

Invasion of non-native grasses causes a drop in soil carbon storage in California grasslands

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Abstract

Vegetation change can affect the magnitude and direction of global climate change via its effect on carbon cycling among plants, the soil and the atmosphere. The invasion of non-native plants is a major cause of land cover change, of biodiversity loss, and of other changes in ecosystem structure and function. In California, annual grasses from Mediterranean Europe have nearly displaced native perennial grasses across the coastal hillsides and terraces of the state. Our study examines the impact of this invasion on carbon cycling and storage at two sites in northern coastal California. The results suggest that annual grass invasion has caused an average drop in soil carbon storage of 40 Mg/ha in the top half meter of soil, although additional mechanisms may also contribute to soil carbon losses. We attribute the reduction in soil carbon storage to low rates of net primary production in non-native annuals relative to perennial grasses, a shift in rooting depth and water use to primarily shallow sources, and soil respiratory losses in non-native grass soils that exceed production rates. These results indicate that even seemingly subtle land cover changes can significantly impact ecosystem functions in general, and carbon storage in particular.

Keywords: grassland, California, species invasion, carbon cycle, land cover change, rooting depth, global climate change, plant strategies

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1. Introduction

Historically, land use and land cover change account for one quarter to one half of all terrestrial carbon losses to the atmosphere, and contribute to both positive and negative climate forcing at local and global scales (Brovkin *et al* 2004). Land use and land cover changes are also powerful forces driving global environmental change more broadly, (i.e. biodiversity loss, top soil erosion, desertification...), and can profoundly affect ecosystem structure and function (Chapin *et al* 2000, Vitousek 1994). The invasion of California grasslands by grasses from Mediterranean Europe

is notorious among invasion events because the land area these grasses encompass is so large, and the transformation near complete (Biswell 1956). Non-native annual grasses became widespread in California in the mid-1800s, largely displacing the region's coastal native perennial grasslands, and repopulating the portions of the state's Central Valley not under cultivation (D'Antonio 2007, Hamilton 1997). The objective of this research was to determine how non-native grass invasion has altered carbon cycling and storage in California's coastal grasslands through a direct comparison of carbon pools and fluxes in locations where both grass types are found. We hypothesized that non-native grass invasion would cause a drop

in ecosystem carbon storage due to a shift from a perennial to annual life cycle strategy. Native perennial grasses in California possess a suite of traits that allow them to survive summer drought, including deep roots and high belowground growth, which also promote soil carbon storage.

A growing body of evidence now documents the impacts on ecosystem carbon and nitrogen pools and fluxes brought on by species invasion (Ehrenfeld 2003, Liao *et al* 2008). Non-native species can alter carbon and nutrient cycling through a number of mechanisms. They can affect the size of carbon and nutrient pools or their rate of flux. They can alter the location or vulnerability of carbon and nutrient pools (i.e. from below to aboveground, or from recalcitrant to labile organic matter pools). And, they can affect the ecosystem's ability to acquire, recycle or retain resources (i.e. a shift from deep to shallow-rooted species can reduce the volume of water available to vegetation) (Chapin *et al* 1996, Vitousek 1990, D'Antonio 2000). Documented changes in biogeochemistry with invasion reveal multiple mechanisms of change, often mediated by additional changes in the plant or microbial communities (Domenech *et al* 2006, Dukes and Mooney 2004, Ehrenfeld 2003, Kourtev *et al* 2002, Peltzer *et al* 2010, Strickland *et al* 2010, Wolkovich *et al* 2010). Moreover, because plant species both shape and are shaped by the environment they inhabit via material exchange processes, nutrient shifts may cause a progression of further ecosystem and community-level change, or catalyze further invasion (D'Antonio and Vitousek 1992, Dunne and Williams 2009, Knops *et al* 1999, Wardle *et al* 2008).

Only a small number of studies have looked at carbon cycle impacts of grass invasion into grasslands, yet some patterns have emerged from these investigations. Relative to the native species they displace, grass invaders often possess higher above and lower belowground growth, greater seed production, lower belowground allocation and a shallower rooting depth (Adair and Burke 2010, Christian and Wilson 1999, Pyke 1990, Richards 1984, Ryel *et al* 2010, Wilsey and Polley 2006); traits that as a whole favor reduced soil and ecosystem carbon storage. Grass invasions into forests, a topic that has received relatively greater study, are similar to grassland invasions in that the degree and nature of the impacts may progress over time. In the early stages of invasion, the dominant tree species are not displaced, and impacts to nutrient cycles may be realized through interspecies competition. In such cases, nutrient cycle changes are manifest through invader impacts on nutrient pool sizes or flux rates of other community dominants (i.e. NPP, litter quality, soil respiration) (Mack and D'Antonio 2003, Mack *et al* 2001, Peltzer *et al* 2010). In time, however, shifts in ecosystem-level processes, and particularly disturbances regimes, may cause forest conversion to grassland or the cessation of woody recruitment (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998, Litton *et al* 2006). Nutrient cycle impacts from grass invasion into grasslands may also progress over time. However, in the annual grasslands of California, non-native invasion followed vegetation removal in most cases. As a result, the dominant perennial grasses are significantly reduced within, or absent from, the post-invasion community.

More generally, reviews of invasion impacts on carbon cycle processes have found higher ecosystem NPP and faster litter decomposition rates following plant invasion, although the converse has also been found (Ehrenfeld 2003, Liao *et al* 2008). However, few studies to date have attempted to quantify all major ecosystem pools and fluxes as we have in this research. Net accounting of invasion impacts on carbon cycle processes are important, in part, because local effects are linked to the global carbon cycle and climate through atmospheric mixing. Moreover, climate change and species invasion can act synergistically to further ecosystem change and species loss. Whereas it is broadly accepted that climate change can cause climate to shift more quickly than species can migrate or adapt (Ackerly *et al* 2010, Kueppers and Harte 2005, Parmesan 2006), climate change is also likely to increase the frequency and extent of disturbance (Westerling and Bryant 2008), creating conditions ripe for species invasion (D'Antonio 2000).

1.1. California grasslands

The annual grasslands of California are unique among ecosystems undergoing change in that they are advanced in their progression toward a new steady state with respect to biogeochemical cycles. This is true both by virtue of their dominance by herbaceous species, which establish and mature quickly, and the length of time since the initial invasion occurred. Anecdotal evidence indicates annual grasses were widely established within the Marin Peninsula by the mid-1800s (Bennett 1998). These characteristics allowed us to directly compare the cumulative carbon cycle changes resulting from a wide range of ecosystem processes in a space for time substitution. Given these conditions, we assumed the native grass community to be at steady state, and that differences in pool sizes between native and non-native communities reflect differences in the processes and plant attributes that control mass exchange along the soil–plant–atmosphere continuum.

In grassland ecosystems, the large majority of carbon is stored in the soil (Schlesinger 1997). Therefore, we attempted to quantify how carbon enters and leaves the soil, and to evaluate the factors that govern material flux rates. Vegetation change can affect carbon inputs to soil by altering net primary production (NPP), plant allocation patterns or the depth of carbon inputs to soil. NPP determines the amount of biomass entering the soil carbon pool. Belowground allocation will more likely augment soil carbon pools than aboveground biomass, which is more vulnerable to loss through fire, herbivory, photodegradation, or other means. Shifts in the location of carbon inputs along the soil profile can alter the rate of plant tissue decomposition, and thus its residence time as a soil constituent, due to differences in soil climate at different soil depths (Gill *et al* 1999, Van Dam *et al* 1997). On the output side, plant decomposition and microbial respiration rates are affected by plant tissue chemical composition. Microbial respiration also correlates strongly with soil climate, with warmer and wetter conditions promoting carbon losses (Lloyd and Taylor 1994, Davidson

et al 2002). Shifts in the composition or activity of the microbial community accompanying litter quality changes may also affect the magnitude and direction of soil carbon change (Strickland *et al* 2010). We did not evaluate this mechanism for this research, however, as litter quality differences were found to be small between grass types in all but one comparison.

In most coastal California grasslands, community transformation is so advanced that few locations exist where native grasses remain in large patches (Huenneke *et al* 1989). Yet a few remnant grasslands still occupy the coastal Californian hillsides and terraces in large swaths, interspersed with non-native grasses. Our investigation was performed at two such sites, both in Marin County, where we set up plots in locations of native and non-native grass types.

2. Materials and methods

To address our study objectives, we set up research plots in two grassland sites; the Tennessee Valley site, which resides in the headlands of the Golden Gate National Recreation Area, (N 37.862, W 122.524, elevation 220 m), and the Bolinas Lagoon Preserve site, located on a private preserve outside Bolinas, California, (N 37.931, W 122.673, elevation 168 m). Both sites are within a kilometer of the coast and experience a climate with distinct wet and dry seasons. Mean annual precipitation is approximately 900 mm, with a standard deviation of 300 mm, and exhibits high inter-annual variability. The rainy season typically spans from late October through April of each year. Summers are warm and dry, but moderated by the coastal fog cycle. Vegetation at both sites is predominantly grassland interspersed with patches of shrubs. We set up research plots at Tennessee Valley on slopes that range from flat to 2% and share a northeast aspect. Slopes at the Bolinas Lagoon Preserve range from flat to 5% and are south-facing. This site is drier than the Tennessee Valley site due the extended direct solar exposure this grassland receives. Soils at both sites are composed of a well-drained sandy loam on bedrock derived from sandstone and shale (Soil Conservation Service 1985).

The vegetation at both sites is predominantly grassland. Large areas of the native perennial grass community are intermixed with areas dominated by non-native annual grasses and a variety of native and non-native forb species. Shrubs are encroaching into both sites. The greater California Bay Area landscape is characterized by a shifting mosaic from grassland to shrubland to woodland. Open grasslands are invaded by shrubs; primarily *Baccharis pilularis* (Williams and Hobbs 1989, Williams *et al* 1987, McBride and Hedy 1968), which facilitates the invasion of oaks, *Quercus spp.*, and/ or Bay woodland, *Umbellularia californica* (Callaway 1992, Callaway and Davis 1998, Zavaleta and Kettley 2006).

We set up 2 m × 2 m research plots in relatively pure patches of native perennial and non-native annual grass communities at Tennessee Valley and the Bolinas Lagoon Preserve in the spring of 2003; five in each grass type. Patches were chosen for their apparent similarity in soil properties, land use history, slope and aspect. Through subsequent sampling, however, we did find differences in some soil properties between grass types. At Tennessee Valley, the dominant

non-native grasses are *Avena barbata*, *Lolium multiflorum*, *Briza maxima* and *Vulpia spp.* The dominant native perennial grasses at this site are *Agrostis halli* (a rhizomatous grass) with continuous aboveground cover and *Festuca rubra* (a caespitose or bunch grass). To observe the influence these morphological and physiological differences might have on carbon cycling and storage, we chose to establish plots in both native grass types. However, we note that caespitose grasses are more typical of native perennial grasses in California. At the Bolinas Lagoon Preserve, non-native plots are dominated by the annual grass, *Brachypodium distachyon*, but also contain *Avena fatua* and *Briza maxima*. The native caespitose grass plots at this site are dominated by *Nassella pulchra* and *Bromus carinatus*, or by *Elymus glaucus*.

At each site, we measured the standing pools of soil carbon in 10 cm intervals to 50 cm depth. We measured rates of above and belowground productivity. Aboveground harvests were undertaken in the late spring of 2004 and 2005, and total annual productivity calculated as equivalent to maximum standing biomass in both grass types including live and dead tissue (Corbin and D'Antonio 2004, Lauenroth *et al* 2006, Scurlock *et al* 2002). We harvested roots in 3.5 cm diameter soil cores from 0 to 10 cm, 10 to 20 cm and 20 to 50 cm in January 2004 and April 2004 for non-natives and June 2004 for natives, at minimum and peak biomass for each grass type (Corbin and D'Antonio 2004, 2010). We performed leaf litter decomposition assays in 2003–4 and 2004–5, and tracked root litter decomposition in 2005–6 by quantifying dry mass loss over time in litter bags of known initial mass content. We conducted a carbon fraction analysis of secondary compounds in which plant samples are separated into constituents with different rates of decay by means of a progressive extraction methodology (McClaugherty *et al* 1985, Ryan *et al* 1990). This procedure was performed at the Natural Resources Research Institute at the University of Minnesota in Duluth. We measured soil respiration on a monthly basis from January 2005–June 2006, using a LI-COR 6400 (LI-COR Inc., Lincoln, NE); five collars per plot. For this measurement, we attempted to isolate heterotrophic respiration from the sum of heterotrophic and autotrophic fluxes by removing and maintaining the removal of aboveground vegetation from soil collars where soil efflux measurements were performed. We acknowledge, however, that root respiration accounts for some unknown fraction of the sums we report, as respired CO₂ diffuses to the soil surface both vertically and laterally, and perennial root systems often possess a radial structure that extends beneath adjacent plants. For simplicity, however, we refer to this measurement as soil respiration hereafter. We measured soil moisture in 5 cm intervals to 40 cm depth using a soil moisture profile probe (Delta-T Devices) repeatedly over the course of the study and soil temperature at the soil surface and at 5, 15 and 35 cm depth, hourly, using HOBO dataloggers (2003–6). To integrate periodic measurements into annual sums, we modeled soil respiration for the water years from 2003 to 2006 based on a regression analysis of soil climate variables against measured soil respiration, and performed a refined error analysis using Bayesian statistical methods and the software packages WinBUGS and Matlab (Verbeeck *et al* 2006).

Table 1. Ecosystem carbon pools and annual fluxes, units are kg m⁻². TV = Tennessee Valley. BLP = Bolinas Lagoon Preserve. Soil carbon, annual root, shoot and combined productivity, and soil respiration for native and non-native grass communities at Tennessee Valley and the Bolinas Lagoon Preserve, for the water years 2003–4, 2004–5 and 2005–6. Values in parentheses represent +/– one standard deviation, $n = 5$. ANOVA was used to detect differences between mean values. Different letters indicate significant differences at $p < 0.05$.

Site	Species type	2003–4					
		Shoot productivity (carbon)	Root productivity (carbon)	Root to shoot ratio	Total productivity (carbon)	Soil respiration ^a	Total soil carbon
TV	Agrostis (native)	0.33 (0.11) a	0.21 (0.07) a	0.82	0.54 (0.13) a	0.42 (0.16) a	17.6 (0.4) a
	Festuca (native)	0.35 (0.16) a	0.50 (0.04) b	1.83	0.85 (0.17) b	0.67 (0.20) b	16.9 (0.4) a
	Non-native	0.12 (0.04) b	0.14 (0.02) a	1.65	0.26 (0.05) c	0.44 (0.12) a	14.9 (0.4) b
BLP	Native	0.26 (0.15) a	0.37 (0.05) a	1.45	0.63 (0.16) a	^a	14.7 (0.4) a
	Non-native	0.17 (0.04) a	0.20 (0.03) b	1.36	0.36 (0.05) b	^a	9.5 (0.2) b
2004–5							
TV	Agrostis (native)	0.42 (0.08) a	0.41 (0.14) a	1.29	0.83 (0.16) a	0.72 (0.18) a	
	Festuca (native)	0.37 (0.13) a	1.01 (0.08) b	3.43	1.38 (0.16) b	0.78 (0.26) a	
	Non-native	0.22 (0.04) b	0.14 (0.02) c	0.96	0.35 (0.04) c	0.77 (0.14) a	
BLP	Native	0.26 (0.10) a	0.74 (0.09) a	2.97	1.00 (0.14) a	0.99 (0.13) a	
	Non-native	0.28 (0.07) b	0.20 (0.03) b	0.8	0.48 (0.07) b	0.68 (0.15) b	
2005–6							
TV	Agrostis (native)	0.42 (0.06) a	0.41 (0.34) a	1.29	0.83 (0.35) a	0.74 (0.17) a	
	Festuca (native)	0.37 (0.10) a	1.01 (0.47) b	3.43	1.38 (0.48) b	0.79 (0.18) ab	
	Non-native	0.22 (0.03) b	0.14 (0.12) c	0.96	0.35 (0.12) c	0.84 (0.20) b	
BLP	Native	0.26 (0.08) a	0.74 (0.09) a	2.97	1.00 (0.12) a	0.76 (0.13) a	
	Non-native	0.28 (0.05) b	0.20 (0.03) b	0.8	0.48 (0.06) b	0.64 (0.14) a	

^a These values are derived from soil respiration measurements from soil collars, in which the aboveground vegetation was removed.

Therefore, in the months in which plants are active, the autotrophic respiration component of this value was reduced. The soil carbon values reported here are from a single sampling assay completed in 2005, $n = 7$ cores per plot. Similar values were found in a 2003 sampling.

To test for explanations other than vegetation change that could account for differences in soil carbon between grass types, we also compared the soil properties that influence plant productivity and soil organic matter stability. Discrepancies could indicate that soil carbon differences preceded annual grass invasion. In each grass type, we measured soil porosity, soil texture, pH, C:N, soil depth and mineralogy. We also measured carbon from soils that support small patches of each grass type found within the matrix of the opposite grass type to see if the carbon stored therein more closely resembles the soils of the patch grass type or of the matrix. And, we compared our results with a survey of soil carbon in annual grasslands throughout California. Lastly, upon finding that only non-native grasses grow on soils with rocks below 30 cm, we compared soil carbon storage among samples with and without rocks in the lower soil profile.

3. Results

In the grasslands of our study, we found consistently higher stocks of carbon in soils of the native perennial grass community relative to the non-native annual community, particularly at soil depths below 30 cm, but also near the top of the soil profile at both sites (table 1, figures 1(a) and (c)).

In 2004, we found higher above and belowground productivity in the native perennial community relative to the non-native annual (figure 2). The native bunch grasses in our study, *Festuca rubra*, at Tennessee Valley, and *Nassella pulchra*, *Bromus carinatus* and *Elymus glaucus*, at the Bolinas Lagoon Preserve, produced significantly greater fine root biomass at all soil depths than the non-native annuals,

(figures 1(b) and (d)). The rhizomatous grass, *Agrostis halli*, also produced significantly greater root biomass than the non-native grasses at soil depths below 10 cm, however, root production in this grass type was significantly lower than the other native perennial grasses and possessed a lower root to shoot ratio, (table 1). In 2005, a year in which we measured aboveground productivity and estimated belowground, total production in both grass types was much higher than in 2004, corresponding to a year of high annual rainfall and an extended growing season. In 2006, we assumed that both above and belowground productivity were similar to 2005, given that it was also a high rainfall year (figure 2).

From litter and root decomposition experiments, we concluded that differences in litter quality helped explain differences in soil carbon only for the roots at the Tennessee Valley site. Roots of the native perennial grass, *Festuca rubra*, decomposed significantly more slowly than those of the other two grass types (figure 3(a)). We found that a single exponential model best explained decay rates for all litter types,

$$M_t = M_0 e^{-kt} \quad (1)$$

where M_t is litter mass at time t , M_0 is litter mass at time $t = 0$, and k is a first-order litter decay constant (Wieder and Lang 1982). The analysis of secondary compounds in leaf and root litter also revealed that the lignin to nitrogen ratio, a common metric of tissue recalcitrance, was highest for *Festuca rubra*, intermediate for the other native grass type, *Agrostis halli*, and lowest for the non-native grass type, (figure 3(b)). This analysis generally corroborated the findings of the decomposition assays.

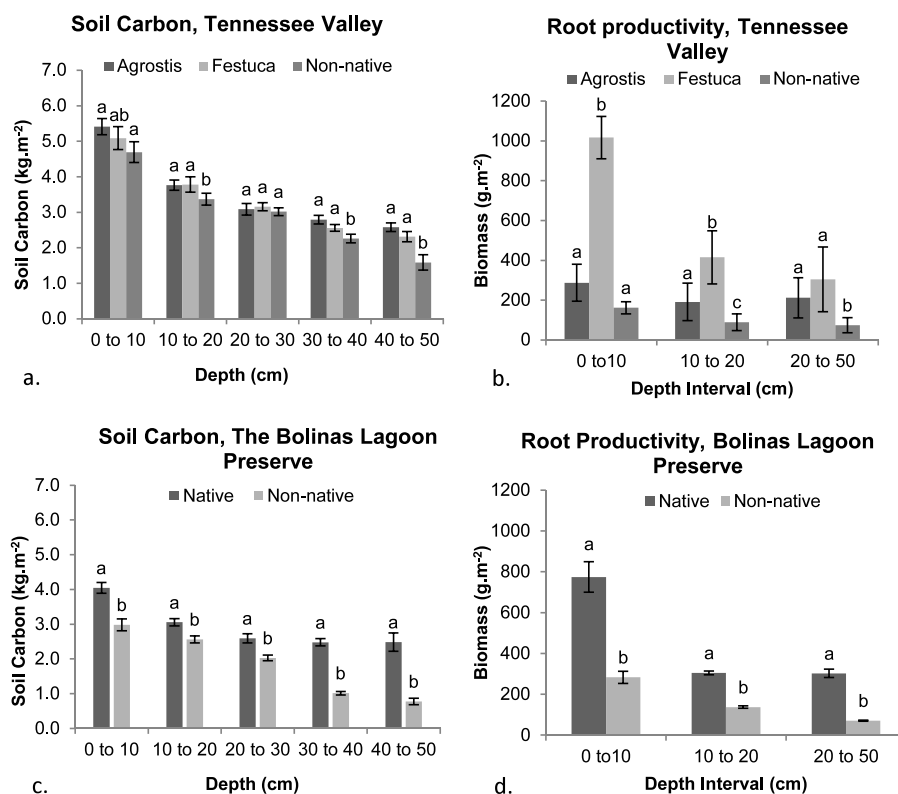


Figure 1. Soil carbon storage and root productivity as a function of soil depth. Soil carbon storage in native perennial and non-native annual grass communities at Tennessee Valley (a) and the Bolinas Lagoon Preserve (c). Annual root productivity for all grass types, averaged between the dry year 2003–4 and the wet year 2004–5 at Tennessee Valley (b) and the Bolinas Lagoon Preserve (d). Error bars represent +/- one standard error.

Modeled soil respiration in all grass types varied by year. At Tennessee Valley, soil respiration was lowest in the water year 2003–4 and significantly higher in the water years 2004–5 and 2005–6 (figure 2). The two latter years were equivalent within the margin of error to each other. At the Bolinas Lagoon site, we report measurements from 2004 to 2006. Native grass soil respiration was higher in the water year 2004–5 than in 2005–6. Non-native grass soil respiration was also higher in 2004–5 at this site, but not significantly so.

Through a regression analysis, we found soil respiration to be correlated with the temporal availability of labile organic substrates, soil carbon pool size, and with the product of soil temperature and moisture, with soil moisture as the dominant factor (r^2 for regression fits = 0.72–0.86). We found soil moisture differs with depth along the soil profile among grass types, and with respect to the location of soil carbon, which is highest at the top of the soil profile and declines with soil depth (figures 1(a) and (c)). At both sites, we found soil moisture to be higher at the top of the soil profile in native grass types relative to non-native grass types and lower deeper in the soil. Differences between pairs of native and non-native grasses over the course of the year and at different depths along the profile appear in (figure 4). Soil temperature was consistently negatively correlated with soil moisture (data not shown).

In testing for possible alternatives to grass invasion to explain differences in soil carbon storage, we found primarily small differences in soil properties between grass types.

However, we did find small, but significant differences in soil texture and soil pH at both sites. We also found lower soil carbon storage in the 20% of samples from the non-native community at the Bolinas Lagoon Preserve with rocks in the lower soil profile compared to non-native-dominated soils without rocks. In comparing carbon stored in the soils from small patches in the matrix of the opposite grass type with findings from the broader soil carbon survey, we found grass type to be more deterministic of soil carbon storage than the matrix of vegetation the patch is found in. These results are discussed in greater depth in the supplemental document (available at stacks.iop.org/ERL/6/044001/mmedia).

4. Discussion

Our findings indicate that the invasion of California grasslands by non-native grasses have caused a drop in soil carbon storage. We find the evidence compelling that non-native grass invasion is the cause of the drop in soil carbon that we document, which we attribute to the difference in the cumulative annual net carbon flux between native and non-native grass types since the time of annual grass invasion. However, we note that additional or alternative explanations are possible (i.e. differences in soil texture) and point the reader to the supplemental document (available at stacks.iop.org/ERL/6/044001/mmedia).

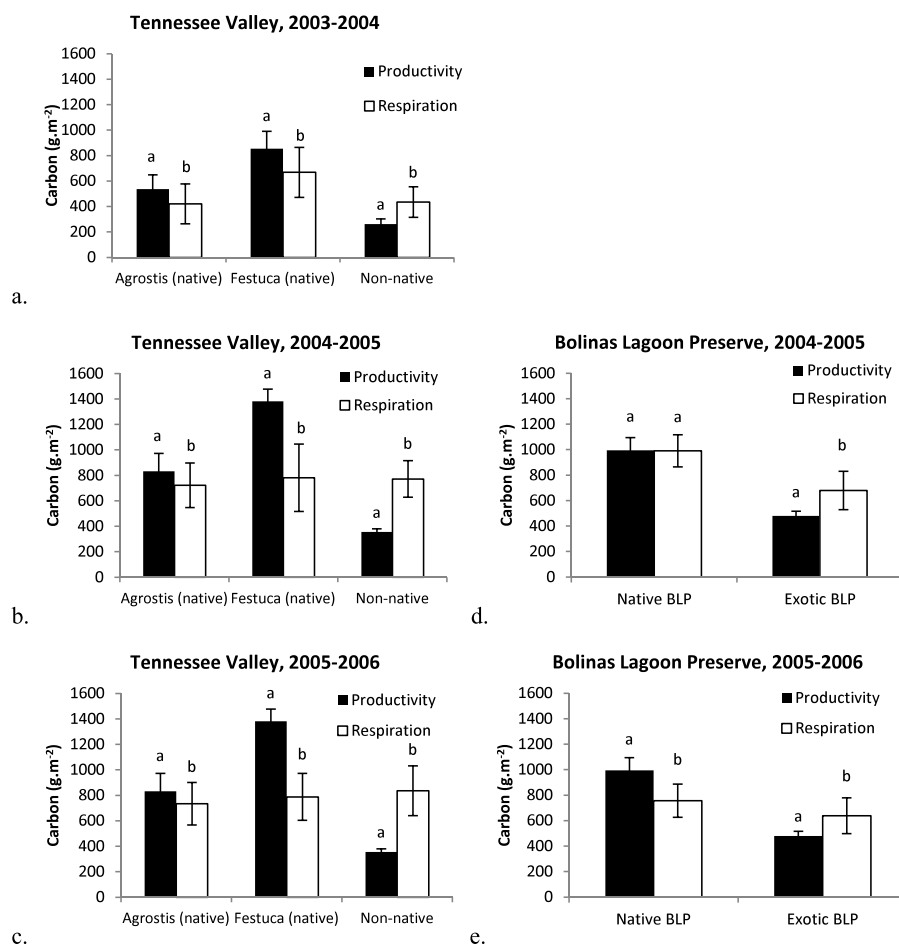


Figure 2. Annual productivity and soil respiration for perennial and annual grasses, Tennessee Valley and the Bolinas Lagoon Preserve. Annual production of biomass carbon and annual soil respiration for the water years extending from October through September for 2003–4 (a), 2004–5 (b), and 2005–6 (c), for the Tennessee Valley and Bolinas Lagoon Preserve Field sites, native perennial and non-native annual grass communities. Error bars represent $\pm$ one standard deviation. Different letters represent significant differences at $p < 0.05$.

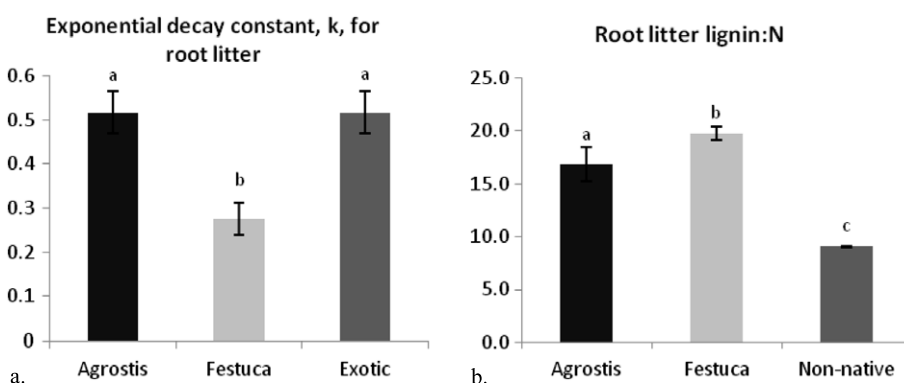


Figure 3. Two metrics for rates of root litter decomposition, Tennessee Valley. The exponential decay constant, k , for the root litter of different species types from the Tennessee Valley field site from an *in situ* litter incubation from 2004–5, $p = 0.001$, based on a simple exponential model of litter decay, equation (1), (a) and, the lignin to nitrogen ratio of root litter (b). Error bars represent $\pm$ one standard error.

The loss of soil carbon appears to stem from key differences in plant traits between grasses with annual and perennial life cycle strategies that evolved in response to seasonal periods of water scarcity. California's native grasses are perennials, maintaining an unbroken interaction with the soil and atmosphere on a perennial basis. The traits that

enable them to survive the summer drought include deep roots to exploit the full soil volume for water, a dense aboveground structure that inhibits soil evaporation, and high root production (table 1, figures 1 and 5). Soil carbon accumulation also fits into a strategy of water conservation, as soil organic matter is highly charged and bonds with

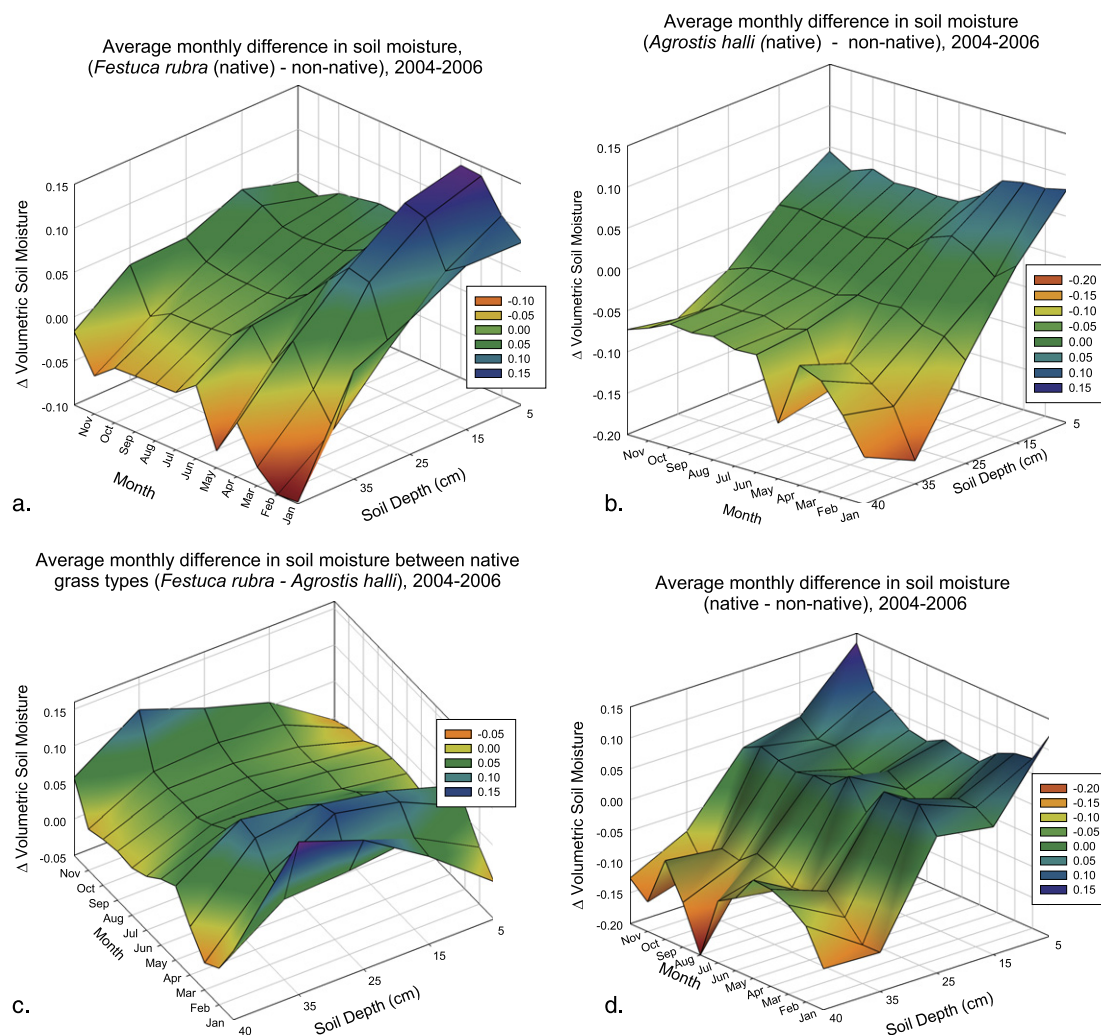


Figure 4. The difference between grass types in volumetric soil moisture along the soil profile. Differences between the native grass *Festuca* community and the non-native community at Tennessee Valley (a), between the native grass *Agrostis* community and the non-native community at Tennessee Valley (b), between the two native grass communities, *Festuca* and *Agrostis* at Tennessee Valley (c), and the native and non-native communities at the Bolinas Lagoon Preserve (d).

polar water molecules (Hudson 1994). In contrast, the non-native grasses are annuals. They avoid summer water scarcity by completing their life cycle before the onset of summer drought; growing from seed each year when autumn rains begin. Aboveground, annual grasses are sparse relative to most perennial grasses, allowing radiation to penetrate to the soil surface and leading to warming and drying of the upper soil profile. Soil desiccation near the surface also results from the structure of the annual grass root system, which is concentrated in the top 10–20 cm of soil. Below the primary rooting zone where roots are absent or sparse, however, soil moisture tends to be higher beneath annual grasses relative to perennial grasses (Holmes and Rice 1996) (figure 4).

These differences in plant traits have several implications for the drop in soil carbon storage following non-native invasion of California grasslands. Because native grasses are perennial, they have a longer growing season than the non-native annuals and maintain a perennial structure capable of resource storage and rapid water and nutrient acquisition when rain begins each autumn (Corbin and D'Antonio 2004, Holmes

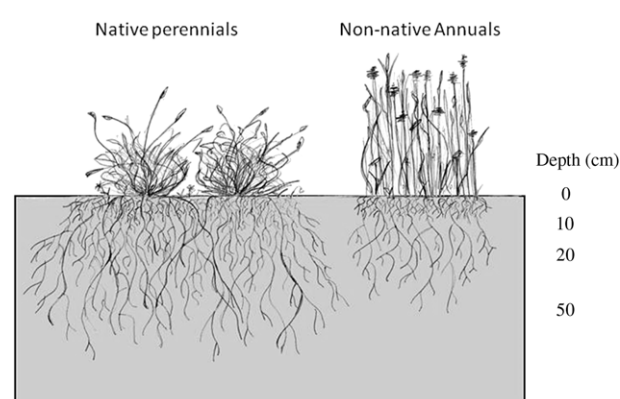


Figure 5. California native perennial and non-native annual grasses. Grass morphology at the time of peak biomass in spring in the native perennial grass community (left) and non-native annual grass community (right).

and Rice 1996). As a result, they are more productive than non-native annuals, despite lower relative growth rates, and thus shed higher amounts of plant matter to the soil each year.

The difference in growing season length also helps explain the loss of soil carbon following non-native grass invasion through its effect on the balance between NPP and soil respiration in each grass type, especially in years of high rainfall. Both productivity and soil respiration vary positively with water availability in native perennial grasses³. Soil respiration also varies with water availability in soils dominated by non-native annuals (Ma *et al* 2007, Zhang *et al* 2010). However, the timing of annual grass senescence is, at least in part, internally set by the necessity of reproduction to occur regardless of environmental conditions, and senescence closely follows flowering in this grass type (Jackson and Roy 1986, Jackson *et al* 1988). Therefore, productivity is capped in the annual grass type by constraints on growing season length, whereas soil respiration is not. Our findings indicate that this imbalance in soil inputs and outputs accounts for the loss in soil carbon that has occurred over time in the annual grass type (figure 2). The timing of summer dormancy can also vary in California perennial grasses by taxa (Laude 1953), but in general, perennial grasses are better able to respond with increased growth in wetter years than annuals. And, the higher NPP in years of high rainfall counteracts, and in most cases supersedes, the loss of soil carbon due to higher soil respiratory losses, leading to net soil carbon accumulation where native perennial grasses are found. We note, however, that our interpretation is subject to our assumptions about the fraction of heterotrophic respiration and autotrophic respiration that make up our soil respiration measurements, and we discuss this issue more fully in section S-11 of the supplemental document that accompanies this manuscript (available at stacks.iop.org/ERL/6/044001/mmedia).

The differences in plant strategies with regard to water use also suggest explanations for the pattern of soil carbon differences between grass types in the upper and lower soil profiles (figure 6). Near the soil surface, soil carbon storage is greater in the perennial grass community. However, the difference is small given the large differences we see in total productivity between grass types, and not significant in all comparisons (figures 1(a) and (c)). This outcome is consistent with the interpretation that both biomass inputs and soil respiration are high in the upper soil profile of the perennial grass type and relatively low in the non-native grass type, leading to only small differences in soil carbon storage between them. We attribute differences in soil respiration rates to differences in soil moisture in upper soil layers between grass types, as soil moisture strongly correlates with soil respiration in these grasslands. The dense aboveground cover and deeper root system of perennial grasses leads to a relatively even draw-down of soil moisture along the depth of the soil profile. The sparser aboveground cover of non-native grasses produces a soil moisture profile that is dry for much of the year near the soil surface, suppressing soil respiration. Deeper in the soil, the size of carbon pool sizes diverges between grass types with significantly greater carbon storage present

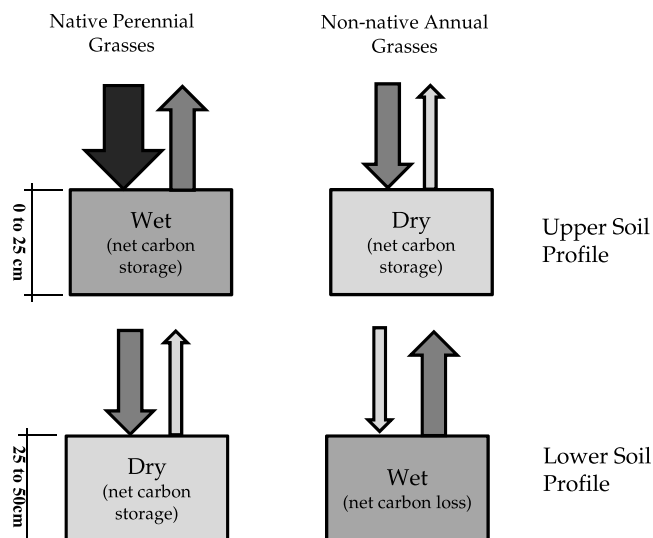


Figure 6. Contrasting carbon cycling dynamics in coastal native perennial and non-native annual grass communities within individual research sites. Diagram of theorized annual carbon inputs and outputs to and from the soil. Terms indicating soil moisture status and flux size are relative to other terms in the same depth profile and indicate average conditions over the course of the annual cycle. Soil depth divisions between the upper and lower soil profile are approximate and vary by species. The size of the soil respiration term is highly correlated with the soil moisture content. See text for a detailed discussion of the contrasting plant strategies that produce differences in soil moisture content and biomass inputs.

where native perennial grasses are found. At these depths, perennial grasses have both greater biomass inputs to soil due to their deeper root system and high belowground allocation, and probably lower respiratory losses as well. In contrast, very low inputs from shallow-rooted annual grasses, coupled with high soil respiratory losses associated with untapped soil moisture beneath the rooting zone, have caused a loss in soil carbon at these depths. The pattern of soil carbon differences we observe are consistent with a progressive loss of soil carbon since the time of non-native grass invasion.

Our investigation of alternatives to plant invasion to explain soil carbon differences was two pronged. On the one hand, we directly measured the main soil properties that could affect plant productivity or soil organic matter stability. On the other, we sought indirect measures to verify or disprove the results from our broader investigation of soil carbon pools and fluxes. With regard to the latter exploration, all of the indirect measures confirmed our original thesis that plant invasion explains the drop in soil carbon. With regard to the former, the tendency toward larger mineral particle sizes in the soils of the non-native grass type could affect plant productivity by speeding soil drainage, thus reducing the period of plant access to soil water. It could also affect soil organic matter stability, as smaller soil particles have greater surface area on which to sorb organic material. However, these difference were small at both sites. We point the reader to the supplemental document for additional discussion of this matter (available at stacks.iop.org/ERL/6/044001/mmedia).

In most respects, our findings are consistent with those of other studies investigating grass invasions into grasslands.

³ For the years of our study, annual precipitation was below average for the water year 2003–4, (89 and 83% of average for Tennessee Valley and the Bolinas Lagoon Preserve, respectively), and higher than average for the water years 2004–5 (117% and 131%), and 2005–6 (162% and 144%).

Generally, similar research has found invaders to possess higher aboveground and lower belowground productivity, greater seed production, lower belowground allocation and a shallower rooting depth in comparison to the native grasses they displace (Adair and Burke 2010, Christian and Wilson 1999, Pyke 1990, Richards 1984, Ryel *et al* 2010, Wilsey and Polley 2006). Our findings differ in that we also found higher aboveground productivity in the native grasses of this research. In the year 2004, the root to shoot ratio was lower in the native *Agrostis halli* grass type than that of non-native grasses, which also represents a departure from the findings of similar research. However, the ratio of root to shoot production was higher in the *Agrostis* grass type in subsequent years and in all other native/non-native grass comparisons.

Lastly, we note that the changes we document in the grasslands of northern coastal California are similar to changes that have occurred elsewhere in the state, and in many temperate grasslands worldwide where deep-rooted vegetation has been replaced by shallow-rooted crop species, such as cereal crops, for example. Therefore, in documenting the change in soil carbon storage within coastal California grasslands, we are focusing on a phenomenon that may be much more widespread.

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