

Invasive grass litter facilitates native shrubs through abiotic effects

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Abstract

Questions: Plant invasions are considered one of the top threats to the biodiversity of native taxa, but clearly documenting the causal links between invasions and the decline of native species remains a major challenge of invasion biology. Most studies have focused on impacts of invaders' living biomass, rather than on mechanisms mediated by litter. However, invasive plant litter, which is often of a very different type and quantity than a system's native plant litter, can have multiple important effects on ecosystem processes – such as nitrogen cycling and soil microclimate – that may influence native plants.

Location: We studied effects of litter of invasive grass species that are widespread throughout western North America on native shrubs in southern California's semi-arid habitat of coastal sage scrub.

Methods: We combined a 3-year field manipulation of non-native litter with structural equation modeling to understand interacting effects on non-native grasses, native shrubs, soil nitrogen (available and total), and soil moisture.

Results: Litter addition facilitated non-native grass growth, revealing a positive feedback likely to enhance invasion success. Contrary to a major paradigm of invasion biology – that competition with invasive plant species causes declines of native plants – we found that litter also facilitated growth of the native dominant shrub, a result supported by observational trends. Structural equation models indicated that enhanced soil moisture mediated the positive effects of litter on shrub growth.

Conclusions: We demonstrate that invasive plants, via their litter, can facilitate dominant native plants by altering soil moisture. Our results highlight that understanding the impacts and mechanisms of plant invasions may be enhanced by considering the role of invasive plant litter on native plants and ecosystem properties.

Keywords: Coastal sage scrub; Competition; Exotic grasses; Grass-shrub interactions; Mediterranean;

Nitrogen; Plant invasions; Positive feedback; Semi-arid; Soil moisture.

Introduction

Plant invasions cost billions of dollars annually to manage (Mooney & Hobbs 2000), yet our understanding of the causes and impacts of most invasions is lacking (Levine et al. 2003). This is partly because it is difficult to isolate the effects of invasions from concurrent landscape changes such as altered disturbance regimes (Didham et al. 2005). Consequently, differentiating among mechanisms for the impact of invasions on native plants, such as greater competitive ability of invasive species for soil resources (Levine et al. 2003) or altered disturbance regimes (Mooney & Hobbs 2000), is often impossible without experiments that clearly link invasive plants to species decline.

Additionally, research has concentrated on the competitive effects of the invaders, instead of the often dramatic abiotic alterations that can be caused by the detritus of invasive plants (Levine et al. 2003). Inclusion of detritus in community analyses can alter fundamental conclusions about system stability and diversity (Moore et al. 2004), and empirical studies of native litter have long documented its positive effects on soil moisture and variable effects on soil nutrients (Dyksterhuis & Schmutz 1947; Hobbie 1992; Boeken & Orenstein 2001), plant diversity, and growth (Facelli & Pickett 1991; Queded & Eriksson 2006). For plant invasions, several studies have found, *a posteriori*, that invasive litter alters ecosystem dynamics (Ogle et al. 2003; MacDougall & Turkington 2005), but few studies have focused on the role of plant litter in the dynamics of invasions.

Invasions of species that are a different functional type than the dominant native community have great potential to alter detrital dynamics

(Eviner 2004), and include most of the large-scale invasions in western North America. Examples include annual grasses displacing perennial grasslands in California (Seabloom et al. 2003) and the spread of *Bromus tectorum* L. (cheatgrass) throughout Great Basin shrublands (Chambers et al. 2007). Additional examples come from the invasion of non-native annual grasses into Mediterranean climate shrublands around the world (D'Antonio 1993). In these arid systems, invasion often results in the replacement of woody plants by annual grasses (Minnich & Dezzani 1998) and the conversion of extensive bare ground and cryptogamic crust into litter layers (Booth et al. 2003). These changes can greatly alter soil moisture and associated nutrient regimes, possibly producing alternative stable states (Borgogno et al. 2007).

Grass invasion into shrub habitats, such as southern California's coastal sage scrub habitat (hereafter CSS), can intensify belowground competition for limited resources, especially nitrogen and water, to the detriment of the native shrubs (D'Antonio et al. 1998). In many invaded systems, invasive grasses take up resources before they reach the deeper roots of shrubs, or share shallow rooting depths with native shrubs (Melgoza et al. 1990; Montana et al. 1995; D'Antonio et al. 1998), as is the case in CSS for most native shrubs, including *Artemisia californica* Less. (Hellmers et al. 1955; Eliason & Allen 1997). In the semi-arid habitats of the Great Basin (Booth et al. 2003) and CSS (Eliason & Allen 1997) competition for soil nutrients is hypothesized to cause the observed decline in native shrubs following grass invasion. Invasive grass litter may also modulate competition for water by altering soil moisture – a major limiting resource in arid systems, and controller of nutrient cycling. Litter can intercept rain and reduce soil moisture, or it may act as mulch and reduce evaporative loss (Facelli & Pickett 1991), possibly facilitating native plants (Holzapfel & Mahall 1999).

We hypothesized that non-native grass litter in CSS increases soil moisture, but decreases soil nitrogen, resulting in overall reduced growth of adult native shrubs. We expected soil nitrogen to decrease due to greater uptake by rapidly growing non-native grasses. To test these hypotheses we conducted a 3-year manipulation of non-native annual grass litter surrounding the native dominant shrub, *A. californica*. We followed soil moisture, total soil nitrogen, and nitrogen mineralization, and compared alternative causal models linking non-native grass litter with shrub growth using structural equation modeling (Didham et al. 2005).

Methods

Study site and system

CSS habitat extends from northern California to Baja California along the coast, and up to 100 km inland at elevations <500 m, with chaparral often adjoining it at higher elevations (Mooney 1977). It is characterized by a number of soft-leaved, drought-deciduous and evergreen sub-shrubs, and in southern California is generally dominated by *A. californica* (drought-deciduous) and *Eriogonum fasciculatum* Benth (mainly evergreen) (Schroenherr 1992).

Native CSS is dominated by shrubs in a matrix of forbs, perennial grasses, and soil crusts. After invasion, sites often convert to annual grasslands or shrublands with all interstitial space filled by invasive grasses and persistent grass thatch (Wolkovich et al. in press). Grass invasion is negatively correlated with adult shrub cover and seedling growth of *A. californica* (Eliason & Allen 1997; Stylinski & Allen 1999), which is hypothesized to be due to competition for soil nitrogen (Zink & Allen 1998; Padgett & Allen 1999) and possibly altered fire regimes (Keeley et al. 2005a). The dominant invasive grasses (*Bromus madritensis* L. ssp. *rubens* (L.) Husnot, *Avena barbata* Link, *Brachypodium distachyon* (L.) Beauv) are shared with other well-studied California perennial grasslands (Seabloom et al. 2003).

We conducted all work in a 50-ha area of the San Diego National Wildlife Refuge (Sweetwater Unit), located 20 km inland in San Diego County, California, US. Vegetation cover at the site is 56% shrub, with the remaining area covered by a mosaic of bare ground, soil crusts, and mostly non-native grasses and herbs (Morrison & Bolger 2002). Soils at the study site are classified as part of the friant series (66% sand, 20% silt, and 14% clay) (United States Department of Agriculture: Natural Resource Conservation Service 2008). Percentage slope ranges from 3% to 40% (E. Wolkovich, unpubl. data).

Litter manipulation

To examine the effects of non-native grass litter on native shrubs and non-native grasses in CSS, we conducted a two-factor experiment. We selected 56 *A. californica* shrubs of similar size ($\sim 1 \text{ m}^3$, which is typical for the area) separated from one another by 10–50 m; these focal shrubs were randomly selected from the approximately 70 shrubs identified as being of appropriate size and distance from one another. We centered 3 m \times 3 m plots around each focal shrub in areas that were either already highly invaded by

grass (>40% non-native grass cover, assessed by point intercept) or with low (<5%) amounts of grass (factor 1, *Invasion Level*: pre-manipulation High or Low Invasion). Abundance of non-native grasses varied considerably across the study area, such that plots in the pre-manipulation high- versus low-invasion treatments were well interspersed, and not clustered into discrete areas. We then added, removed or left grass litter unchanged at the end of two growing seasons (factor 2, *Litter*: Addition, Removal, or Control) in a fully crossed design, with each of the six treatment levels (*Invasion Level* × *Litter*) replicated eight times. In areas of pre-manipulation High Invasion, we also included a Removal Control treatment, where we removed all grass litter then immediately returned it to the plot. Any Removal effects are not due to artifacts of disturbance by raking or cutting: Removal Control treatments did not differ from Controls for any response variables ($P > 0.2$). All plots were on east- or west-facing slopes and located at least 0.5 km from any road.

We based the timing and magnitude of our manipulation on yearly growing season conditions. Manipulations were conducted at the end of the 2005 and 2006 growing seasons (late May-June) after senescence and desiccation of annual grasses. To gather litter for the manipulation we used hand-held battery-powered shears and rakes. On removal plots, we cut all non-native grass litter at ground level, removed the entire stalk and seed head then shook the litter to remove any loose seeds. We used this litter combined with litter from non-study areas for Addition plots. For Additions, we brought all plots (pre-manipulation High and Low Invasion) to two times the pre-manipulation abundance of non-native litter on our High Invasion plots for that year, placing litter to mimic natural conditions. We chose our levels (i.e. 2 × high abundance and complete removal) to provide contrasts to our High and Low Invasion × Control plots, to mimic litter levels in areas of extremely high invasion, and to examine the possible effect of litter removal. We estimated total litter moved by collecting 0.025 m³ of litter, measuring in the field how many units of this volume we were moving for one Low Invasion × Addition plot, then sorting three volumes of the litter (total of 0.075 m³) in the lab, and drying and weighing it. In the first year of the manipulation (2005), an above-average rainfall year (521 mm, 190% of the 50-year mean), we removed approximately 2.4 ± 0.14 kg/plot (mean ± SE) from High Invasion × Removal plots and added this litter to High Invasion × Addition plots; we

added twice this amount to Low Invasion plots. In 2006, a below-average rainfall year (74% of the mean), we added ~10% of the 2005 amounts. We removed only small amounts of litter from pre-manipulation Low Invasion areas, as they were not heavily invaded. Rainfall in 2007 was 59% of the mean.

Vegetation sampling

We measured vegetation characteristics of all plots before and after the manipulations (2005 to 2007). We estimated ground cover and total standing plant density by point intercept sampling, taking data every 0.5 m along two diagonal transects in each plot (18 total points). The 0.5-m distance was chosen after pilot sampling showed that it gave very similar results to collecting data every 0.25 m (E. Wolkovich, unpubl. data). At each point, we recorded (A) ground cover as grass litter, forb litter, or native and bare ground cover, and (B) living plant density by species to intersect the point intercept line, with a maximum of three hits per 0.1 m per species (Barbour et al. 1999). We converted data (A) to percentage ground cover by dividing ground cover hits by the total number of points (18/plot), and (B) to a plant density index by dividing plant hits by the maximum number of hits of all species of any one plot (92, which occurred in 2005). These estimates are thus comparable across years and scale to 100.

To measure the effect of litter on native shrubs, we recorded the size and growth of each focal *A. californica* shrub. We estimated cylindrical volume each year from one height and two width measurements. In May of 2006 and 2007, we estimated total aboveground biomass by clipping a small section (~5%) of the shrub and estimating the number of similarly sized sections present on the shrub. For each clipping, we separated, dried, and weighed current (foliage and non-lignified stem; hereafter referred to as “shrub growth”) and previous (woody, hereafter “initial shrub mass”) growth in the lab. *A. californica* shrubs have no central stem and this method has been found to be quite robust compared to volume or other estimates (Wolkovich in press).

Soil sampling

We sampled soil to determine how litter alters soil processes. We took three cylindrical soil cores per plot (3-cm diameter, 10-cm deep) in mid-growing season (29 April 2005, 30 March 2006, and 13 March 2007). To determine percentage soil moist-

ure, we sieved samples through 2-mm mesh to remove roots and rocks, then weighed, dried at 60°C for 3 d, and re-weighed (Robertson et al. 1999) the samples. In 2005 and 2007, we also measured total soil nitrogen (Carlo Erba NA 1500 series 2 elemental analyzer), nitrate/nitrite, and ammonium mineralization on fresh, undried soils via standard lab incubations (Robertson et al. 1999) lasting 30 d, using 2 M KCl for extraction, followed by colorimetric analysis (QuikChem 8500 Series FIA+ autoanalyzer). Additionally, we compared below-ground temperatures in two Control and two Addition plots for 8 d before and after the 2005 initial manipulation to assess effects of litter addition. We used HOBO Pro Temp/External temperature devices (H08-30-08, Onset Computer Corporation) installed 5 cm belowground in one pre-manipulation Low Invasion×Addition and one pre-manipulation High Invasion×Addition plot, as well as in one Low and one High Invasion×Control plot.

Statistical analyses

To analyze responses to our experiment, we used a combination of approaches and JMP version 5.0 (SAS Institute Inc.) and R version 2.5.1, including the packages *car*, *nlme* and *sem* (R Development Core Team 2007). We used Pearson correlation coefficients to evaluate pre-manipulation associations between percentage non-native grass litter, soil moisture, soil nitrogen metrics, and native shrub volume. We used repeated measures (RM)-ANOVA to test for effects on vegetation and soil; plot ID was the only random effect, and we selected the best fitting variance-covariance matrix for each response variable via AIC (Wolfinger 1996). We used multiple regression to examine the role of soil moisture and nitrogen variables on shrub growth, including the initial shrub mass as a covariate. For soil temperature, we fitted a simple one-way ANOVA to mean temperature differences (per plot) before minus after manipulation. We square-root transformed percentage non-native grass litter cover, percentage native and bare ground cover, living grass density, shrub growth, and initial shrub mass to equalize variance across treatments. Although we conducted multiple statistical tests in this study, we did not adjust alpha or our *P*-values because such corrections greatly inflate the Type II error rate, especially when response variables are correlated (Moran 2003; Gotelli & Ellison 2004), as in this study.

We used path analysis, which is a subset of structural equation modeling that allows estimation of possible direct and indirect effects among variables (Shipley 2002), to evaluate six alternative

models of the interacting effects of non-native litter, soil moisture, and soil nitrogen on native shrub growth at the end of the experiment (2007). Model A had the greatest number of links (Fig. 5a), and the five other models are nested within it. Compared to model A, the sub-models vary the extent that nitrogen is determined by litter and moisture and controls shrub growth (Table 1). Because all models had a minimum of six observations per link with variance inflation factors values <2.0, our models had reasonable power and little to no effects of multicollinearity (Petraitis et al. 1996). To include multiple forms of nitrogen, but reduce dimensionality, we used principal component analysis on nitrate/nitrite mineralization, ammonium mineralization, and total soil nitrogen. PC 1 explained 53% of the variation, with eigenvectors of 0.63 for ammonium mineralization, -0.61 for nitrate/nitrite mineralization, and 0.48 for total soil nitrogen. Because models varied the pathways and not the number of variables, we used the Bayesian information criterion (BIC) to select the best-fitting model (Rafferty 1993).

Results

Non-native litter

We successfully altered the non-native grass litter abundance in both years after manipulation as a function of pre-manipulation invasion level (Year×Invasion Level×Litter of RM-ANOVA, $P < 0.0001$, Table 2). In areas of High Invasion, Removal decreased litter cover by 40% compared to Controls (Fig. 1a), while in Low Invasion plots, Additions resulted in a >70% increase in litter cover in the following 2 years compared to Controls (Fig. 1b). However, manipulations that reinforced the pre-manipulation state – Additions to High Invasion areas and Removals from Low Invasion plots – showed only minor effects (Fig. 1a-b). Percentage native and bare ground cover (combining bare soil, cryptogamic crust, and the common native spike-moss *Selaginella cinerascens*) mirrored changes in litter cover (Fig. 1c-d, Year×Invasion Level×Litter of RM-ANOVA, $P \leq 0.01$, Table 2), as most Removals resulted in sustained bare ground and Additions covered bare ground, moss, and soil crusts.

Non-native grass growth

Living non-native grass increased 15-fold in litter Additions to Low Invasion areas and decreased 6-fold in Removals from areas of High Invasion (Fig. 1e-f, Year×Invasion Level×Litter of RM-

Table 1. Comparisons of six *a priori* path models varying relationships between soil moisture, nitrogen, shrub growth, and non-native grass litter. A *P*-value of >0.05 indicates the model is a good fit to the data, while low BIC values highlight the best fitting model (D, in bold). Indirect effect gives the total significant indirect effect of non-native grass litter on shrub biomass; a “–” indicates there was no significant path.

Model	Description	Goodness of fit				
		χ^2	<i>df</i>	<i>P</i>	BIC	Indirect effect
A	Full model	3.66	1	0.06	–0.25	0.31
B	As in A, but without moisture to nitrogen path	3.78	2	0.15	–4.05	0.31
C	As in A, but without litter to nitrogen path	3.72	2	0.16	–4.10	0.31
D	As in B, but without litter to nitrogen path	4.10	3	0.25	–7.63	0.31
E	As in C, but without nitrogen to shrub growth path	6.35	3	0.10	–5.38	0.32
F	As in C, but without moisture to shrub growth path	19.90	3	<0.001	8.17	–

Table 2. Summary of RM-ANOVA for effects on litter cover, native and bare ground cover, living non-native grass density, and soil moisture for a 3-year non-native grass litter manipulation crossing pre-manipulation *Invasion Level* with *Litter* treatment. Variance–covariance matrices are either compound (c), autoregressive (ar), or unstructured (u). Bold indicates significance of $\chi \leq 0.01$

	<i>df</i> num	<i>df</i> den	Percentage non-native grass litter cover ^{1/2} (c)		Percentage native and bare ground ^{1/2} (ar)		Living non-native grass density ^{1/2} (u)		Soil moisture (c)	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Between subjects</i>										
Invasion level (High/Low)	1	42	227.63	<0.0001	0.49	0.49	77.37	<0.0001	41.10	<0.0001
Litter (Add/Rem/Con)	2	42	91.60	<0.0001	30.79	<0.0001	22.08	<0.0001	7.43	<0.0001
Invasion level×Litter	2	42	23.54	<0.0001	1.81	0.18	4.94	0.0118	1.55	0.22
<i>Within subjects</i>										
Year	2	81	126.56	<0.0001	53.57	<0.0001	26.07	<0.0001	300.86	<0.0001
Year×Invasion level	2	81	0.87	0.42	54.85	<0.0001	86.86	<0.0001	0.08	0.93
Year×Litter	4	81	37.06	<0.0001	24.67	<0.0001	9.32	<0.0001	6.54	0.0001
Year×Invasion level×Litter	4	81	9.20	<0.0001	3.30	0.01	3.73	0.0077	1.50	0.21

ANOVA, *P* = 0.008, Year×Invasion Level of RM-ANOVA: *P* < 0.0001, Table 2). Treatments that were similar to the pre-manipulation condition (Additions to High Invasion areas, Removals from Low Invasion areas) had little effect (Fig. 1e-f).

Native shrub growth

Non-native grass litter enhanced growth of the dominant native shrub, *A. californica*. In 2005, shrubs that began the study in High Invasion areas were markedly larger than those in Low Invasion areas (estimated volume: 0.95 versus 0.65 m³, *F*_{1,54} = 11.28, *P* = 0.0014). This pre-manipulation effect disappeared following the manipulation (Invasion Level, RM-ANOVA, *P* ≥ 0.15), as litter treatments had altered shrub growth after one year (2006), and this effect continued through 2007 (Litter, RM-ANOVA: *F*_{2,38} = 5.73, *P* = 0.007). In 2007, the effect varied marginally by pre-manipulation Invasion Level (Invasion Level×Litter of RM-ANOVA: *F*_{2,40} = 3.48, *P* = 0.04). In areas of Low Invasion, Additions more than doubled shrub growth in 2007 (Fig. 2). Removals from areas of pre-manipulation High Invasion showed sharply re-

duced shrub growth, while Removals from areas with only low levels of invasion did not (Fig. 2). A total of three shrubs died during the experiment, all from within experimentally or naturally low, non-native grass litter plots.

Soil moisture and temperature

Addition of non-native litter increased soil moisture by ~20% (Year×Litter of RM-ANOVA: *F*_{4,81} = 6.54, *P* = 0.0001, Table 2, Fig. 3a), independent of the pre-manipulation level of invasion (Year×Invasion Level×Litter of RM-ANOVA, *P* = 0.21, Table 2), as assessed by spring measurements. Mean soil temperature decreased by 2.06 ± 0.61°C following litter addition (*F*_{1,2} = 42.43, *P* = 0.02). Following this trend, daily maximum temperatures decreased by 2.68 ± 1.32°C following litter addition (*F*_{1,2} = 22.99, *P* = 0.04), however daily minimums were unchanged by addition (*F*_{1,2} = 0.51, *P* = 0.55).

Soil nitrogen

Available soil nitrogen (total nitrogen mineralization) was not affected by the litter treatment

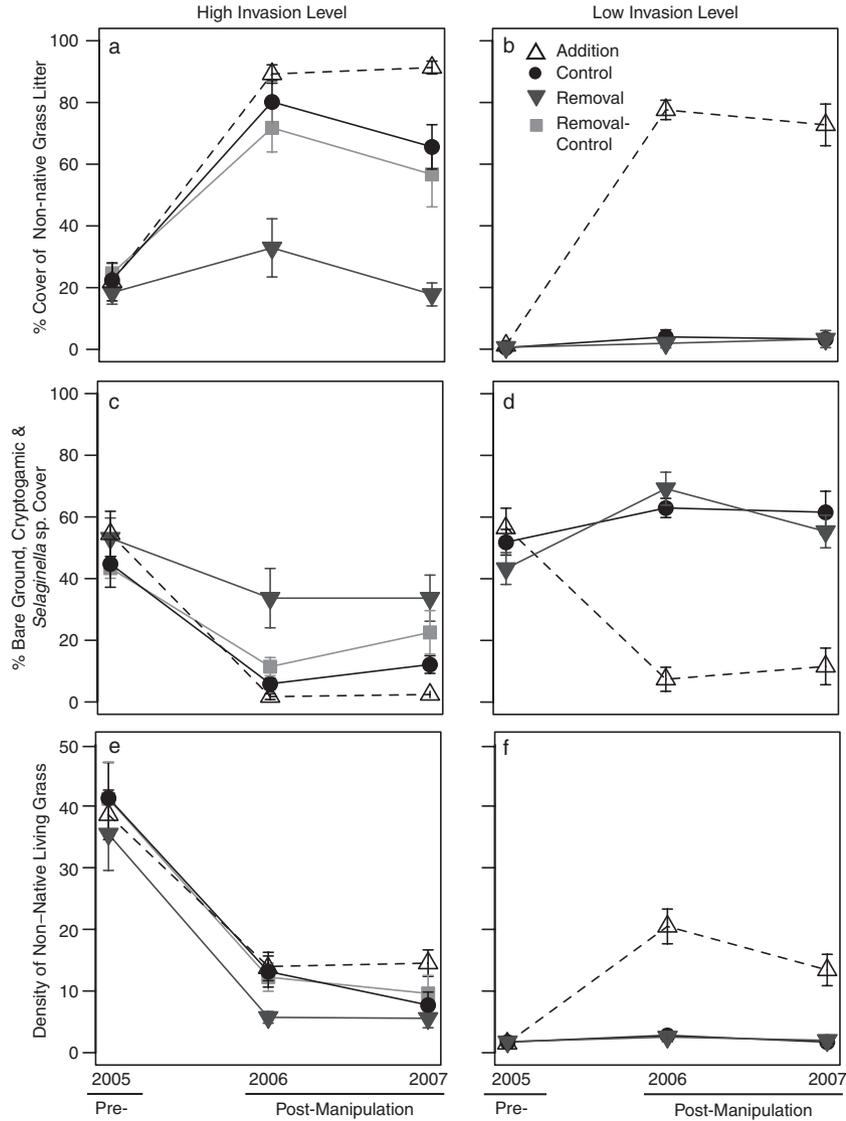


Fig. 1. Non-native grass litter treatments altered mean ground cover (a-d) and living grass density (e-f) in both areas of pre-manipulation High Invasion (left) and Low Invasion (right) during the 3-year study (see Table 2 for statistics). For c-d, bare ground was generally 75.4% while *Selaginella* (mostly *cinerascens*) was 18.5% and cryptogamic crust was 6.1%. Bars are ± 1 SE.

(Year \times Litter of RM-ANOVA: $F_{2,41} = 0.84$, $P = 0.44$, Fig. 3b), invasion level, or year (all other effects of RM-ANOVA: $F_{1-2,41-42} < 0.63$, $P > 0.5$, Fig. 3b). Total soil nitrogen also did not vary due to the litter manipulation (Year \times Litter of RM-ANOVA: $F_{2,37} = 1.95$, $P = 0.16$, data not shown), although it changed dynamically – increasing or decreasing by over 20% – during the experiment (Wolkovich et al. in press). Additionally, total soil nitrogen was greater in areas of high grass invasion (0.14 ± 0.005 versus $0.11 \pm 0.004\%$ soil nitrogen, Invasion Level of RM-ANOVA: $F_{1,42} = 13.72$, $P = 0.0006$), both before and after the experiment

(all interactions with Year in RM-ANOVA: $F_{1-2,37} < 0.37$, $P > 0.7$).

Inter-annual variation

All vegetation measures and soil moisture levels varied by year (Year of RM-ANOVAs, all $P < 0.0001$, see also Table 2), mirroring the large differences in annual precipitation. Non-native living grass was greatest in 2005, a year when rainfall was 190% of the 50-year mean, and was lower in 2006 and 2007 when rainfall was more moderate – 74% and 59%, respectively (Fig. 1e-f).

This naturally large production of non-native grass in 2005 contributed to high non-native grass litter cover in High Invasion areas in 2006 and 2007 including Control plots (Fig. 1a), with concomitant reductions in other types of ground cover (Fig. 1c). Native shrub growth was reduced in 2007 compared to 2006 (Fig. 2), consistent with reduced rainfall in 2007. Finally, soil moisture also varied by year (Fig. 3a); however, since we measured moisture only once during the spring, it is difficult to compare our measurements directly to year-to-year patterns in rainfall.

Path analysis of non-native litter on native shrub growth

Before manipulation, shrubs were larger in areas of higher litter cover ($r = 0.26$, $t_{54} = 1.98$,

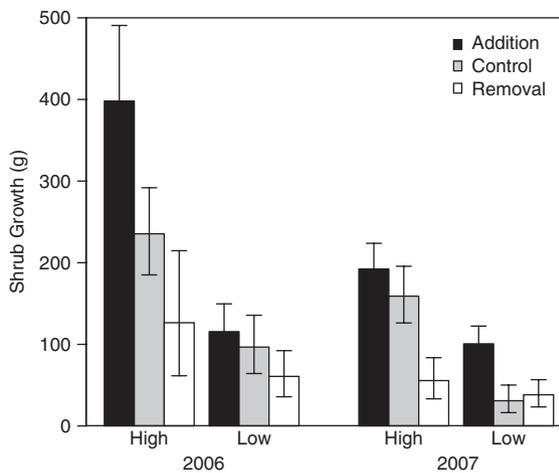


Fig. 2. Mean total shrub growth (± 1 SE) was greater in areas of high invasive grass litter cover (Addition; High Invasion \times Control) compared with lower litter plots (Removal; Low Invasion \times Control). “High” and “Low” refer to pre-manipulation level of grass invasion. Figure republished with permission from Wolkovich 2009 (in press).

$P = 0.052$) and greater soil moisture ($r = 0.46$, $t_{54} = 3.82$, $P = 0.0004$), but shrub size was not related to total ($r = 0.17$, $t_{53} = 1.26$, $P = 0.22$) or available soil nitrogen ($r = -0.05$, $t_{50} = -0.36$, $P = 0.72$). Also, before the manipulation, soil moisture was itself positively correlated with litter cover ($r = 0.46$, $t_{54} = 3.79$, $P = 0.0004$). Concordant with these pre-manipulation observational trends, following our litter manipulation we found that shrub growth was positively related to soil moisture (Fig. 4a), but not to soil nitrogen (Fig. 4b).

Path analyses suggested that non-native litter affected shrub growth indirectly through its effect on soil moisture. In the best fitting path model (Fig. 5b), non-native litter positively affected soil moisture, which then positively affected native shrub growth. Although neither non-native litter nor soil moisture were linked to soil nitrogen in this model, models with such links were also feasible (χ^2 tests non-significant, Table 1) but had inferior fits to the data ($\Delta BIC \geq 2$, Table 1). Effects of soil nitrogen on shrub growth were weak and non-significant ($P \geq 0.1$) in all models. Results did not depend upon specifics of the particular year or chosen metric of nitrogen used: analyses with 2005 (pre-manipulation) data and with 2007 data using various nitrogen metrics clearly supported soil moisture as the dominant link between non-native litter and native shrub growth (E. Wolkovich, unpubl. results). Furthermore, standardized coefficients for paths from litter to soil moisture to shrub growth were similar across models (see indirect effects in Table 1).

Discussion

Our results demonstrate how changes in a system’s detritus due to plant invasion can have

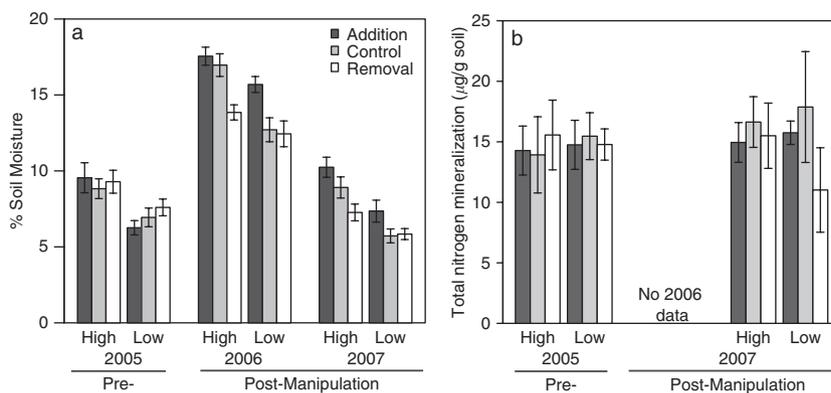


Fig. 3. Mean soil moisture (a) increased with additions of non-native litter and decreased with removals in both years (2006 and 2007) following manipulation (see Table 2). Total available soil nitrogen (b) did not vary due to treatments. Bars are ± 1 SE.

dramatic and interacting abiotic and biotic effects throughout the system. Contrary to expectations – that invasive plants would decrease growth of the native shrub – we found that the native dominant shrub, *A. californica*, was larger in areas of high invasive grass cover, and we experimentally linked this increase to invasive grass litter. Shrubs grew 3.1-times more with grass litter added than with litter removed (Fig. 2), despite the fact that living invasive

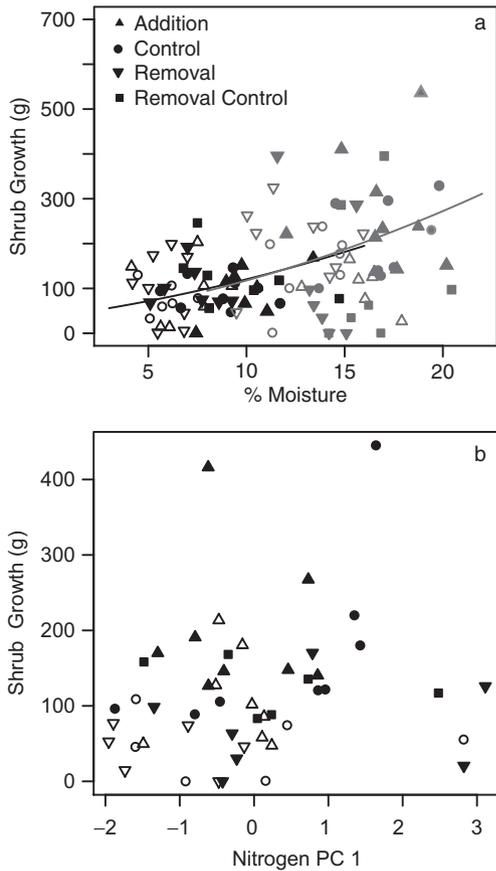


Fig. 4. Total annual shrub (*A. californica*) growth increased with soil moisture (a), with the same slope (comparison of slopes test: $t_{101} = 0.19$, $P = 0.85$) in both years post-grass litter manipulation (for 2006: Soil Moisture: $F_{1,49} = 4.12$, $P = 0.048$, Initial shrub mass^{1/2}: $F_{1,49} = 26.18$, $P < 0.0001$; for 2007: Soil Moisture: $F_{1,50} = 6.60$, $P = 0.013$, Initial shrub mass^{1/2}: $F_{1,50} = 33.11$, $P < 0.0001$). Shrub growth was not related to a combined nitrogen metric (b, for 2007: $F_{1,46} = 0.002$, $P = 0.97$, Initial shrub mass^{1/2}: $F_{1,46} = 55.11$, $P < 0.0001$) or to any of its components (ammonium, nitrate/nitrite mineralization, total nitrogen: $F_{1,46} < 0.15$, $P > 0.7$, Initial shrub mass^{1/2}: $F_{1,46} > 48.43$, $P < 0.0001$). Filled versus open symbols represent High versus Low Invasion. Gray symbols represent 2006, while black symbols represent 2007. Points and line fits are back-transformed with the effect of initial shrub mass removed so that only the influence of moisture or nitrogen remains.

grass cover (Fig. 1e-f), and thus potential competition between shrubs and non-native grasses, also increased dramatically. Further, although we attempted to control for shrub size prior to the manipulation, shrubs in High Invasion areas were 1.5-times larger than those in Low Invasion plots at the beginning of the experiment. This effect persisted in control plots throughout the experiment: shrubs in Low Invasion Control plots grew substantially less than those in High Invasion Control plots (1.6-fold less in 2006 and 5.1-fold less in 2007), demonstrating that the facilitation of native shrubs also occurs in un-manipulated invaded areas. Structural equation modeling suggests that an increase in soil moisture due to invasive grass litter caused the increase in shrub growth. Thus, our results show that non-native grass litter has positive effects on shrubs over several years, and suggests that field experiments considering the role of litter can reverse relationships expected between native and invasive plants based on observational studies (Didham et al. 2005; MacDougall & Turkington 2005).

Non-native litter’s greatest effect on shrub growth was via increased soil moisture, as shown by

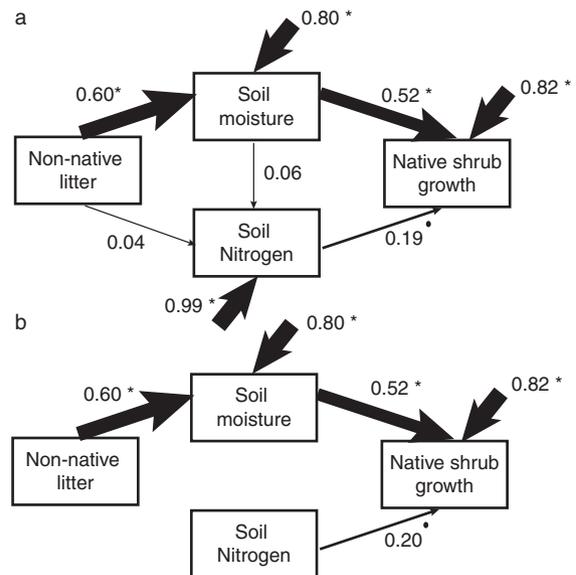


Fig. 5. Full (Model A – a) and the best (Model D – b) of six possible path models describing the effect of non-native grass litter on native shrub growth (see Table 1). In all models, the dominant path of litter to shrub growth was via soil moisture. All lines represent positive effects. Path coefficients are given and also represented by line widths. Asterisks denote significance at $P < 0.05$, while dots denote $P \leq 0.1$. Nitrogen PC 1 combines soil data on total nitrogen and nitrogen mineralization. Path coefficients varied little from (a) in the other four models (described in Table 1).

structural equation modeling. Litter increased soil moisture, most probably by decreasing evaporation. To cause the observed increase in moisture, this evaporative decrease must have been greater than the loss due to increased transpiration from the greater grass growth. While previous studies in CSS have examined competition between non-native grasses and *A. californica* for nitrogen (Zink & Allen 1998; Padgett & Allen 1999; Cione et al. 2002) or water (Eliason & Allen 1997), they did not assess the relative importance of nitrogen versus water limitation. We found the effect of soil moisture was stronger than any influence of soil nitrogen on shrub growth: we do not attribute this lack of an effect to the short duration of the experiment limiting changes in soil nitrogen metrics because we also found large (20%) changes in many soil organic matter variables. Total carbon and nitrogen responded especially strongly during this experiment, and suggest our findings of higher soil nitrogen in High Invasion areas were driven by abiotic and biotic changes produced by non-native grass litter (Wolkovich et al. in press). While the positive effect of litter via moisture is contrary to hypotheses regarding non-native grasses and *A. californica* (Padgett & Allen 1999), it supports models showing non-native grass litter can benefit native forbs through its effect on soil moisture (Levine & Rees 2004), evidence that water is the major structuring force for plant communities in Mediterranean systems (Vila & Sardans 1999), and recent studies suggesting invasive plants may sometimes benefit native plants by altering nutrient cycling (Gomez-Aparicio & Canham 2008; Rout & Callaway 2009).

Importantly, we found consistent effects of grass litter across several years of significant inter-annual variation in rainfall and plant production. CSS, like many semi-arid systems, is punctuated by irregular, high precipitation years, often followed by several years of drought (Morrison & Bolger 2002). Our manipulation coincided with one such irregular, high rainfall year (2005, 190% mean rainfall), resulting in high non-native grass and litter production, and was followed by two moderately dry years with lower production. The role of litter was clearly important to native shrubs in these two moderately dry years, but further research designed to disentangle the roles of litter and rainfall pulse dynamics is needed (Walters et al. 1988).

Our results contrast with studies documenting negative correlations between non-native grass cover and native shrub cover in CSS (DeSimone & Zedler 2001). These observational studies may reflect longer-term processes in which factors such as

fire and disturbance play greater roles than interactions between invasive and native species (Keeley et al. 2005b). Additionally, such patterns of shrub decline may reflect the possibility that interactions between *A. californica* and invasive grasses vary with the shrub life-stage, moving from competition to facilitation as shrubs mature. Manipulative restoration studies have documented negative relationships between non-native grasses and *A. californica* only at early shrub life-stages (Eliason & Allen 1997): after 1 year of shrub growth all such negative effects disappeared (Eliason & Allen 1997; Cione et al. 2002). As shrubs mature, grasses may create more favorable soil conditions for shrub growth through litter-induced soil shading. The possibility that the sign of interactions between shrubs and grasses may change through shrub life-stages (Aguilar & Sala 1994; Armas & Pugnaire 2005) has not been considered in plant invasions (Daehler 2003); however, our results suggest the importance of considering the entire life history of plant species – from germination to senescence – in invasion biology.

Our results may provide an opportunity to both apply and extend theories on interactions between plant functional types. Studies and models of coexistence of native grasses and shrubs support facilitation of grasses by shrubs (Aguilar & Sala 1994; Armas & Pugnaire 2005), especially in water-limited systems (Maestre et al. 2003; Brooker et al. 2008). Here, we documented the reverse: that grasses can facilitate native shrubs. Because litter can alter microclimate (Maestre et al. 2003) and ecosystem processes (Hobbie 1992), it may be a major mechanism controlling grass-shrub interactions within and across seasons, and could alter conclusions about such interactions. Moreover, although we found the dominant effect of non-native grass litter on shrubs was via soil moisture effects, non-native grasses and their litter also substantially changed soil temperature, as well as ecosystem carbon and nitrogen (Wolkovich et al. in press), demonstrating that the traits of this invasive grass have multi-level effects (Eviner & Chapin 2003).

Our finding that non-native grass litter enhanced non-native grass success, especially in Low Invasion plots, may indicate an important positive feedback for invasion. The data suggest that a main mechanism for this enhancement may be altered microclimate: litter decreased soil temperature and increased soil moisture, probably due to an altered light regime on the soil surface. Any of these changes could increase germination or seedling success of non-native grasses in this semi-arid climate. The litter additions unavoidably added a small amount of

seeds – those few still fully attached in seed heads – that could have contributed to the observed increase in grass cover. However, we believe this potential artifact did not drive the increase: seeds were unlikely to be limiting because small plot size (3m×3m) and close proximity to areas of dense non-native grass ensured high seed rain into all plots. Furthermore, Removal from pre-manipulation High Invasion areas left an extremely high abundance of seeds, yet these areas showed decreased living grass in the first year after manipulation. The positive response of non-native grasses to litter suggests that the benefits in terms of soil moisture outweigh any negative impacts due to shading. Living grass cover increased following Additions to areas of already High Invasion (Fig. 1e), indicating that even at very high densities (~0.25 kg dry weight per m² in 2005), litter benefits non-native grasses; however, Additions to Low Invasion areas showed far more dramatic effects (Fig. 1f). Several other studies of similar widespread invasive grasses have found grass litter positively associated with the success of grasses (Heady 1956; Clements et al. 2007), for example, thatch reduction decreases non-native plant cover in California grasslands (Meyer & Schiffman 1999).

Our results have implications for restoration of invaded landscapes. Research suggests that many semi-arid grasslands and shrublands may have tendencies towards alternative stable states with contrasting amounts of bare ground (Borgogno et al. 2007). If this is the case in CSS, targeted thatch reduction may help return systems to their pre-invasion state. Thatch reduction is already used to reduce fuel load in many Mediterranean climate invaded shrublands (Meyer & Schiffman 1999; Allen et al. 2005). Our findings suggest it may also decrease non-native growth and thus future thatch production. However, because we also found litter removal decreased native shrub growth, managers need to consider their ultimate goals when designing de-thatching programs, and may wish to manage thatch under adult shrubs. Because our results were conducted at only one site, further research is needed. However, if the interaction of non-native grass litter and native shrubs varies by life-stage, thatch removal programs combined with applications of native seeds or seedling plantings may be an effective strategy to increase native plant success (Seabloom et al. 2003).

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