $A_p = \pi \times D^2/4$ and D is the average plant diameter calculated from measurements of plant width at the longest axis and width perpendicular to that longest axis. Average absolute cover of each species was calculated by summing the cover of each species and dividing by the plot area. Relative cover of each species was calculated as the absolute cover per species divided by the total cover of all species.

Aboveground biomass of woody shrubs was estimated from shrub A_p using regression equations that were developed for a variety of chaparral shrub species (Vourlitis and Pasquini 2009). In addition, shoot samples were collected from all measured shrubs on 1 February, 2016 for C and N analysis (described in section 2.3.).

Aboveground biomass of herbaceous annual and perennial plants was measured on 1 February and 18 April, 2016 in the control and seeded plots. For herbaceous biomass the aboveground portion of each plant rooted within a 0.5 x 0.5m (0.25 m²) quadrat that was randomly located within each 12.56 m² plot was clipped at ground level, dried at 72°C for 1 week, and weighed using a digital balance.

Root biomass in the upper 0-10 cm soil layer was quantified from PVC soil cores obtained on 1 February, 2016. Root fragments > 2 mm were removed from the soil cores using a sieve, washed with DI water, dried at 72°C for a period of 1 week, and weighed using a digital balance.

2.3. Laboratory analyses

Soil samples were passed through a 2 mm mesh sieve to remove roots and other debris. After sieving, 10 g of the fresh soil sample was extracted in 40 ml of 0.5M K₂SO₄ to quantify soil extractable NH₄ and NO₃. Extractable N was measured using automated Flow Injection Analysis (FIA) (Quikchem 3000, Lachat Instruments, Milwaukee, WI, USA). Another portion of the soil sample was dried at 105°C until constant weight. Gravimetric soil moisture (θ) was calculated as the difference in fresh and oven-dry soil mass divided by the dry soil mass.

Oven-dried aboveground woody, herbaceous, and root biomass samples collected from each plot on 1 February were ground to a fine powder using a ball mill (MM200, Retsch, Düsseldorf, Germany), and analyzed for total N and C using dry combustion (ECS 4010,

Costech Analytical Technologies, Inc., Valencia, CA, USA). Aboveground N pool sizes for woody, herbaceous, and total (woody + herbaceous) vegetation components were calculated by multiplying the biomass standing crop of each component by its corresponding N concentration. Similarly, root biomass N pool size for each plot was calculated by multiplying the root mass per unit area by N concentration.

Microbial biomass was assessed using the chloroform fumigation and extraction method (Brookes et al. 1985). Soil samples were exposed to chloroform for a period of 5 days and extracted with 0.5M K₂SO₄ after incubation. Non-fumigated samples were also incubated in a chloroform-free environment and extracted with K₂SO₄ after incubation. Fumigated and non-fumigated extracts were analyzed for dissolved C using a modified version of the Walkley-Black method (Sims and Haby 1971), and absorbance was measured at 600 nm using a spectrophotometer (Lambda 20, Perkin-Elmer Ltd., Buckinghamshire, UK). The difference in absorption between the fumigated and un-fumigated samples was taken as the microbial C content based on a standard curve generated from glucose (Brookes et al. 1985).

2.4. Net N mineralization

Net N mineralization was assessed from a 37 day laboratory incubation experiment that was performed using soil samples acquired on 28 September, 2015 from unburned and burned plots. A portion of the fresh soil obtained from the upper 10 cm soil layer in each plot per site (n=10 plots/site) was combined and mixed to yield 1 composite soil sample from each site. Twenty grams (fresh weight) of the composite soil sample was weighed into a sterile microcosms (90 ml urine specimen cups, Thermo Scientific, Inc., Waltham, MA, USA), for a total of 18 microcosms per site. Soil moisture was adjusted to 15% by weight by adding DI water, and microcosms were incubated in the dark at a constant temperature of 25°C. Soil water content

was maintained by periodically weighing each microcosm and adding DI water as needed to bring each microcosm back to its initial weight. Extractable N (NH_4^+ and NO_3^-) was measured as described above (section 2.3.) on 3 randomly sampled microcosms per site beginning on the day that the soil water content was adjusted to 15% and continuing on approximately weekly intervals over the 37 d incubation.

2.5. Statistical analysis

Differences in woody, herbaceous, and total (woody + herbaceous) aboveground biomass between burned sites (seeded and control) were analyzed using a repeated-measures ANOVA (RM-ANOVA), with site and time as fixed effects. Differences in absolute plant cover between burned sites and post-fire regeneration pattern (resprouting or re-seeding) were also analyzed using RM-ANOVA with site, regeneration, and time as fixed effects. Post-fire regeneration pattern was defined from personal observations and from descriptions by Wells (1969) and Keeley (2000; 2006). Box's M and Mauchly's tests were used to test the assumptions of equality and compound-symmetry (sphericity), respectively ($p \leq 0.10$) of the between-group covariance matrices, and probability values were calculated using the Geisser-Greenhouse corrections for data that violated these assumptions (Hintze, 2004).

Variations in absolute and relative cover as a function of plant functional group (woody shrubs, herbaceous perennials, annual forbs, and grasses) and site (control and seeded) were analyzed using a 2-way ANOVA with plant functional group and site as fixed effects. Rates of change in absolute cover as a function of post-fire regeneration (resprouting or re-seeding) and site (control and seeded) were analyzed using a 2-way ANOVA with regeneration and site as fixed effects. Variations in plant species richness, aboveground biomass increment, and biomass N concentrations and pools between the control and seeded stands were analyzed using two-

sample *t*-test. Data were checked for normality and homogeneity of variances, and data violating these assumptions were LN-transformed as indicated. Analyses were conducted using NCSS statistical software (Version 7, NCSS, LLC, Kaysville, UT, USA).

Sampling multiple sites over a variety of sampling dates resulted in an unbalanced design for many of the soil variables including extractable NH₄ and NO₃, microbial C, soil water content, and net mineralization rate. In these cases, mean $\pm$ 95% confidence intervals (95% CI) were calculated by bootstrapping over 1000 iterations, and means were considered to be significantly different if confidence intervals did not overlap.

3. Results

3.1. Precipitation patterns

Precipitation data was not available on site, so data was obtained from the Western Regional Climate Center (<http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?caCSPQ>) for San Pasqual, CA located approximately 16 km ESE of the CSUSM study area. The “Cocos” fire occurred during a year when annual precipitation (209 mm) was 60% of the long-term (30 year) average (365 mm) for the San Marcos-Escondido, CA region (Fig. 2). Precipitation increased to 104 mm in December of 2014, which is when the hydroseeded slope was treated. More than half of the annual rainfall occurred during the months of December and January, while rainfall for the other months was < 50 mm (Fig. 2). Precipitation totals for 2015 and 2016 were 252 and 345 mm, respectively, which were 71 and 97% of the long term average, respectively, indicating that the first two years of post-fire recovery were relatively dry years.

3.2. Effects of post-fire management on vegetation recovery

Pre-fire vegetation abundance was not measured; however, measurements made in April 2015 (11 months post-fire) indicate that the density of resprouted shrubs was not significantly different

(2-tailed $t_{18} = 0.91$; $p = 0.38$) between the naturally regenerating (control) and hydroseeded (seeded) slopes (mean $\pm$ se; $n = 10$ plots; $= 0.42\pm0.23$ and 0.18 ± 0.14 shrubs/m² for the control and seeded slopes, respectively). Areal images (Fig. 1) also indicate complete canopy cover before fire on both slopes (Fig. 1), and personal observations suggest that vegetation in the unburned, control, and seeded stands was similar before fire. Both stands were be completely denuded of vegetation immediately after fire in May 2014, and areal images suggest that vegetation regeneration was qualitative similar in the control and seeded slopes over time (Fig. 1).

A total of 24 plant species were observed on the burned slopes during the study period (Table 1). According to personal observations and published descriptions of species growth habit and regeneration patterns, 50% (12) of all plant species were shrubs or sub-shrubs, 21% (5) were herbaceous perennials, 21% (5) were annual forbs, and 8% (2) species were grasses (Table 1). Most of the plant species (19, or 79%) regenerated primarily from seeds while the rest (6) regenerated primarily by resprouting after fire. More than half of the plant species (13) were found on both the control and seeded slopes, while 4 were only found on the control slope and 7 were only found on the seeded slope (Table 1). Of the plant species unique to the seeded slope, 6 were part of the hydroseed mix, while the other two (*Nicotiana glauca* and *Salsola turgus*) are exotic weedy species.

Vegetation cover varied significantly as a function of vegetation type and post-fire management after nearly 1 year of post-fire recovery, and there was a significant group x stand interaction (Table 2). The control stand had significantly higher herbaceous perennial and woody shrub cover, while the seeded stand had the highest grass cover (Table 2). Because of the high grass cover, the seeded stand also had significantly higher total vegetation cover than the control stand. Woody shrubs and herbaceous perennials comprised approximately 77% of the

combined relative cover of all vegetation types in the control stand but < 2% of the combined relative cover of the seeded stand (Table 2). In contrast, grasses made up over 97% of the relative vegetative abundance on the seeded stand but < 6% in the control stand. Woody shrub species richness was > 6-times higher in the control stand than in the seeded stand (Table 2). Differences in total species richness were smaller, but total species richness in the control stand was still 2-times higher than in the seeded stand (Table 2).

Shrub cover was separated by species post-fire regeneration pattern (resprouting vs. seeding; see Table 1) to see if shrub recovery in the control and seeded slopes was influenced by regeneration pattern. Absolute cover varied significantly as a function of slope (control vs. seeded) and time and there was a significant slope x time interaction (Fig. 3). However, regeneration (seeders vs. resprouts) did not significantly effect cover nor were there significant interactions between regeneration, slope, or time. The control slope had significantly higher cover of resprouting and reseeding shrubs than the hydroseeded slope in April 2015 and April 2016, but not in February 2015, which probably accounts for the significant slope x time interaction (Fig. 3). The rate of increase in absolute cover over time was also significantly higher in the control stand, but there was no difference between resprouting or seeding shrubs nor was there a statistically significant stand x regeneration interaction (Fig. 4).

Aboveground woody biomass varied significantly between stands and over time (Fig. 5a). Both stands exhibited an increase in aboveground woody biomass over time, but the biggest increase was observed in the control stand during the 2016 wet season. The control stand had nearly 8-times more aboveground woody biomass than the seeded stand in April 2015, but by February 2016, this difference declined to only 2-fold. However, by April 2016 the control slope had nearly 3-times the aboveground woody biomass than the seeded stand (Fig. 5a). In contrast,

herbaceous biomass during the 2016 wet season was significantly higher in the seeded stand than in the control stand (Fig. 5b). The higher woody biomass in the control stand was compensated by the higher herbaceous biomass observed in the seeded stand, causing differences in the total aboveground (woody + herbaceous) standing crop between the seeded and control stands to be negligible (Fig. 5c). Both stands exhibited significant increases in woody, herbaceous, and total aboveground biomass over time (Fig. 5a-c); however, only the aboveground woody biomass increment was significantly different between the control and seeded stands (Fig. 6).

Root biomass sampled on 1 February, 2016 varied significantly (2-tailed $t_{18} = -2.77$; $p < 0.05$) between control and seeded plots. Seeded plots had ca. 2.5 times higher root density than control plots (mean $\pm$ se; $n = 10$ plots; 51.3 ± 13.3 and 132.3 ± 26.0 g/m² for control and seeded plots, respectively).

Herbaceous vegetation in seeded plots had a significantly higher tissue N concentration than control plots in February 2016 (Table 3). The higher tissue N concentration, combined with a higher herbaceous standing crop (Fig. 5b), led to a higher aboveground herbaceous N pool size as well (Table 3). N pool size of woody shrubs was significantly higher in control plots even though differences in woody N concentration between control and seeded plots were negligible (Table 3). As with standing crop, the higher woody N pool of the control stand was compensated by a higher herbaceous N pool in the seeded stand causing total (woody + herbaceous) N pools to be similar in the control and seeded stands (Table 3). Root tissue N concentration was slightly higher ($p < 0.10$) in the seeded than control stands; however, because of the higher root biomass, seeded plots had a higher root N pool than control plots (Table 3).

3.3. Soil extractable N, net N mineralization, and microbial C

Soil water content was similar for all stands (Fig. 7a). The unburned chaparral stand had significantly lower extractable NH_4^+ (Fig. 7b) than the burned stands; however, differences in extractable NH_4^+ between the burned stands were not statistically significant. The control stand had significantly higher extractable NO_3^- than the seeded stand; however, the unburned stand had similar extractable NO_3^- to both burned stands in September 2015 (Fig. 7c).

Laboratory soil incubations indicated net consumption of NH_4 for both burned stands and no statistically significant change for the unburned stand over the 37 day laboratory incubation, and net NH_4 consumption was significantly higher for the control stand than the seeded stand (Fig. 8a). All soils accumulated NO_3 over the 37 day laboratory incubation, and net nitrification rates were significantly higher for the burned stands than the unburned stand, but differences between the control and the seeded stands were not statistically significant (Fig. 8b). All soils exhibited a net increase in total N mineralized ($\text{NH}_4 + \text{NO}_3$) over the laboratory incubation but there were no statistically significant differences between burned and unburned stands (Fig. 8c).

Microbial C was similar in each stand in September 2015 and ranged between 28-59 $\mu\text{gC/g}$ dry soil); however, in February 2016 microbial C increased significantly in the seeded stand and was >4-times higher than in September 2015 (Fig. 9). Microbial C also increased in the control stand in February but the increase was not significantly different from values obtained in September.

4. Discussion

4.1. Effects of post-fire management on vegetation recovery

Our results support the hypothesis that hydroseeding inhibits the recovery of native woody shrubs after almost two years of post-fire stand recovery. While total aboveground biomass stranding crop was not significantly different between control and seeded areas, woody shrub

biomass, cover of resprouting and reseeding vegetation, rates of increase in shrub cover and biomass, and plant species richness were significantly lower in the seeded area. While long-term trends in vegetation recovery are unknown, if these trends persist, our data suggests a possible ecosystem type conversion from a dense, diverse chaparral shrubland to a more open, species-poor grass-dominated ecosystem.

While this study had a limited spatial and temporal scale, our results, together with others, indicate that hydroseeding may have long-term implications to post-fire ecosystem recovery and plant species composition. Hydroseeding was effective at increasing total plant cover; however, nearly all (ca. 98%) of the cover of the seeded stand was dominated by an annual grass (*Festuca microstachys*), which did not exist in the control stand. While *F. microstachys* is a native grass, fast-growing annual grasses have been shown to reduce post-fire recovery of native perennial forbs and suffrutescent and woody shrubs because of high rates of seed production and effective competition for water and/or nutrients (Elliot and White 1987; Keeler-Wolf 1995; Keeley 2004). In particular, there is evidence that hydroseeding reduced available N (described below), and given the fact that post-fire recovery occurred during a record drought in southern California, it is also possible that competition for soil moisture was intense. If this type conversion persists, post-fire seeding with annual grasses may have important consequences for the future chaparral fire regime (Zedler et al. 1983).

4.2. Effects of post-fire management on N cycling and microbial C

The burned sites had significantly higher extractable NH_4 than the unburned stand after 1 year of post-fire recovery, which is consistent with results reported for other semi-arid shrublands and woodlands (Stock and Lewis 1986; Vourlitis and Pasquini 2008; Hanan et al. 2016), and is attributed to an abundance of NH_4 -rich ash and a reduction in plant uptake (Carreira et al. 1994;

Neary et al. 1999; Knicker 2007). However, post-fire increases in NH_4 are often gone after ca. 1 year as nitrification, plant uptake and losses consume the initial pulse of NH_4 (Carreira et al. 1994; Neary et al. 1999; Hanan et al. 2016). Thus, it is striking to see such high levels of extractable N in these burned stands after nearly 2 years of post-fire recovery, which is presumably due to copious amounts of ash still present and the relatively low amount of biomass cover. In contrast, extractable NO_3 concentrations were more similar in burned and unburned sites even though the burned stands had consistently higher rates of nitrification than the unburned stand. Presumably, the burned stands lost more NO_3 from leaching and/or gaseous efflux (Riggan et al. 1994; Meixner et al. 2006; Vourlitis and Hentz 2016), thus reducing concentrations of soil extractable NO_3 .

Our data support the hypothesis that NO_3 (but not NH_4) was lower in hydroseeded stand than in the naturally recovering stand. The significantly higher herbaceous and root N pool sizes for the seeded stand suggests that the lower extractable NO_3 concentration in the seeded stand was due in part to higher plant N uptake (Dickens and Allen 2014). Thus, hydroseeding appeared to be effective at increasing ecosystem N retention in this post-fire chaparral stand.

Finally, we hypothesized that higher herbaceous biomass in hydroseeded areas would increase microbial biomass and N immobilization because microbial N activity in chaparral soils is C limited (Jenerette and Chatterjee 2012; Vourlitis and Fernandez 2015). In our laboratory incubation, the fixed pool of NH_4 was consumed in all stands, and the relative amount of consumption was closely related to the initial stand NH_4 pool. In turn, the relative differences in nitrification reflected the differences in NH_4 consumption; however, nitrification rates in the control and seeded stands were not significantly different. Thus, fire stimulated rates of nitrification, a result that has been observed from other chaparral stands during the initial stages

of post-fire recovery (Carreira et al. 1994; Neary et al. 1999; Hanan et al. 2016), but hydroseeding did not appear to significantly affect nitrification rate.

These mineralization dynamics were unrelated to the soil microbial biomass C during the time that the soil samples for the laboratory incubation were obtained, suggesting that net ammonification and nitrification were driven more by existing available N pools and not by differences in microbial population size. Soil microbial C was generally low (ca. 25-65 $\mu\text{gC g dry soil}^{-1}$) in September 2015, and was similar for the burned and unburned stands. The similarity between the burned and unburned stands is in contrast to Hanan et al. (2016) who reported a large decline in chaparral soil microbial C after fire. However, soil microorganism responses to fire can vary substantially due to fire intensity, ash content, and the rate of vegetation recovery (Knicker 2007; Fonturbel et al., 2012).

Microbial C increased in the spring (February 2016) but only significantly in the seeded plot, which presumably reflects an increase in C availability from the higher herbaceous and/or root biomass associated with the seeded stand and/or an increase in C quality (Dickens and Allen 2014). Root C:N ratios were significantly lower in the seeded plots than in the control plots (mean $\pm$ se; $n = 10$; 26.2 ± 1.5 and 36.5 ± 2.3 for the seeded and control stands, respectively, 2-tailed $t_{18} = 3.75$; $p < 0.01$). Similarly, vegetation C:N ratios calculated as a weighted average of both woody and herbaceous vegetation were on average 29.6 ± 2.2 and 17.8 ± 1.9 for the control and seeded stands, respectively (2-tailed $t_{18} = 4.15$; $p < 0.001$). These data suggest a potentially higher proportion of labile C in the seeded plots, which should stimulate microbial growth and/or activity (Gallardo and Schlesinger 1995; Jenerette and Chatterjee 2012), and presumably microbial N immobilization (Goodale et al. 2005; Vourlitis and Fernandez 2015; Dickens and Allen 2014).

Conclusions

Our data indicate that hydroseeding significantly increased ecosystem N storage during the initial stages of post-fire succession but at the expense of native shrub regeneration and species richness. The increase in ecosystem N retention will likely result in a decline in NO₃ export to downstream water bodies that often occurs during the immediate stages of chaparral post-fire succession. However, if the trajectory of grass-dominance and slow shrub recovery continues, the hydroseeding treatment used here may result in a vegetation type conversion from a shrub- to a grass-dominated system. An increase in annual grass dominance has the potential to increase fire frequency (Zedler et al. 1983) such that native shrubs may not be able to regenerate following fire (Keeley and Brennen 2012). Such a type conversion could have significant implications for chaparral plant species diversity.

If hydroseeding has such potentially large consequences to native vegetation regeneration, what options are available to land managers that are concerned with high soil erosion and nutrient losses following intense fires? While not evaluated here, organic mulching may fulfill many of the same anti-erosion and nutrient retention goals of seeding without altering natural post-fire regrowth. For example, Zink and Allen (1998) found that organic mulch applied during coastal sage scrub restoration increased microbial N immobilization and survival rates of replanted native shrubs. Hubbert et al. (2012) reported that mulching accelerated the post-fire regrowth of chaparral shrubs and forbs and reduced post-fire erosion during the first 4 months of stand recovery. Thus, organic mulching may represent an alternative to short-term erosion control and nutrient retention for post-fire chaparral stands when such management interventions are warranted. However, natural regeneration is likely to be a better alternative in areas not susceptible to erosion.

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414 **Acknowledgements**

415 This research was supported in part by California State University San Marcos (CSUSM) and the
416 USDA-NIFA-HSI (2010-38422-21241) program. Permission to conduct field sampling on
417 university property, and use of graduate and undergraduate instructional labs, was graciously
418 granted from CSUSM. The authors thank students from G Vourlitis's BIOL 354; BIOL 390L,
419 and BIOL 386L courses for helping with the field data collection and laboratory analysis.
420 Special thanks to George Martinez of CSUSM Facilities Management and Rob McGann,
421 President, HydroPlant Hydroseeding, Inc., for providing information on the hydroseed mix.

422

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Figure captions

- Fig. 1.** Google Earth images of the north-facing burned slope showing the approximate locations of the naturally regenerating (control) and hydroseeded sites (a) before fire in May 2014, (b) 7 months post-fire in December 2014, and (c) 22 months post-fire in March 2016. The scale in the bottom right-hand corner of each image depicts 100 feet (30.5 m). The unburned stand is located approximately 500 m NNW of the burned sites and is not visible on the images. Images accessed on January 25, 2017 using Google Earth Pro (Version 7.1.5.1557).
- Fig. 2.** Monthly rainfall totals for San Pasqual, CA located approximately 16 km ESE of the CSUSM study area showing the month of the Cocos fire (May 2014), the month when seed

was applied to the hydroseeded slope (hydroseeding), and the study period for the vegetation and soil analyses described here (grey shaded region). Rainfall data are from the Western Regional Climate Center (<http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?caCSPQ>), accessed January 20, 2017.

Fig. 3. Mean ($\pm$ se; n = 10) absolute cover for shrubs that primarily regenerate from fire by resprouting or reseeding (see Table 1) in the naturally regenerating (control) and hydroseeded burned chaparral sites in April 2015 (open bars), February 2016 (light-grey bars), and April 2016 (dark-grey bars). Also shown are the results (F-statistic, factor and error degrees of freedom) of a repeated-measures ANOVA with site (S), regeneration (R), time (T), and their interactions. Only significant ($p < 0.05$) direct effects or interactions are displayed $^{*}(p<0.05)$, $^{**}(p<0.01)$, $^{***}(p<0.001)$.

Fig. 4. Mean ($\pm$ se; n = 10) rate of increase in absolute cover between April 2015 and April 2016 for shrubs that primarily regenerate from fire by resprouting or reseeding (see Table 1) in the naturally regenerating (control) and hydroseeded burned chaparral stands. Also shown are the results (F-statistic, factor and error degrees of freedom) of a 2-way ANOVA with slope (S), regeneration (R), and their interaction (SxR). $^{*}(p<0.05)$.

Fig. 5. Mean ($\pm$ se; n = 10) aboveground woody (a), herbaceous (b), and total (herbaceous + woody) biomass (c) for naturally regenerating (control) and hydroseeded burned chaparral stands in April 2015 (open bars), February 2016 (light-grey bars), and April 2016 (dark-grey bars). Also shown are the results (F-statistic, factor and error degrees of freedom) of a repeated-measures ANOVA with slope (S), time (T), and their interaction (SxT). $^{*}(p<0.05)$, $^{**}(p<0.01)$, $^{***}(p<0.001)$.

Fig. 6. Mean ($\pm$ se; $n = 10$) aboveground woody biomass growth rate for naturally regenerating (control) and hydroseeded burned chaparral stands calculated between February and April 2016. Also shown is the result of a 2-tailed t-test (t-statistic and degrees of freedom). $*(p < 0.05)$.

Fig. 7. Mean ($\pm$ 95% confidence interval) gravimetric soil moisture (a) and extractable NH_4 (b) and NO_3 (c) for the surface 0-10 cm soil layer in unburned and burned slopes chaparral slopes that were naturally regenerating (control) and hydroseeded in September 2015 (open bars) and February 2015 (grey bars). Confidence intervals were calculated using bootstrap randomization techniques (see section 2.5). Means with confidence intervals that do not overlap are significantly ($p < 0.05$) different from each other.

Fig. 8. Mean ($\pm$ 95% confidence interval) net ammonification (a), nitrification (b), and total ($\text{NH}_4 + \text{NO}_3$) N mineralization (c) rates measured over a 37-day laboratory incubation experiment for surface (0-10 cm) soil collected from unburned and burned slopes chaparral slopes that were naturally regenerating (control) and hydroseeded in September 2015. Confidence intervals were calculated using bootstrap randomization techniques (see section 2.5). Means with confidence intervals that do not overlap are significantly ($p < 0.05$) different from each other.

Fig. 9. Mean ($\pm$ 95% confidence interval) microbial carbon concentration in the surface 0-10 cm soil layer of unburned and burned slopes chaparral slopes that were naturally regenerating (control) and hydroseeded in September 2015 (open bars) and February 2015 (grey bars). Confidence intervals were calculated using bootstrap randomization techniques (see section 2.5). Means with confidence intervals that do not overlap are significantly ($p < 0.05$) different from each other.

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Table 1. List of the observed species and their growth habit (AF = annual forb; G = grass; HP = herbaceous perennial; S = shrub, and WS = woody shrub), most common type of post-fire regeneration (S = seeding; RS = resprouting), and the location where the species was observed (C = control; H = hydroseeded). Growth habit and regeneration based on personal observation and Wells (1969), Keeley (2000), and Keeley (2006). Species names in bold font were part of the seed mix applied to the hydroseeded site.

Scientific name	Growth habit	Post-fire regeneration	Location observed
<i>Acmipson glaber</i>	HP	S	C/H
<i>Adenostoma fasciculatum</i>	WS	RS	C/H
<i>Artemisia californica</i>	WS	S	H
<i>Bromus carinatus</i>	G	S	H
<i>Cammissonia sp.</i>	AF	S	C/H
<i>Ceanothus sp.</i>	WS	S	C/H
<i>Dichelostemma capitatum</i>	HP	RS	C
<i>Eriodictyon sp.</i>	S	S	C/H
<i>Eriogonum fasciculatum</i>	WS	S	C/H
<i>Festuca microstachys</i>	G	S	H
<i>Gnaphalium sp.</i>	AF	S	C/H
<i>Helianthemum scoparium</i>	S	S	C/H
<i>Isocoma menziesii</i>	S	S	C/H
<i>Lupinus succulentus</i>	AF	S	H
<i>Malosma laurina</i>	WS	RS	C/H
<i>Marah macrocarpus</i>	HP	RS	C
<i>Mimulus aurantiacus</i>	HP	S	H
<i>Nicotiana glauca</i>	WS	S	H
<i>Phacelia grandiflora</i>	AF	S	C
<i>Rhus integrifolia</i>	WS	RS	C/H
<i>Salsola tragus</i>	AF	S	H
<i>Salvia apiana</i>	S	S	C/H
<i>Salvia mellifera</i>	WS	S	C/H
<i>Solanum xanthii</i>	HP	S	C

Table 2. Mean ($\pm$ se; $n = 10$) post-fire absolute and relative cover for woody shrub, herbaceous perennial, annual forb, and grass components, total absolute cover, and woody shrub and total plant species richness for the control and hydroseeded slope aspects on the CSU San Marcos campus on April 16, 2015. F -statistics for absolute and relative cover of vegetation types are from a 2-way ANOVA with slope (S) and vegetation type (V) as fixed-effects, while t -statistics for total absolute cover and total and woody shrub species richness are from a 2-sample t -test. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

$F(df)$	Component	Control	Hydroseeded
		Absolute cover (%)	
$F_S(1,72)=22.4***$	Woody shrub	4.0 $\pm$ 1.2	0.7 $\pm$ 0.5
$F_V(3,72)=10.3**$	Herbaceous perennial	10.0 $\pm$ 4.3	0.1 $\pm$ 0.1
$F_{S \times V}(3,72)=3.2***$	Annual forb	4.0 $\pm$ 2.1	0.1 $\pm$ 0.1
	Grass	0.4 $\pm$ 0.2	42.3 $\pm$ 6.0
$t_{18}=-2.8^*$	Total	18.3 $\pm$ 6.6	43.3 $\pm$ 6.1
Relative cover (%)			
$F_S(1,72)=27.3***$	Woody shrub	34.9 $\pm$ 7.1	1.3 $\pm$ 0.9
$F_V(1,72)=0.0$	Herbaceous perennial	42.0 $\pm$ 8.8	0.5 $\pm$ 0.3
$F_{S \times V}(1,72)=76.7***$	Annual forb	17.4 $\pm$ 7.5	0.3 $\pm$ 0.2
	Grass	5.6 $\pm$ 4.0	97.9 $\pm$ 1.0
Species richness (# species)			
$t_{18}=5.1***$	Woody shrub	2.7 $\pm$ 0.4	0.4 $\pm$ 0.2
$t_{18}=3.5**$	Total	7.3 $\pm$ 0.9	3.6 $\pm$ 0.5

Table 3. Mean ($\pm$ se; n = 10 plots) aboveground tissue nitrogen concentration and pool size for woody, herbaceous, root (0-10 cm soil layer) and total (woody + herbaceous) vegetation components in control and hydroseeded chaparral stands on the CSU San Marcos campus on February 1, 2016. T-statistics (t) were calculated from a 2-tailed t -test with 18 degrees of freedom. N pool size data for woody, herbaceous, and total components were LN-transformed to achieve normality and homogenous variance. † ($p < 0.10$); $*$ ($p < 0.05$); $**$ ($p < 0.01$); NA = not analyzed.

	N concentration (%)			N pool size (g/m ²)		
	Control	Hydroseed	t_{18}	Control	Hydroseed	t_{18}
Woody	1.61 $\pm$ 0.12	1.52 $\pm$ 0.16	0.45	0.45 $\pm$ 0.16	0.17 $\pm$ 0.06	2.67*
Herbaceous	2.37 $\pm$ 0.33	3.29 $\pm$ 0.33	-3.30**	0.45 $\pm$ 0.20	1.34 $\pm$ 0.47	-2.43*
Root	1.14 $\pm$ 0.04	1.31 $\pm$ 0.08	-2.00 †	0.59 $\pm$ 0.16	1.78 $\pm$ 0.42	-2.63*
Total	NA	NA	NA	0.90 $\pm$ 0.30	1.51 $\pm$ 0.45	-1.35