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Soil nitrogen cycling is resilient to invasive annuals following restoration of coastal sage scrub

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ABSTRACT

Southern California coastal sage scrub (CSS) is highly invaded by Mediterranean annual grasses and undergoing extensive restoration efforts. Exotic plant invasion alters ecosystem structure and function through plant-soil feedbacks that can be detrimental to native plants. Assessments of CSS restoration have focused on aboveground plant communities, while belowground effects have received less attention. We examined CSS soil resilience following restoration of native CSS species using ecosystem property divergence in restorations from an invaded state as a measure of exotic plant impacts. We hypothesized that exotic annual plants compete with native species for nutrients and change nutrient cycling, and exotic plant removal and native plant restoration would allow soil recovery under native plant-soil inputs. Nitrogen (N) cycling was resilient but not resistant to vegetation changes. Exotic annual plants increased N mineralization and nitrification but did not affect total soil carbon (C) and N and extractable phosphorus. Extractable N was reduced in invaded plots, and immediately increased following weeding. These changes suggest that exotic plants are directly competing with native plants for N. Impacts to N cycling were reversible after exotic plants were removed and native shrubs reestablished, which may have important implications for recovery of other ecosystems invaded by annual grasses.

1. Introduction

Invasion of exotic species offers the opportunity to assess ecosystem resistance to invasion-caused impacts, and resilience of the system once invasives are removed. Resistant ecosystems would remain unaltered by an invading species such that soil nutrient pools would remain unchanged. Ecosystems that are not resistant to invasion may still be resilient following restoration (Lake, 2013; Westman, 1978). Exotic plants have traits that can alter native ecosystem processes, including different quality, quantity and timing of litter deposition; root exudates; phenology; and microbial associations (Christian and Wilson, 1999; Ehrenfeld, 2003; Klironomos, 2002; Yoshida and Allen, 2004). Exotic plants can alter plant-soil feedbacks to facilitate their persistence by fostering a microbial community or soil nutrients that hinder natives, facilitates exotics, or both (Batten et al., 2008; Ehrenfeld, 2003; Hawkes et al., 2006; Klironomos, 2002; Kourtev et al., 2002; Kulmatiski et al., 2008). Exotic plants can directly impact natives through competition for space, light, water and soil nutrients (D'Antonio et al., 1998; Ehrenfeld, 2003; Eliason and Allen, 1997). Comparison of short- and long-term restorations in invaded and restored lands can be used to identify soil characteristics that are more sensitive to invasion (Callaway and Ridenour, 2004). For instance, removal of exotics could increase availability of mobile and faster-cycling nutrients, such as nitrate, within a single growing season, while longer term impacts might include changes in slower cycling organic N and carbon (Schlesinger, 1997; Scott and Morgan, 2012; van der Putten et al., 2007). If removal of the invading species leads to recovery of natural soil resource levels, then soils are believed to be resilient to the initial impact of the invading, exotic species.

Coastal sage scrub (CSS) is a semi-deciduous, Mediterranean-type shrubland distributed from coastal, central California to northern Baja California, Mexico. Most of the remaining CSS that has not been converted to urban or agricultural uses has been invaded by Mediterranean annual grasses and forbs. It is one of the most endangered ecosystems in the United States (Klopatek et al., 1979; Rubinoff, 2001; Westman and Oleary, 1986), making it a priority ecosystem for preservation and restoration. Regional, uninvaded CSS references are becoming increasingly rare, so much so, that many Southern California CSS restoration projects lack a

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local reference site upon which to base goals and gage change. In such cases, the invaded site may act as a baseline from which the level of divergence of system properties from the invaded to the restored state can act as a proxy for a measure of exotic impacts (Alverez and Cushman, 2003; Díaz et al., 2003). Restoration studies have focused on aboveground competition (Eliason and Allen, 1997), but the effects of invasive species on CSS soils and their resilience following restoration has received little attention. The removal of exotic plants will have direct effects on competition with natives, but may also have indirect effects through changes to soil biogeochemical cycling.

Exotic annual grasses may have phenology, rooting structure and depth (Eliason and Allen, 1997; Wolkovich et al., 2009; Wood et al., 2006), and tissue nutrient composition (Wolkovich et al., 2010) that differ greatly from native CSS shrub species. This difference in species traits gives exotic grasses the potential to change the shrub ecosystem significantly. Restoration of CSS typically consists of controlling invasive plants and reintroducing a mature shrub community via seeding or planting of container plants (Bowler, 2000). In a successful restoration native litter inputs to the soil along with the rooting structure and microbial associations of native plant species will return. In this study, our hypotheses were: (1) CSS soils are not resistant to exotic plant invasion and therefore will experience changes in the chemical properties of soils due to altered litter chemistry inputs following restoration from the invaded state and (2) if exotics are controlled and native CSS species restored, chemical properties will return to pre-invaded conditions due to the resilience of CSS soils and the restoration of native CSS plant species inputs.

2. Methods

2.1. Study sites and experimental design

Research was conducted at White Point Preserve located in San Pedro, Los Angeles County, California, USA. The site receives 30 cm precipitation annually, most from November to April, with a winter growing season and warm, dry summers (temperature range of 8–26 °C). Soils are classified as clay loam of the Diablo Clay Adobe series (Nelson et al., 1919). Soil texture was 33% sand, 33% silt and 34% clay. The preserve is located on a 121-ha decommissioned Department of Defense missile facility in CSS vegetation that has been invaded for several decades by exotic annual grasses with a lesser coverage of exotic forbs. White Point Preserve lacks a local, uninvaded reference site against which invaded and restored sites can be compared; therefore, we examined the divergence of two restorations of differing age from an invaded baseline. Approximately half of the site was restored to CSS beginning in 2000, leaving stands of invasive plants that we used to compare restored and invaded areas for this study. The original restoration consisted of exotic plant control (mowing and herbicide spot application), seeding native shrubs and forbs, planting native shrub seedlings, and irrigation. This original restoration is termed the long-term restoration study, and was used to determine the effects of long-term re-establishment of native plants on soil chemistry. Nine replicate 1 m^2 plots per treatment (invaded and restored) were established on a southwest-facing slope. The restored and invaded sites were adjacent, and located on the same slope and soil type. Plots of the restored treatment were randomly located under shrubs between the shrub base and drip-line. Plots of the invaded treatment were located randomly within large unrestored patches adjacent to the restored area. Restored sites had successful native shrub re-establishment since 2000 and <50% exotic species cover, while invaded areas contained >50% exotic plant species cover.

To address more rapid effects of exotic plant competition, we established two additional sets of nine 1 m^2 plots in the invaded areas. We termed this our short-term restoration, which used two treatments: Seed, in which native seed was gently raked into invaded plots, and Weed/Seed, in which plots were weeded free of all exotics and then seeded with native species. Hand-weeding of all exotic species was maintained up to three weeks prior to data collection and seeding occurred following the first rains in the fall of 2007. Due to drought in the 2006–2007 season, much of the seed was lost to granivory, so seeding was repeated in 2008. Seeds of two shrubs, *Artemisia californica* (California sagebrush; 100 seed/m^2), *Eriogonum fasciculatum* (California buckwheat; 200 seed/m^2) and an annual forb, *Phacelia ramosissima* (branching phacelia; 100 seed/m^2) were evenly distributed over the plot and raked into the soil. Seed was donated by Palos Verdes Peninsula Land Conservancy and collected on site 2004–2006.

2.2. Plant community composition

To identify differences in plant species composition between invaded, long-term restoration and short-term restoration, species percent cover and species richness were measured three times annually (germination, peak growth and senescence) and percent cover of litter was measured annually at peak growth from 2007 to 2009. Net annual productivity of annuals was determined by collection of biomass clipped at soil level from 0.25 m^2 plots and scaled up to 1 m^2 using regression models of mass and percent cover (biomass = 0.0546*cover+7.9695; R^2 = 0.144, P = 0.0013). Additional biomass was collected for vegetative plant tissue chemical analysis at that time. Biomass was oven dried at 60 °C, weighed, ground and analyzed for total C and N on a combustion analyzer system (Thermo-Finnigan model: Flash AIIIZ).

2.3. Soil chemistry, respiration and mineralization

To identify effects of exotic plant invasion on soil chemical characteristics, three soil cores (10 cm deep by 2.5 cm diameter) were collected from each plot at the time of plant species percent cover and richness sampling and composited within each plot (n = 36 plots) three times annually 2007–2009. Soils were air dried and passed through a 2 mm sieve for analysis of total C and N using the combustion method. Soil pH was determined with a 2:1 soil:-water slurry. Phosphorus (P) was determined in sodium bicarbonate extracts by the UC Davis Analytical Laboratory (anlab.ucdavis.edu). Extractable N (NH_4^+ and NO_3^-) was measured on soil cores collected in August of 2006 at germination, peak and plant senescence periods of the 2007–2008 growing season. Nitrogen was extracted in 1 M KCl, shipped on dry ice and analyzed using the flow injection method at the UC Davis Analytical Laboratory.

Laboratory incubations for N mineralization were performed on soils collected in March and August of 2008 and incubated over a 30 day period maintaining 25 °C and 60% humidity. Soil NH_4^+ and NO_3^- were extracted with a 2 M KCL 4:1 solution (Riley and Vitousek, 1995) and shipped on dry ice for analysis to the UC Davis Analytical Laboratory. Net mineralization was calculated as the change in NH_4^+ minus the change in NO_3^- over time and net nitrification as the change of NO_3^- over time following Riley and Vitousek (1995). Potential soil respiration rates were determined with laboratory incubations. Soils were maintained at 20% soil moisture and 25 °C in sealed mason jars for 10 days. Jar headspace concentrations of CO_2 (ppm) were determined using a LiCor 800 infrared gas analyzer (Lincoln, USA) and converted to a rate function of mg CO_2–C g soil^{-1} day^{-1} (Chatterjee et al., 2008).