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Carbon and nitrogen storage in California sage scrub and non-native grassland habitats

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ABSTRACT

Human activity has altered global carbon and nitrogen cycles, leading to changes in global temperatures and plant communities. Because atmospheric carbon (C) and nitrogen (N) concentrations are affected by storage in terrestrial vegetation and soil, it is critical to understand how conversions from native to non-native vegetation may alter the C and N storage potential of terrestrial landscapes. In this study, we compared C and N storage in native California sage scrub, non-native grassland, and recovering California sage scrub habitats in the spring and fall by determining the C and N content in aboveground biomass, litter, and surface soil. Significantly more C and N were stored in intact and recovering California sage scrub than in grassland habitats. Intact and recovering sage scrub did not differ significantly in C or N storage. Our results highlight that preserving and restoring California sage scrub habitat not only provides habitat for native biodiversity, but also increases carbon and nitrogen storage potential even without restoration to intact sage scrub.

1. Introduction

Carbon dioxide and N_2O concentrations are increasing in the atmosphere, leading to increases in global temperatures and changes in the hydrological cycle (Ciais et al., 2013). Terrestrial vegetation is a volatile carbon and nitrogen sink which is heavily influenced by human activity through habitat conversions including the introduction of non-native species and alteration of vegetation (Aber and Melillo, 2001). The impacts of these changes on nutrient storage cannot be well explained without first determining how different terrestrial habitat types store carbon (C) and nitrogen (N). As such, studies that examine storage in different habitats are critical to our understanding of global C and N cycling and how habitat modifications influence storage (Bradley et al., 2006; Hobbs and Mooney, 1986; Jackson et al., 2002; Knapp et al., 2008; Wolkovich et al., 2010).

The California sage scrub ecosystem (hereafter sage scrub) is native to areas of Southern and Baja California on lower elevation hillslopes (Rundel, 2007). It is characterized primarily by drought-deciduous shrubs such as *Artemisia californica* Less. (coastal sagebrush), with a few evergreen shrubs in some stands (Mooney, 1977; Rundel and Gustafson, 2005). The drought deciduous species are largely dormant in the hot, dry summer months and resume growth in the winter and spring, following the rainy season (Mooney, 1977). The California sage scrub ecosystem is listed as endangered (85–98% lost) by the USGS (Noss et al., 1995), and as critically endangered by the World Wildlife Fund (Olson et al., 2015). More than thirty years ago, Westman (1981) estimated that the then extant stands of sage scrub reflected less than 10% of their original distribution. Replacement by non-native species following disturbances (primarily fire and high levels of N deposition) and human development currently threaten remaining sage scrub (Cox et al., 2014; Mooney, 1977; Riordan and Rundel, 2014).

In Southern California, much of the remaining native sage scrub habitat has been replaced or invaded by non-native grass species (Cox et al., 2014; Jackson et al., 2002; Wolkovich et al., 2010). Grass-dominated communities differ in structure from native sage scrub, which likely affects their nutrient storage potential. While sage scrub contains woody shrubs, non-native grasslands in Southern California are primarily composed of introduced European annual

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grasses, which affect the above and belowground biomass as well as the litter composition in these communities (Schlesinger, 1997). For example, woody litter takes significantly longer than leafy litter to decompose and to release stored nutrients back into the soil and atmosphere (Aber and Melillo, 2001). Additionally, vegetation functional type has been found to significantly influence soil C concentration, including surface soil horizons as well as deeper horizons where C is less likely to be quickly released into the atmosphere (Jobbágy and Jackson, 2000).

While the C storage profile for sage scrub has been measured (Gray and Schlesinger, 1981), the differences in C storage between sage scrub and non-native grasslands are not yet well quantified and are sometimes contrary to expectations. There have been studies both of shrubs invading grasslands (Hobbs and Mooney, 1986; Jackson et al., 2002; Knapp et al., 2008) and of grasses invading shrublands (Bradley et al., 2006; Wolkovich et al., 2010), which present conflicting interpretations of the effects of changing from one habitat type to the other on C storage. Two recent studies on C storage in California shrubland and grassland habitats are contradictory, with Wolkovich et al. (2010) finding increased storage in coastal sage scrub systems invaded by grasses and Bradley et al. (2006) finding decreased storage in cheatgrass-invaded native California shrublands. Due to the inevitable complexity of nature and differences in study priorities, many studies on grass versus shrub dynamics contain confounding factors such as fire (Bradley et al., 2006), limited consideration of plant species (Wolkovich et al., 2010), and short establishment of habitat types (Knapp et al., 2008), which make it difficult to compare true C storage differences between sage scrub and type-converted grassland habitats.

While several studies have investigated differences in C storage between these habitat types, N storage in sage scrub and type-converted grassland has been less thoroughly researched. Type conversion is likely to influence N storage, but interactions between high N deposition and conversion make storage predictions difficult. High rates of N deposition often facilitate conversion of sage scrub to non-native grassland and slow the recovery of shrubs after fire or invasion (Cox et al., 2014; Fenn et al., 2003; Kimball et al., 2014), and California shrublands experience rates of N dry deposition as high as 29 kg N ha^{-1} y^{-1} (Bytnerowicz and Fenn, 1996). High N has also been shown to reduce plant species richness and promote non-native species over natives in shrublands and grasslands (Clark and Tilman, 2008; Huenneke et al., 1990; Kimball et al., 2014). While increased N addition can also increase primary production, it is unclear how changes in plant diversity and functional types associated with high N deposition may interact with increased primary productivity to influence N storage potential in these habitat types in Southern California. Determining current N storage potential of Southern California shrubland and grassland systems would provide estimates of N storage in different habitat types against which to measure future change and monitor the N saturation of these systems.

Here we report on a study to address a knowledge gap in the current understanding of C and N biogeochemical cycles in intact sage scrub, recovering sage scrub, and non-native grassland ecosystems, the three primary non-urban/suburban habitat types in the greater Los Angeles basin. We compared these habitats by measuring and modeling the amount of C and N stored in three major terrestrial components: aboveground biomass, litter, and soil. The fourth major component, belowground biomass, was excluded from this analysis due to difficulty of sampling or modeling C and N concentrations, particularly in the fall after the senescence and death of annual grasses. We hypothesized that intact sage scrub would store more C and N than non-native grassland, but due to the contradictory findings of previous studies, had no strong predictions about whether intact or recovering sage scrub would have higher C and N storage. The results of this comparison between habitat types are needed to evaluate how type conversion from sage scrub to non-native grassland impacts C and N storage and whether preserving or restoring native sage scrub habitat areas has a C and N storage benefit.

2. Materials and methods

2.1. Study system

This study was conducted at the Robert J. Bernard Biological Field Station (hereafter, field station) in Claremont, CA, on the eastern edge of Los Angeles County (Appendix A, Fig. A1). The climate in Claremont is xeric (Mediterranean) and has been specifically classified as the Intermediate Valley type, with average temperatures between 32 °C in the summer and 4 °C in the winter with most precipitation occurring in the winter (Bailey, 1966). There were three primary habitat types within the field station: intact sage scrub, non-native grassland, and a transitional habitat where sage scrub shrubs had begun to recolonize a non-native grassland area. Sage scrub habitat at the field station was defined by the dominance of shrub species including *Artemisia californica*, *Eriodictyon crassifolium* Benth. (thickleaf yerba santa), and *Eriogonum fasciculatum* Benth. (Eastern Mojave buckwheat). Other shrub species in the field station sage scrub habitat included *Salvia apiana* Jeps. (white sage), *Rhus integrifolia* (Nutt.) W.H. Brewer & S. Watson (lemonade sumac), *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (Pacific poison oak), *Lepidospartum squamatum* (A. Gray) A. Gray (California broomsage), *Ericameria pinifolia* (A. Gray) H.M. Hall (pinebush), *Malosma laurina* (Nutt.) Nutt. ex Abrams (laural sumac), *Sambucus nigra* L. (black elderberry), and *Ribes aureum* Pursh (golden current). The field station grassland habitat was by definition dominated by non-native annual *Bromus* spp. Also common in this grassland were patches of *Croton setigerus* Hook. (dove weed), which were more prevalent in the fall prior to the sprouting of the grasses. The transitional habitat contained plant species from both the sage scrub and grassland communities in roughly even proportions. As shown by aerial photographs and satellite imagery, none of the studied habitat areas had experienced a fire for at least 40 years previous to this study, and each had been established as the current habitat type for at least as long (Hamlett, 2012).

Soil morphology and taxonomy were described as part of this study following the protocols of Schoenenberger et al. (2002, 2012) and Soil Survey Staff (2014), using small, 1 m^3 test pits (see Appendix A for soil profile descriptions and laboratory characterization data). Soils were similar among the three communities sampled in this study and were best characterized as mixed, sandy-skeletal Humic Haploxerepts, which are simple, young, weakly developed soils with thin (~10–15 cm) surface horizons. Parent material consisted of alluvial sands and gravels derived from granitic and metamorphic rocks in the San Gabriel Mountains.

2.2. Sample collection and processing

To determine total carbon and nitrogen storage in these three habitats, we sampled aboveground biomass, litter, and soil in each habitat in the fall (Oct–Dec 2012), when plants were dormant, and again in the spring (Apr–May 2013), when new growth had emerged. In each of the three habitats, we computer-generated random points to select eight and six 2 × 2 m plots in the fall and spring respectively. Upon visiting the sites we intentionally avoided sites with trees, poison oak, and highly disturbed areas such as paths. Because we avoided trees such as *Sambucus nigra* in the sage scrub habitat, our estimations of aboveground biomass in sage scrub are thought to be conservative.

Three 0.1 m^2 area subplots located along the diagonal of the larger plots were used to sample herbaceous aboveground biomass, litter, and soil. In each subplot, any living non-shrub vegetation was cut at the base (mineral soil surface) and harvested. These aboveground biomass clipped samples included any grasses, herbaceous intershrub species, and small woody plants other than the main shrub species (see below). All remaining material in the litter layer (O horizon) was collected and sorted into woody and leafy litter. Aboveground biomass and litter samples were then dried at 50 °C for at least 48 h and weighed to determine biomass. The three leafy litter subsamples from each plot were homogenized and then analyzed with the aboveground biomass samples for total C and N content using an Elementar vario elemental analyzer (Elementar, Mt. Laurel, New Jersey). For the woody litter, we used a conservative estimate of 45% C content (Lamlom and Savidge, 2003).

Once litter was collected, two types of soil samples were taken from the top of the mineral soil surface (A horizon) in each subplot. First, an intact soil aggregate was collected to measure bulk density using the clod method (e.g., Burt, 2004, method 3a1), with IXAN PVDC copolymer resin (Chempoint, Inc.) instead of Dow Saran resin. Another soil sample (not necessarily aggregated) was taken from the top 10 cm of the A horizon for C and N analysis. These samples were refrigerated before processing, then sieved to remove large rocks and roots and analyzed for C and N using an Elementar vario elemental analyzer (Elementar, Mt. Laurel, New Jersey).

Aboveground shrub biomass was determined for each large plot using empirically derived linear models (e.g., Brown, 1976; Northup et al., 2005; Whittaker and Woodwell, 1968) created from shrub samples collected at the field station (Table 1; Appendix B). *Artemisia californica*, *Eriodictyon crassifolium*, and *Eriogonum fasciculatum*, the three main shrub species at the field station, were each modeled separately. Species branch models were used to predict masses for branches between 5 and 12 mm in basal diameter, and a separate model was used to determine the mass of branches with basal diameters greater than 12 mm (Appendix B). Midpoint diameter and branch length were measured for these larger branches, and their volume was then found by considering them as uniform cylinders. Models of branch mass for *A. californica* and *E. fasciculatum* included leaf and flower mass as well as wood mass because leaves for these species were very small and numerous. *Eriodictyon crassifolium* leaves were modeled separately from branch masses since leaves were larger and more robust.

All shrubs within each plot were measured and their biomass was calculated using the developed species models (Table 1). Shrubs with branches (>5 mm diameter) entering or leaving the plot were incorporated by measuring their diameter at the point of entrance as the basal diameter and either adding or subtracting a modeled branch of that diameter, depending on whether the branch originated from a shrub based inside or outside of the plot. Additionally, all living *E. crassifolium* leaf lengths within a plot were measured to estimate *E. crassifolium* leaf biomass.

Combined wood and leaf samples of *A. californica* and *E. fasciculatum* and leaf samples of *E. crassifolium* were collected, dried at 50 °C for at least 48 h, and analyzed for nutrient content. Again, conservative wood values of 45% C (Lamlom and Savidge, 2003) and 0.1% N (Northup et al., 2005) were used for cylinder branches and *E. crassifolium* branches.

2.3. Scaling

Carbon and N measurements of each type were scaled to give C and N per meter squared. All shrubs within a 2 × 2 m plot were measured and modeled, so shrub C and N content were divided by 4 to give mass per square meter. Measurements of non-shrub aboveground biomass, litter, and soil C and N from the three quadrats within each plot were averaged for each plot. These averages of C and N per 0.1 m^2 were then multiplied by 10 to give estimated C and N per square meter for each of these three components. Once each component was scaled to square meters, all four components were summed to give the total C and N.

2.4. Statistical analyses

All statistical analyses were conducted in R (v. 3.2.2, R Core Team, 2015). Differences between total, aboveground, soil, and litter C and N in the three habitat types and two seasons were tested for using generalized linear models with a Gamma distribution, as the data did not meet assumptions of normality and homogeneity of variance. Habitat type and season were included as fixed factors. Pairwise differences between treatments were tested using Dunn's test with a Bonferroni correction. This statistical method is conservative, which is in line with our conservative sampling approach.

3. Results

The three habitat types differed in total C (GLM; $F_{[5,36]} = 9.7$, $p < 0.0001$; Fig. 1) and total N (GLM; $F_{[5,36]} = 6.3$, $p = 0.0003$; Fig. 2). There was no significant difference between total C or N storage in spring and fall (GLM; C $F_{[5,36]} = 9.7$, $p = 0.4$; N $F_{[5,36]} = 6.3$, $p = 0.2$).

Total C storage was significantly higher in the sage scrub (Dunn's test; $z = 4.3$, $p < 0.0001$) and transitional (Dunn's test; $z = 3.7$, $p = 0.0003$) habitats than in the grassland. Averaged among plots and seasons, sage scrub stored 4.3 kg C m^{-2} and 228 g N m^{-2}, transitional habitat stored 4.1 kg C m^{-2} and 268 g N m^{-2}, and grassland stored 1.9 kg C m^{-2} and 128 g N m^{-2}. The sage scrub and transitional habitats did not differ significantly in their total C or N storage (Dunn's test; C $z = 0.5$, $p = 0.9$; N $z = 0.7$, $p = 0.7$). Total N storage was also significantly higher in sage scrub (Dunn's test; $z = 2.8$, $p = 0.008$) and transitional (Dunn's test; $z = 3.5$, $p = 0.0006$) than grassland (Fig. 2).

Aboveground and litter biomass differed markedly between communities (Fig. 3), driving some differences in C and N storage in these pools. Litter C was higher in sage scrub and in transitional areas than in grassland (Dunn's test; sage scrub $z = 5.2$, $p < 0.0001$; transitional $z = 3.1$, $p = 0.003$). Litter N was also higher in both of these communities than in the grassland (Dunn's test; sage scrub $z = 4.8$, $p < 0.0001$; transitional $z = 3.5$, $p = 0.0009$). Neither litter C nor litter N differed by season.

Table 1
Shrub branch and leaf models. W is weight in g, D is branch basal diameter in mm, V is cylindrical branch volume in cm^3, and L is leaf length in mm.

Species	Transformation	Intercept	Predictor	R^2
Artemisia californica	$W^{1/3}$	0.3 ± 0.1	(0.31 ± 0.01)*D	0.89
Eriodictyon crassifolium − branches	$W^{1/2}$	−1.7 ± 0.3	(0.55 ± 0.04)*D	0.91
Eriodictyon crassifolium − leaves	$W^{1/3}$	0.19 ± 0.03	(0.0057 ± 0.0003)*L	0.89
Eriogonum fasciculatum	W	−49 ± 6	(11 ± 1)*D	0.90
Cylinders	W	6 ± 1	(0.39 ± 0.01)*V	0.96

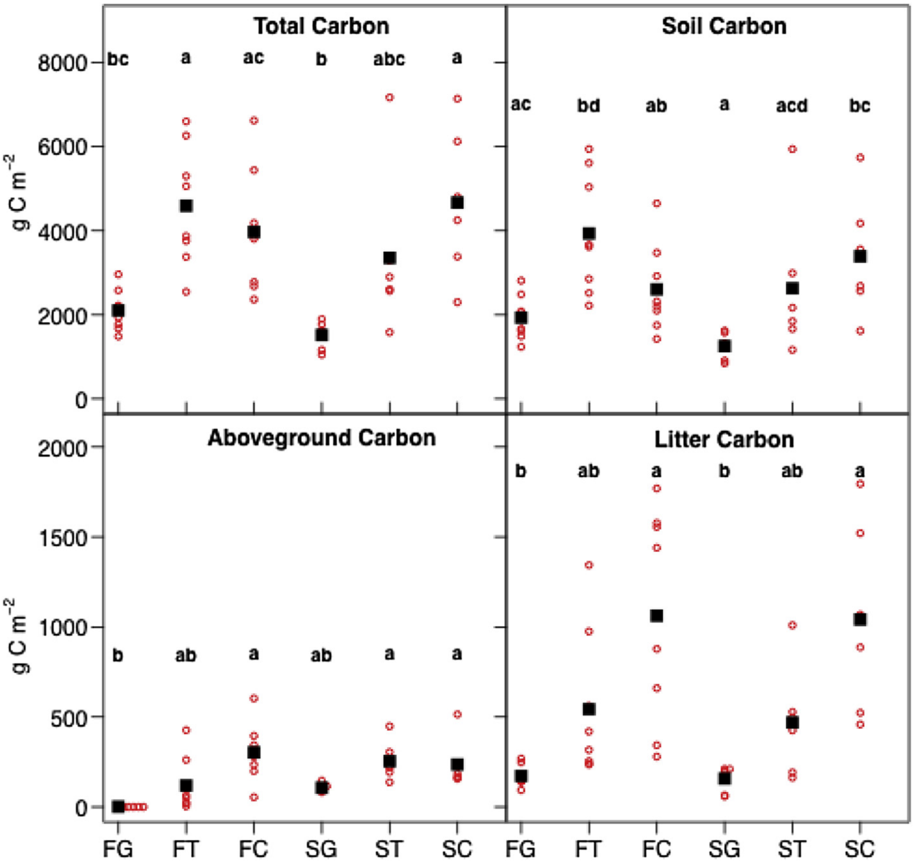

Fig. 1. Fall and spring total, soil, aboveground, and litter carbon in California sage scrub, grassland, and transitional habitats. Values for each plot are shown as open red circles with mean values shown as larger filled black squares. Where multiple plots had the same measurement, points are displayed side-by-side. Treatments marked with the same letter do not differ significantly ($\alpha = 0.05$). "FG" = fall grassland, "SG" = spring grassland, "FT" = fall transitional, "ST" = spring transitional, "FC" = fall sage scrub, and "SC" = spring sage scrub. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Very little living aboveground biomass was recorded in the grassland in the fall, resulting in significantly less C and N in fall grassland aboveground biomass than in fall sage scrub (Dunn's test; C $z = 4.5$, $p < 0.0001$; N $z = 4.1$, $p = 0.0004$), spring sage scrub (Dunn's test; C $z = 3.6$, $p = 0.003$; N $z = 4.1$, $p = 0.0003$), or spring transitional habitat (Dunn's test; C $z = 3.9$, $p = 0.0008$; N $z = 3.6$, $p = 0.002$). However, spring grassland aboveground C and N did not differ significantly from any of the other communities.

While there were differences in litter and aboveground C and N storage among communities, soil was by far the largest pool of C and N and thus had the greatest weight in determining overall storage. Mineral soils accounted for 54–96% of the C (mean: 79%) and 71–99% of the N (mean: 91%) stored in each plot (Fig. 4). In contrast, litter accounted for 4–37% of C (mean: 16%) and 1–27% of N (mean: 7%) and aboveground biomass accounted for only 0–17% of C (mean: 5%) and 0–8% of N (mean: 2%). There were relatively few significant differences between soil pools of C (Fig. 1) and N (Fig. 2). The fall transitional soil stored significantly more C than the fall grassland (Dunn's test; C $z = 2.8$, $p = 0.03$) or spring grassland (Dunn's test; $z = 4.1$, $p = 0.0003$) and more N than the spring grassland (Dunn's test; $z = 3.9$, $p = 0.0007$). Sage scrub stored more C than grassland in the spring (Dunn's test; $z = 3.2$, $p = 0.009$).

4. Discussion

Total C storage was higher in transitional and sage scrub habitats than in non-native grasslands, and did not differ between transitional and intact sage scrub. This corroborates the findings of Bradley et al. (2006) that shrub communities store more C than grassland communities. However, sage scrub and transitional habitats did not differ in C storage, contrary to the findings of Wolkovich et al. (2010). Non-native grasslands stored less C than sage scrub habitats in our study, suggesting that while partial invasion of sage scrub by grasses may increase C storage, type conversion of sage scrub to a non-native grassland may lead to a decline in C storage.

Following a trend similar to C, N was higher in the transitional and sage scrub habitats than in the non-native grasslands. Our results in the transitional habitat are consistent with previously demonstrated increases in soil N caused by non-native grass invasion of sage scrub (Wolkovich et al., 2010). However, our research indicates that type conversion to grassland will lead to declines in N storage. Soil and vegetation perform a key ecosystem service of storing N and preventing it from leaching into groundwater (e.g., Brady and Weil, 2008), but high N deposition may lead to increased type-conversion to grassland and subsequent declines in N storage. Fertilization by dry deposition of N can range from 0.5 to 29 kg ha^{-1} y^{-1} in California (Bytnerowicz and Fenn, 1996) and has been shown to significantly increase the probability of type conversion of sage scrub to non-native grasslands (Cox et al., 2014). Greater availability of N favors non-native grass species, particularly through competition following a disturbance like fire (Goldstein and Suding, 2014; Kimball et al., 2014), which could ultimately lead to a decrease in N storage following conversion to grassland. Additionally, lower and potentially more transient storage of N in aboveground biomass and litter in grasslands than in

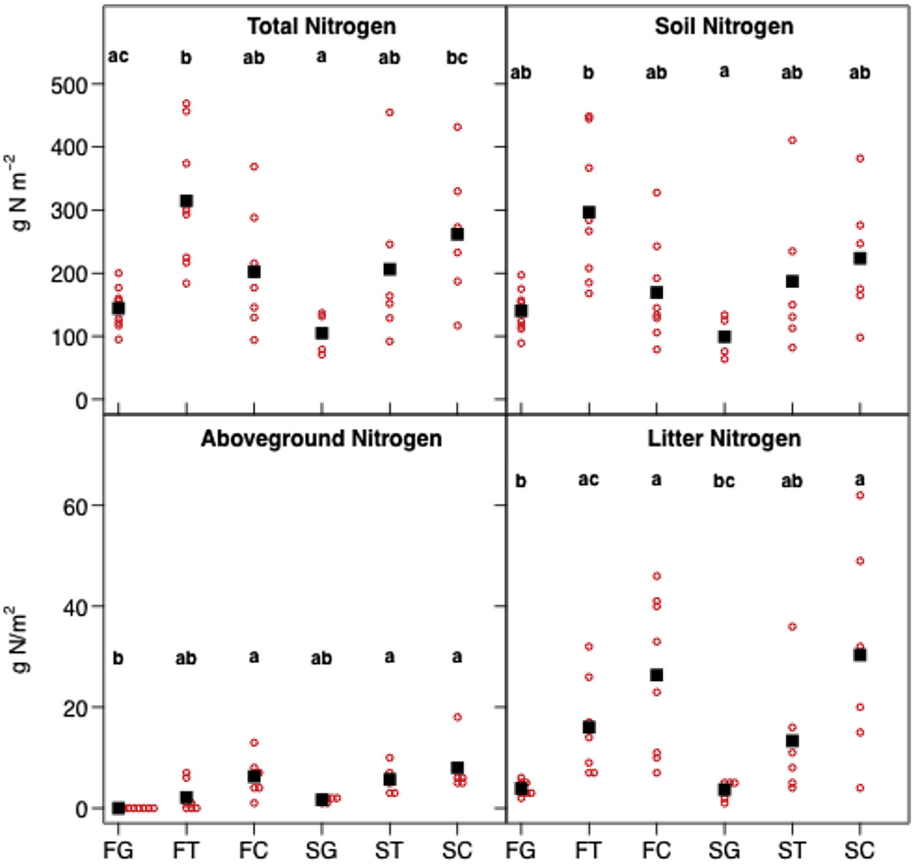

Fig. 2. Fall and spring total, soil, aboveground, and litter nitrogen in California sage scrub, grassland, and transitional habitats. Values for each plot are shown as open red circles with mean values shown as larger filled black squares. Where more than one plot had the same measurement, points are displayed side-by-side. Treatments marked with the same letter do not differ significantly ($\alpha = 0.05$). "FG" = fall grassland, "SG" = spring grassland, "FT" = fall transitional, "ST" = spring transitional, "FC" = fall sage scrub, and "SC" = spring sage scrub. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

sage scrub may lead to higher availability of N if deposition rates remain high, which could favor continued persistence of grasslands.

Interestingly, established sage scrub and the transitional habitat did not differ in total stored C or N, indicating that partially grass-invaded sage scrub is much more similar to intact sage scrub than to type-converted grassland in terms of C and N storage. This result has important implications for conservation and restoration, showing that nutrient storage benefits from sage scrub restoration efforts may begin even before sage scrub is fully re-established. However, grass invasion has been shown to slow restoration of sage scrub and reduce the ability of sage scrub to recover from fire (Dickens and Allen, 2014). Thus, while transitional habitat demonstrated the same C and N storage capacity as sage scrub, it may prove more vulnerable to fire and other perturbations.

No significant differences were found between seasons, indicating little seasonal change in C and N storage in any of these pools or habitats. There were some seasonal changes in the relationships among habitats, with total C and N storage differing significantly between sage scrub and grassland in spring but not fall and between transitional and grassland in fall but not spring. These patterns are driven by trends in soil C and N, which show the same relationships. These trends are most likely the result of variation within communities, especially the transitional community, which may have had a strong influence due to our small sample size. Additional sampling, particularly in the transitional community type, would be necessary to better capture within-community variability and compile stronger evidence for or against seasonal

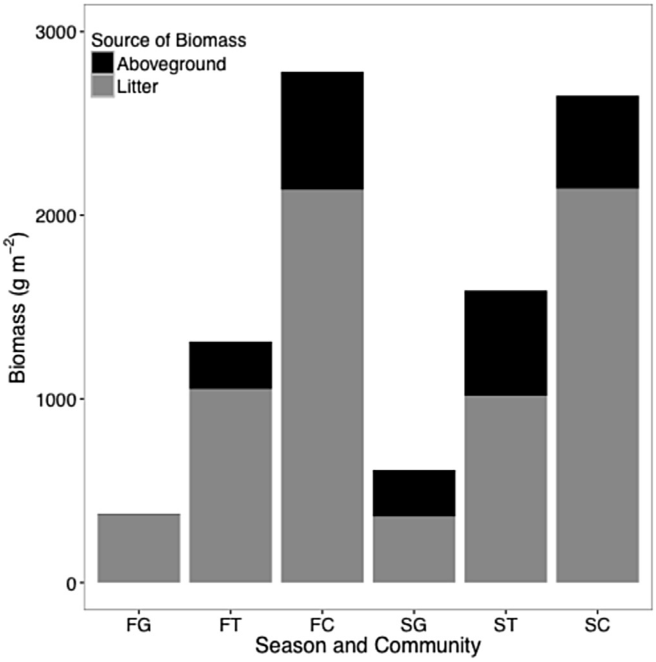

Fig. 3. Fall and spring average aboveground and litter biomass in California sage scrub, grassland, and transitional habitats. "FG" = fall grassland, "SG" = spring grassland, "FT" = fall transitional, "ST" = spring transitional, "FC" = fall sage scrub, and "SC" = spring sage scrub.

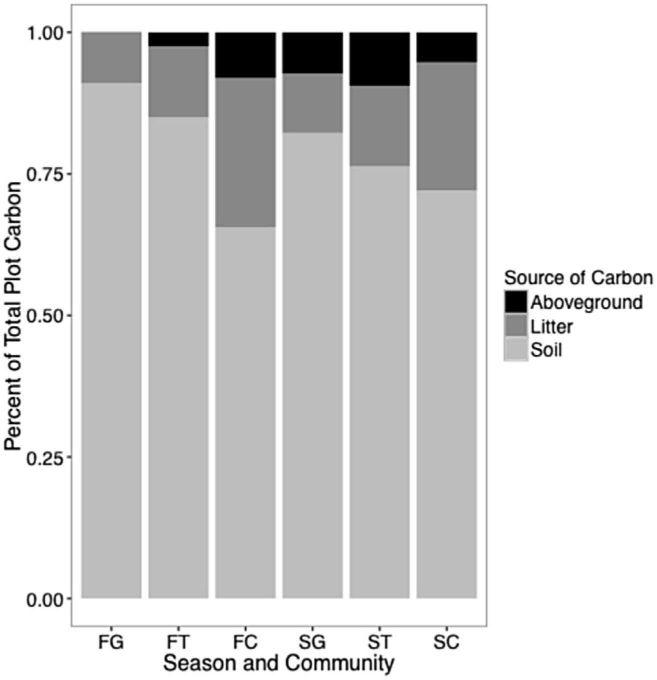

Fig. 4. Fraction of total carbon storage in aboveground, litter, and soil pools in fall and spring in California sage scrub, grassland, and transitional habitats. "FC" = fall sage scrub, "SC" = spring sage scrub, "FT" = fall transitional, "ST" = spring transitional, "FG" = fall grassland, and "SG" = spring grassland.

differences in relative C and N storage.

In all three habitats, most C was stored in the soil, which is the most long-lived of our three considered C pools (Aber and Melillo, 2001). Sage scrub and transitional habitats contained more and higher percentages of C in aboveground biomass and litter than did grassland, but most of this biomass was woody material, and so would not turn over as quickly as C stored in annual grasses. This suggests that while more C and N are stored in aboveground biomass and litter in sage scrub and transitional habitats than in grassland, turnover of these nutrients would likely be much slower in sage scrub and transitional habitats than in grassland (Aber and Melillo, 2001).

This study does not include C and N storage in belowground biomass due to experimental constraints. Root biomass has been shown to differ between grass-dominated and shrub-dominated communities, with lower root-to-shoot biomass ratios in shrub communities than in grassland communities (Jackson et al., 1996). Ongoing studies focused solely on sage scrub and non-native grassland at our study site are examining microbial biomass and diversity, and suggest that more active bacteria in the non-native grassland than sage scrub habitat in the spring may cause more C to be metabolized in this habitat type (Dipman and Meyer, unpublished results). While all of these factors influence C and N storage in grassland and sage scrub communities, soil processes influenced by plant communities are likely to remain the driving component that explains differences between habitat types.

Our study examined C and N storage in the fall of 2012 and spring of 2013, a single rainfall season with below average precipitation. Additional studies are needed to assess annual variability and interannual dynamics of C and N storage in these communities, especially in years with normal to high amounts of precipitation. Additionally, all samples came from a single small field station, and so were subject to similar abiotic conditions apart from the current habitat type. As such, further sampling is required to confirm that the observed differences between these communities are consistent throughout Southern California, particularly along the coastal to inland gradient which differs significantly in temperature, N deposition, and precipitation.

To determine the importance of C storage in these habitats, we must also consider how they compare with other prominent ecosystems. Los Angeles County, CA, is mostly suburban development, typically planted with ornamentals. Urban forests in Los Angeles store 4.59 kg C m^{-2}, somewhat lower than the average storage of 7.69 kg C m^{-2} for urban areas in general (Nowak et al., 2013). Total carbon storage in urban areas can be much higher, for instance 25 kg C m^{-2} stored in residential areas of Chicago when all plant life as well as the top 60 cm of soil were considered (Jo and McPherson, 1995). Our measurements show that sage scrub and transitional habitats store 4.3 kg C m^{-2} and 4.1 kg C m^{-2} on average, respectively, while grasslands store 1.9 kg C m^{-2} on average. While sage scrub habitats store less C than many suburban habitats, they store more than invasive grassland habitats and are not insignificant in comparison to urban storage. Furthermore, we specifically excluded trees from our analyses to simplify our ability to model C and N storage and to ensure that differences observed among habitats were robust. Incorporating trees and other larger shrubs would certainly increase our estimates of C storage in sage scrub. Finally, it is critical to remember that the habitats studied here receive no artificial irrigation, unlike many urban/suburban habitats. Tradeoffs between water use and C storage need to be considered in arid and semiarid regions.

5. Conclusions

Our results highlight the significant C and N storage benefits of preserving and restoring California sage scrub and suggest that these benefits can begin even before the community is entirely recovered. On average, our measured sage scrub stored 130% more C and 80% more N than the non-native grassland, indicating a clear C and N storage benefit to sage scrub preservation and restoration. Since type conversion is so widespread throughout Southern California (Cox et al., 2014), such differences in C and N storage among habitat types may reveal a potentially significant change to regional scale C and N dynamics. In addition to nutrient storage benefits, native vegetation restoration also facilitates the return of native communities of arthropods, birds, reptiles, and other animals, thereby positively affecting biodiversity and native species persistence (Bowler, 2000; Burger et al., 2003). The added benefit of increased C and N storage makes California sage scrub restoration and preservation even more desirable.

Contributions

MMW, WMM, and CRR designed the experiment. MMW, MMD, TAA, AVR, CRR, and WMM conducted the experiment and collected the data. MMW, CRR, and WMM analyzed the data. MMW, WMM, and CRR wrote the manuscript. All authors reviewed, edited, and approved the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2016.02.013.

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