RESEARCH ARTICLE

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Differences in root phenology and water depletion by an invasive grass explains persistence in a Mediterranean ecosystem

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PREMISE: Flexible phenological responses of invasive plants under climate change may increase their ability to establish and persist. A key aspect of plant phenology is the timing of root production, how it coincides with canopy development and subsequent water-use. The timing of these events within species and across communities could influence the invasion process. We examined above- and belowground phenology of two species in southern California, the native shrub, *Adenostoma fasciculatum*, and the invasive perennial grass, *Ehrharta calycina* to investigate relative differences in phenology and water use.

METHODS: We used normalized difference vegetation index (NDVI) to track whole-canopy activity across the landscape and sap flux sensors on individual chaparral shrubs to assess differences in aboveground phenology of both species. To determine differences in belowground activity, we used soil moisture sensors, minirhizotron imagery, and stable isotopes.

RESULTS: The invasive grass depleted soil moisture earlier in the spring and produced longer roots at multiple depths earlier in the growing season than the native shrub. However, *Adenostoma fasciculatum* produced longer roots in the top 10 cm of soil profile in May. Aboveground activity of the two species peaked at the same time.

CONCLUSIONS: The fact that *Ehrharta calycina* possessed longer roots earlier in the season suggests that invasive plants may gain a competitive edge over native plants through early activity, while also depleting soil moisture earlier in the season. Depletion of soil moisture earlier by *E. calycina* suggests that invasive grasses could accelerate the onset of the summer drought in chaparral systems, assuring their persistence following invasion.

KEY WORDS chaparral; global change; invasion; Poaceae; roots; Rosaceae; soil; water-use.

Shifts in vegetation composition due to invasion are an aspect of global change that alters ecosystem processes and function across the world (D'Antonio and Vitousek, 1992; Walther et al., 2002; Gonzalez et al., 2010). Terrestrial plant invasion often leads to vegetation community type conversion, such as from native shrubland to invasive grassland, which can be accompanied by changes in soil resource availability. Globally, Mediterranean ecosystems may face the greatest losses of biodiversity because of their susceptibility to multiple global change drivers, such as precipitation variability and biotic introductions (Sala et al., 2000; Stocker et al., 2013).

Invasive grasses are establishing and persisting post-disturbance in the dominant Mediterranean-type shrubland in California, USA, the chaparral (Stylinski and Allen, 1999; Keeley and Brennan, 2012; Dickens and Allen, 2014; Meng et al., 2014). Invasive grasses often possess flexible resource acquisition strategies that can facilitate rapid phenological responses, which may enable them to invade chaparral systems (Willis et al., 2010; Wolkovich and Cleland, 2014; Ashbacher and Cleland, 2015). Specifically, these strategies could include acclimation to earlier spring temperatures, unseasonably early rains, and the ability to respond to an increase in nutrient availability (Willis et al., 2010). Flexible responses to precipitation could make invasive plants stronger competitors in a changing climate compared to native shrubs, especially when climate interacts with global change drivers that promote invasion, such as frequent fire, vegetation removal, or anthropogenic nitrogen deposition (D'Antonio and

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Vitousek, 1992; Bradley et al., 2010; Fenn et al., 2010; Willis et al., 2010). Loss of chaparral vegetation to invasive grasses could affect ecosystem structure both above- and belowground, with potential cascading effects on ecosystem services (Ehrenfeld, 2010). To improve our ability to predict risk to invasion and vegetation type conversion in California's chaparral, it is critical to address gaps in understanding related to how phenology enables invasion success in the chaparral and the relationship between above- and belowground phenology in invaded systems.

In Mediterranean ecosystems, the frequency and magnitude of rain events has the potential to affect the production of fine roots for some vegetation types (Palacio and Montserrat-Martí, 2007). Root phenology might enable invasion success through differences in the timing of root development with respect to resource availability (McCormack et al., 2014). Specifically, invasive grasses, whether annual or perennial, may escape drought through the production of short-lived, dense, fine roots for rapid water and nutrient uptake (Williamson et al., 2004a, b; Wolkovich and Cleland, 2011; Wainwright et al., 2012). Alternatively, drought tolerant shrubs may be highly dependent on seasonal precipitation events for recharge through the soil profile (Schwinning and Ehleringer, 2001), and are likely to possess long-lived, relatively less efficient fine roots (Chen and Brassard, 2013). In a high elevation Mediterranean forest, root growth preceded aboveground activity as soil moisture and temperature were increasing (Kitajima et al., 2010). Further, if rain events are not large enough for deep recharge, shrubs may engage in hydraulic redistribution (the movement of water from wetter to drier regions of soil) from wet upper layers to deep drier layers to maintain existing plant physiological function and foliage throughout the summer drought (Querejeta et al., 2003, 2007, 2009; Ryel et al., 2004; Kitajima et al., 2013). These phenology patterns and rooting architecture may allow chaparral shrubs to better tolerate Mediterranean-climate summer drought.

Although multiple studies have shown that invasive plants may display flexible phenological responses, most studies focus on aboveground responses (Willis et al., 2010; Wainwright et al., 2012). When belowground work is included, the inherent challenge of studying root activity can limit understanding of belowground dynamics (Palacio and Montserrat-Martí, 2007; Steinaker and Wilson, 2008; Steinaker et al., 2009; Du and Fang, 2014; McCormack et al., 2014, 2015; Smith et al., 2014; Wilson, 2014). Generally, grass roots of these Mediterranean-type ecosystems tend to be shallow, and plants senesce early in the growing season (e.g., Davis and Mooney, 1985; Eliason and Allen, 1997; Hooper and Vitousek, 1998) whereas shrubs including *Adenostoma fasciculatum* Hook. & Arn. [Rosaceae] sustain leaves during the dry season, depending on deep roots that penetrate cracks in the bedrock (e.g., Hubbert et al., 2001; Egerton-Warburton et al., 2003). To our knowledge, no studies to date integrate invasion ecology with simultaneous measurements of above- and below-ground phenology. In our study, we emphasized temporal dynamics at a fine scale to understand water use through the profile and over time (Allen et al., 2007), to determine if belowground phenological activity differs from aboveground landscape-scale phenology using remote sensing and stand-level phenology using sap-flux measurements. These species characterize the differences in rooting depth and aboveground phenology shifts of other grass-invaded, type-converted shrublands, where grasses senesce early in the growing season compared to shrubs (Davis and Mooney, 1985; Williamson et al., 2004b; Dickens and Allen, 2014; Rundell, 2018).

In this study, we examined normalized difference vegetation index (NDVI), a measure of canopy greenness, across the landscape coupled with sap-flux measurements to assess phenological differences between the most abundant invasive grass (*Ehrharta calycina* Sm. [Poaceae]) and the dominant native chaparral shrub (*Adenostoma fasciculatum*) at our study site. Most native chaparral shrubs, including our study species are evergreen, meaning that they maintain a relatively constant NDVI throughout the year, whereas invasive grasses senesce in summer causing them to exhibit larger seasonal variations in NDVI (Gamon et al., 1995). Therefore, our unique approach allows us to disentangle the phenological differences between *A. fasciculatum* and *E. calycina*, by using in situ transpiration (sap-flux) measures and NDVI, respectively. To determine if there was a rooting phenology offset, we contrasted aboveground phenology with intensive root image and in situ environmental and physiological measurements at one site to differentiate *A. fasciculatum* and *E. calycina* water relations and root as well as shoot phenology. We also explored what water source (surface or deep) *A. fasciculatum* was accessing using stable isotopes. We predicted that (1) *E. calycina* will deplete soil moisture at shallower depths given (2) production of shallower and longer roots as compared to *A. fasciculatum*. We also predicted that (3) *A. fasciculatum* will be able to access deeper water sources at the onset of the summer drought, potentially driving (4) later peak aboveground production in *A. fasciculatum* as compared to *E. calycina*.

MATERIALS AND METHODS

Site Description

The study was conducted in the San Gabriel Mountains of California, USA, at San Dimas Experimental Forest (34°12' N, 117°46' W, and 50 km east of Los Angeles) at 830 m a.s.l. The soils consist of loam in the A horizon (0–8 cm), gravely sandy loam in the B and C (8–43 cm), and weathered bedrock in the Cr (43–53 cm) with a parent material of residuum weathered from granodiorite (NRCS Web Soil Survey, 2016). The soils possess many rock outcroppings and have moderate concentrations of macronutrients (total N = 0.17%, Ulery et al., 1995; extractable P = 30 ug/g and extractable K = 200 μg/g, Egerton-Warburton et al., 2001). The site exhibits a typical Mediterranean climate with cool winters, variable winter rainfall, and hot, dry summers. Mean annual precipitation is 68 cm, however during our seven-month study period (November 2015 – June 2016) which occurred over one growing season there was a total of 41 cm of precipitation. Mean annual temperature is 14.4° C and summer temperatures regularly exceed 37.8° C but minimum winter temperatures rarely drop below −3° C (Dunn et al., 1988). The site consists primarily of chaparral shrubland, which is one of the most widespread vegetation types in California (Parker et al., 2016), but some areas were deliberately type converted by seeding *Ehrharta calycina* to grassland during the 1960s (Dunn et al., 1988). Overall the site is composed of chaparral species from the genera, *Salvia* [Lamiaceae]*, Arctostaphylos* [Ericaceae]*, Eriogonum* [Polygonaceae]*, Rhamnus* [Rhamnaceae], and *Ceanothus* [Rhamnaceae]. *Ehrharta calycina* is by far the most abundant invasive grass at this site, though there are also species of *Bromus* [Poaceae] and *Avena* [Poaceae]. Adjacent nearly monotypic stands of native shrub, *Adenostoma fasciculatum,* and the invasive perennial grass, *Ehrharta calycina,* were chosen for investigation.

Adenostoma fasciculatum is a tall (>2 m), long-lived (>60 yr) shrub, while *Ehrharta calycina* is relatively short-statured (<75 cm) and short-lived (~5 yrs). We manually removed all *Ehrharta calycina* that was present in the *Adenostoma fasciculatum* stand before the start of the experiment (about 15 individuals, taking care to minimize soil surface disturbance) and continued to remove subsequent seedlings for the duration of the experiment. *Adenostoma fasciculatum* is widespread and dominant throughout California chaparral, and *Ehrharta calycina* is an abundant invasive grass primarily on the coast (e.g., Cushman et al., 2011).

Environmental measurements

We deployed and maintained Campbell CS-616 volumetric water content (VWC) sensors (Campbell Scientific Inc., Logan, Utah, USA) from December 2015 until June 2016 in one stand of invasive and one stand of native vegetation. The stands were adjacent and on the same soil type, slope, and aspect. We chose a site that was relatively level (<10% slope) to facilitate instrument installation. The two stands were 10 m apart and each plot within the stand was at least 5 m from other plots to avoid edge effects. Because of the intensive nature of root observations coupled with plant and soil observations, only the two stands were studied.

Three replicate soil moisture were installed 30 cm deep either underneath the root crown individual *Adenostoma fasciculatum* shrubs, under monotypic *Ehrharta calycina* or under bare soil where we manually removed the grass vegetation. We co-located soil moisture sensors with minirhizotron tubes. Additionally, for *A. fasciculatum,* we chose three individuals that were ~5 m away from each other to avoid overlapping root systems. Bare ground and *E. calycina* plots were 1 m^2 and paired and adjacent with an unsampled edge of 0.5 m around bare ground plots to avoid edge effects. We compensated for changes in albedo and surface temperature resulting from grass removal by the replacing grass leaf litter on ground. Within the grass and bare ground sub-plots, Campbell CS-650 soil VWC sensors (Campbell Scientific) were deployed at 30 cm depth. For each plot type (n = 3), we calculated diurnal soil VWC and applied a two-week running average to remove spikes caused by rain events. Daily precipitation data for the entirety of the study period was acquired from PRISM (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA, website http://prism.oregonstate.edu, created 3 July 2017).

Aboveground phenological measurements

To understand the phenological activity at the landscape scale, we used remotely sensed imagery sourced from the Operational Land Imager (OLI) onboard Landsat 8 (Roy et al., 2014). We acquired level 2 image top of atmosphere reflectance data using Google Earth Engine (GEE (Chander et al., 2009; Schmidt et al., 2013; Dong et al., 2016; Gorelick et al., 2017). We extracted normalized difference vegetation index (NDVI) values for a 30 m pixel (with ca. 70% grass cover), in which our site was located from all available Landsat 8 images with less than twenty percent cloud cover from 10 October 2015 until 20 June 2016 (n = 16). Seasonal differences in NDVI that we observe can be primarily attributed to *Ehrharta calycina* since the surrounding shrub vegetation is evergreen and therefore maintains relatively consistent NDVI throughout the seasons (Gamon et al., 1995; Park et al., 2019). We compared NDVI measures of *E. calycina* with transpiration measures of *Adenostoma fasciculatum*.

We fit a harmonic regression to the NDVI values using the 'harmonic.regression' function in the 'HarmonicRegression' package in R to account for erroneous NDVI values and increase accuracy of our ability to detect peak NDVI values (Lueck et al., 2015).

To measure transpiration, stem sap flux velocity was measured from January to June 2016 using custom built 10-mm Granier-style thermal dissipation probes (Granier, 1987) singly or in pairs on *Adenostoma fasciculatum* individuals (n = 7). Outputs were recorded every 30 s and averaged every 5 min using a Campbell CR-10x datalogger (Campbell Scientific Inc.). Probes were inserted at the widest knot-free point of the stem 10–35 cm above ground and insulated with a reflective mylar wrap as well as silicone caulking. Conducting sapwood area was determined in December 2017 by taking stem cross-sections, staining active xylem with a dilute solution of safranin, and examining sections at 50× magnification (Sano et al., 2005). Non-conducting sapwood area was determined to be negligible and stem sap flow was calculated by scaling flux velocity by stem cross-sectional area at the point of probe insertion. Stand transpiration was calculated by normalizing stem sap flow by stem basal area across instrumented shrubs. We applied a 14-day running average to transpiration data to capture overall trends. We normalized both our 14-day running average stand transpiration and harmonic regression NDVI values to the maximum of each value to compare changes in response to the peak of both *A. fasciculatum* (stand transpiration) and *Ehrharta calycina* (NDVI).

Belowground imagery (root length)

Seasonality of root length was followed using a manual minirhizotron (MMR, Rhisosystems, LLC., Idyllwild, California, USA; website http://www.rhizosystems.com/Home.php). Sequential belowground images were captured using wireless 100X digital camera that runs through a transparent 5-cm diameter tube buried in the soil (MMR, Rhizosystems, LLC.). Three MMR tubes were installed under *Adenostoma fasciculatum* and three under *Ehrharta calycina* at a 45° angle to the soil surface, capturing root standing crop from 0 to 40 cm below ground. We installed tubes in August 2015 to allow the soil to settle around the tubes and fine roots to grow prior to data collection. Each tube had an airtight seal to prevent water from accumulating and had an additional PVC covering to prevent light from entering the tube. Imagery was taken bi-weekly at consecutive windows from December 2015 until May 2016. We recorded eighty 6.75 mm × 9.00 mm images for each tube at every time step that were then organized into a mosaic using Rootview (Rhizosystems, LLC.) for a total of 6240 images. An example of raw images can be found in Fig. 1A and B. Image processing was done using Rootfly version 2.0.2, (Birchfield and Wells, 2016), where we measured lengths and diameters of all roots observed. We aggregated both the root length into monthly observations and bin by true depth from surface level.

Stable isotope analysis

Depending on the time of year and the type of plant, stem water reflects the water source a plant is using spatially and temporally (Ehleringer et al., 1991). To determine if *Adenostoma fasciculatum* is accessing water sources at different depths seasonally, we collected rainwater and well water in February 2017 as well as stem samples from *A. fasciculatum* in February 2017 and June 2017. Plant stems were collected directly from live plants and immediately placed in
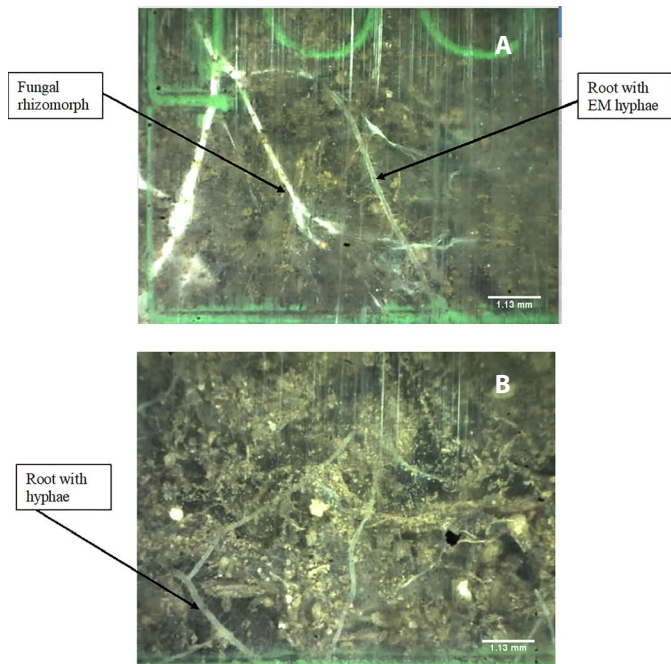
FIGURE 1. Example of image from manual minirhizotron (50× magnification) displaying (A) *Adenostoma fasciculatum* roots and EM (ectomycorrhizal) hyphae in February 2016 at ~35 cm depth and (B) *Ehrharta calycina* roots and arbuscular mycorrhizal hyphae in December 2015 at ~25 cm depth.

10 mL vacutainers (Becton Dickinson #367820, Franklin Lakes, New Jersey, USA), which were capped and sealed with parafilm to prevent evaporation. Samples were subsequently frozen at -20°C until analyzed. Water was extracted from plant stem samples using a cryogenic vacuum distillation line for at least 60 min for stems (Ehleringer et al., 2000; West et al., 2006). Stable isotopic composition of oxygen (δ^{18}O) analyses were conducted at the Facility for Isotope Ratio Mass Spectrometry at the University of California, Riverside using a Temperature Conversion/Elemental Analyzer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) interfaced with a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific). Values for δ^{18}O are reported in delta notation (‰) relative to the Vienna Standard Mean Ocean Water (V-SMOW) standard:

$$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000$$

Statistical analyses

Repeated-measures ANOVA were fit to diurnal soil VWC and root length data using the 'lmer' and 'anova' functions from the 'lme4' and 'stats' R packages (Bates et al., 2015; R Core Team, 2017; Appendix S1). To structure the repeated-measures ANOVAs and account for temporal autocorrelation, we built linear mixed-effects models and included measurement number (day) as a random effect. Then, we used the 'anova' function on the linear mixed-effects model object. For diurnal VWC, candidate predictor variables were vegetation type, month, and the interaction of vegetation type with month. Replicates were treated as random

effects to account for spatial variation. To examine the interaction of vegetation type and month for our VWC model, we calculated the estimated marginal means (least-squares means) using the 'emmeans' function with Tukey's adjustment from the 'emmeans' package in R (Lenth, 2019). For the root length model (0–40 cm), candidate predictor variables were vegetation type, month, depth, the interactions of vegetation type with month, and vegetation type with depth. We use month as a predictor variable because it averages the VWC or root length across multiple measurements which removes some of the temporal autocorrelation structure of the data. Again, we included measurement number (measurements were taken bi-weekly) and replicate as random effects. For model selection, we used the 'step' function from the 'lmerTest' package on full models to do a backwards elimination of fixed effects using Akaike information criterion (AIC). We retained full models for both VWC and root length, as ΔAIC values were less than two.

We used four repeated measures ANOVAs for each depth bin (0-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm) with root length as the response variable and vegetation type and month as the predictor variables. Measurement number (day) and replicate were treated as random effects. We calculated estimated marginal means with Tukey's adjustment to compare the interaction between vegetation type and month on root length for each depth.

ANOVAs were fit to the isotope data using the 'anova' function from the stats' R package (R Core Team, 2017). Tukey's pairwise comparisons were performed on δ^{18}O isotope data using the 'TukeyHSD' function in the 'stats' package. All data conformed to expectations of normality of residuals and homoscedasticity of variance. For δ^{18}O analyses, source (well water, rainwater, stem water in February, and stem water in June) was the predictor variable and δ^{18}O values were the response variable. Analyses were conducted using R version 3.2.1 (R Core Team, 2017). All data and analyses used to generate these results are publicly available as a redistributable R package (website: https://github.com/bmcnellis/SDEF.analysis/releases/tag/v1.1).

RESULTS

Environmental variables

Soil moisture in the *Adenostoma fasciculatum* stand (native vegetation) at 30 cm depth began to increase after rain events (<5 cm) in mid-December 2015 (Fig. 2A). Equipment failure prevented assessment of soil moisture for *Ehrharta calycina* (invasive vegetation) and bare ground plots until mid-January when it was observed that soil moisture across the site steadily increased with multiple rain events (Fig. 2A). We did not include measurements in our statistical analyses before mid-January when sensors in all plots were operating. Soil moisture peaked under native and invasive vegetation during the middle of March, and the peak was marginally less under invasive vegetation.

Based on repeated measures ANOVA, soil moisture values were significantly different by month and there was a significant interaction between vegetation type and month (p = 0.0002 and 0.0007, respectively, Appendix S1). VWC was not significantly different between vegetation type alone over all months (p = 0.8844, Appendix S1). Bare ground plots had lower soil moisture than plots with either native or invasive vegetation in January (native p = 0.0009; invasive
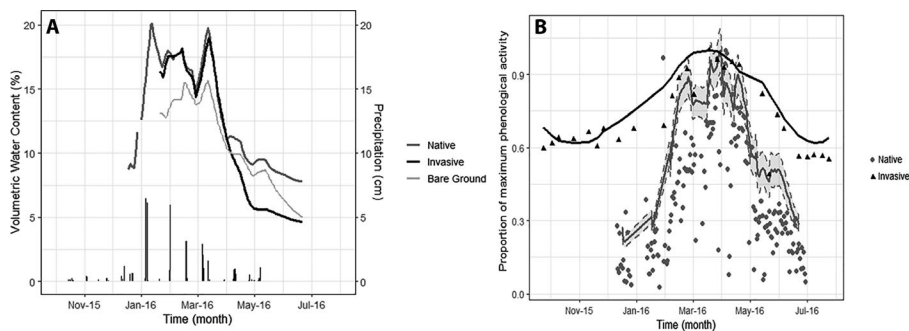
FIGURE 2. (A) Two week running averages of volumetric water content at 30 cm depth for native (*Adenostoma fasciculatum*), invasive (*E.calycina*), and bare ground (all vegetation removed) plots (n = 3). Bars represent precipitation events derived from PRISM data. (B) Two-week running averages of aboveground activity measured as transpiration of native vegetation in grey (*A. fasciculatum*) and aboveground activity measured as NDVI fit to a harmonic regression for the study site (representing invasive grass activity) normalized as a percentage of the maximum observed value for each. Points are values used to fit harmonic regression (NDVI: black triangles) or two-week running average (transpiration: gray circles). Standard error for transpiration values (n = 7) is displayed around two-week running averages (solid gray line) as a grey ribbon with dashed gray lines.

$p = 0.0035$), February (native $p = 0.0039$; invasive $p = 0.0004$), and March (native $p = 0.0023$; invasive $p = 0.0007$, Fig. 2A, Appendix S2). In April, there was no difference in soil moisture under invasive vegetation and bare ground ($p = 0.2814$, Fig. 2A, Appendix S2). Soil moisture did not differ under native and invasive vegetation until April ($p = 0.0191$, Fig. 2A, Appendix S2). After April, soil moisture remained higher under native than under invasive vegetation in May and June ($p = 0.0001$ and 0.0002, respectively, Fig. 2A, Appendix S2). In May, soil moisture in plots with bare ground was higher than under invasive vegetation ($p = 0.036$, Fig. 2A, Appendix S2).

Aboveground phenology

Adenostoma fasciculatum responded to rain events (>5 cm) in early January, with concomitant increased soil water availability and transpiration as measured by sap flux sensors (Figs. 2A, B). Landscape-level aboveground activity (NDVI), which is primarily driven by grass activity, reached its' peak on March 27 and the aboveground activity of *A. fasciculatum* (transpiration using sap-flux) peaked around the same time on March 30 (Fig. 2A). Raw NDVI values ranged from 0.2-0.5, meaning the proportion of activity relative to the maximum range from 0.5 to 1 (Fig. 2B).

Belowground imagery (root length)

During the study period we observed a total of 233 roots of *Adenostoma fasciculatum* with a mean root length of 4.05 mm in the viewing area (0–40 cm in the soil profile around the 5-cm diameter tube). Whereas for *Ehrharta calycina* there was a total of 1596 roots with a mean root length of 4.11 mm. Repeated measures ANOVA showed that root length was affected by the interaction between vegetation type and month ($p = 0.00001$; Fig. 3; Appendix S3), but not by vegetation type alone ($p = 0.2935$; Fig. 3; Appendix S3). Additionally, the interaction of vegetation type with depth affected root length ($p = 0.0045$; Fig. 3;

Appendix S3). Specifically, invasive grasses produced longer roots than native shrubs across our entire observation area within the soil profile (0–40 cm) in December 2015 ($p = 0.0090$; Fig. 3; Appendix S4). We did not observe significant differences in root length across all depths (0-40 cm) during any months after December 2015 ($p > 0.05$; Fig. 3; Appendix S4).

The interaction of vegetation type with month affected root length at 0–10 cm ($p = 0.0001$; Fig. 3; Appendix S3). Invasive vegetation produced longer roots than native vegetation at 0–10 cm and 20–30 cm in December 2015 ($p = 0.002$ and 0.0097, respectively; Fig. 3; Appendix S4). There were no differences in root length at 0–10 cm in January, February or March 2016 ($p = 0.3501$, 0.9545 and 0.5774; Fig. 3; Appendix S4), however native shrubs possessed longer roots at 0–10 cm in May 2016 ($p = 0.0037$; Fig. 3; Appendix S4). Invasive vegetation produced longer roots at 10–20 cm than native vegetation in February 2016 ($p = 0.0501$; Fig. 3; Appendix S4). We didn't observe any significant differences in root length between vegetation types at 20–30 and 30–40 cm for any months ($p > 0.05$; Fig. 3; Appendix S4).

Stable isotope analysis

We used the $\delta^{18}O$ signatures from the two water sources, rainwater and well water (i.e., groundwater), coupled with $\delta^{18}O$ signatures from *Adenostoma fasciculatum* stem water to discern what sources of water *A. fasciculatum* was accessing during the wet and dry seasons. Well water and rainwater samples had similar signatures that were not significantly different ($p > 0.05$, Appendix S5). Stems collected from *A. fasciculatum* in February coinciding with abundant precipitation had significantly lower $\delta^{18}O$ than well-water samples, but not lower than rainwater samples ($p < 0.05$, Fig. 4, Appendix S5). In contrast, the stems collected from the same individuals in June, coinciding with the onset of the summer drought, had significantly higher $\delta^{18}O$ than winter rainy season stem samples and rainwater samples ($p < 0.001$, Fig. 4, Appendix S5).

DISCUSSION

Intensive measurements over time showed that invasive vegetation depleted soil moisture more rapidly toward the end of the rainy season than both native vegetation and bare ground. Greater depletion of soil moisture under *Ehrharta calycina* starting in April and continued into the summer drought when compared to *Adenostoma fasciculatum* supports our first hypothesis. In this study system, 30 cm is considered relatively shallow in the soil profile since chaparral plants possess deep roots (Kummerow, 1983; Schenk and Jackson, 2002; Williamson, Graham et al., 2004). We expected that aboveground activity (NDVI) at the site level—representing invasive grass activity (Gamon et al., 1995)—would peak before *A. fasciculatum* aboveground activity (transpiration), but instead found that they peaked around the same time. We also found support for our prediction that *E. calycina* would produce longer roots at shallower
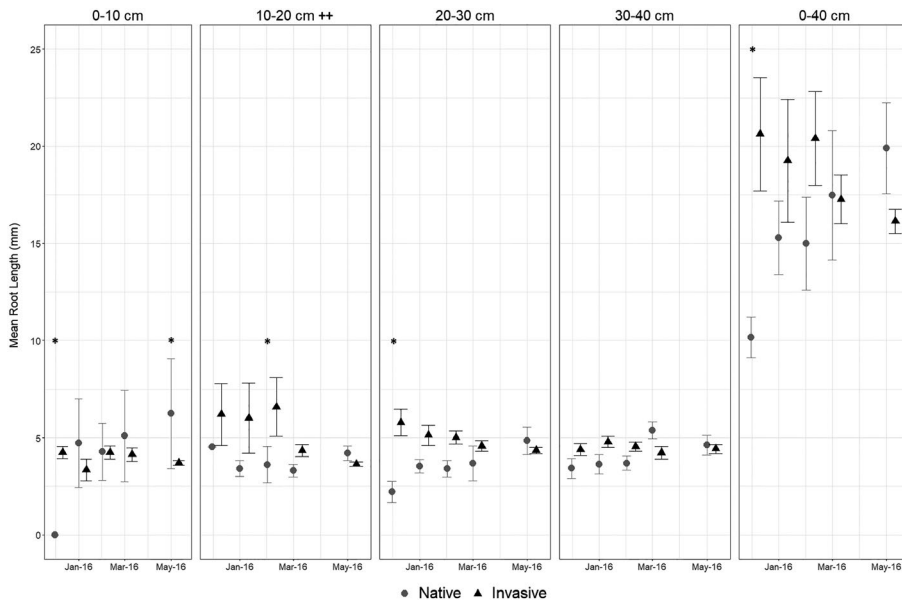
FIGURE 3. Monthly mean root length (mm) of native vegetation (*Adenostoma fasciculatum*; n = 3) and invasive vegetation (*Ehrharta calycina*; n = 3) at four depths within the soil profile and the total observation area (0–40 cm in the soil profile) from the beginning of the rainy season to the beginning of the dry season. Significance at *p* < 0.05 based on estimated marginal means is denoted by *. Significance at *p* < 0.05 for vegetation type is based on repeated measures ANOVA is denoted by ++. Measurements were taken on the same day, but points are jittered for visual representation. Summary statistics can be found in Appendix S4.

is driven by precipitation and more specifically that root responses precede or occur simultaneously with aboveground transpiration responses, as was also observed in high elevation Mediterranean forest (Kitajima et al., 2010). The invasive grass had greater root length values in December than in January, before any substantial rain events (>2 cm), suggesting that it was able to take advantage of small increases in soil moisture and that root activity precedes aboveground activity.

We found support for our hypothesis that invasive grasses would deplete soil moisture more rapidly and produce roots earlier at shallow depths than *Adenostoma fasciculatum*, allowing them to gain a competitive edge through early phenological activity or seasonal priority effects (Willis et al., 2010; Wainwright et al., 2012). *Ehrharta calycina* produced longer roots at multiple depths earlier in the growing season than *A. fasciculatum*. The early presence of longer roots of *E. calycina* suggests that this species may respond rapidly to rain events, but *A. fasciculatum* response was delayed. Our observation that *E. calycina* possessed longer roots earlier in the growing season shows some support for the idea that this invasive plant may be able to respond to early rains faster than natives (Willis et al., 2010).

The invasion literature suggests that functional differences between two species would make them less likely to compete for resources (Funk et al., 2008), and we expected that the deep rooting strategy of *Adenostoma fasciculatum* would allow it to access deep water whereas *Ehrharta calycina* would access shallow soil moisture. However, we observed overlap of root depth between *A. fasciculatum* and *E. calycina* in monospecific stands. *A. fasciculatum* root length
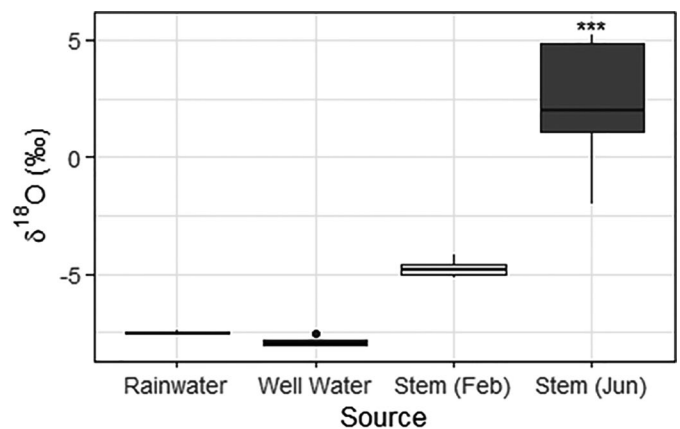
depths than *A. fasciculatum*, because *E.calycina* possessed longer roots in December 2015. Lastly, we expected that *A. fasciculatum* would access deep water sources at the onset of the summer drought, meaning that the $\delta^{18}O$ signature of the stems collected in June would match the well water. However, we found little support for this hypothesis as the $\delta^{18}O$ signature from the stems in June were distinct from both water sources. Overall, we found differences in root length at shallow depths and depletion of soil moisture suggesting that these plant species can differentially affect soil water balance.

During the rainy season (January—March), there were no differences in soil moisture between native and invasive vegetation types, suggesting that *Ehrharta calycina* was not using water more rapidly than *Adenostoma fasciculatum* at 30 cm. Both invasive and native vegetation types had higher soil moisture than bare ground, which indicates that the presence of any vegetation decreases runoff and increases soil water infiltration. This dynamic shifted later in the growing season because soil moisture under invasive vegetation dropped below soil moisture under native vegetation and bare ground starting in April, coinciding with the end of the rainy season. This could lead to an acceleration of the onset of the summer drought in areas where invasive grasses are present (Davis and Mooney, 1985; Eliason and Allen, 1997; Williamson et al., 2004a, b).

Since there were no differences in soil moisture between native and invasive vegetation during the rainy season, this naturally lends to similar peak activity times in aboveground activities. This could be driven by the fact that both species are perennial. Soil moisture increased in response to rain events in early January, and *Adenostoma fasciculatum* responded with increases in root length and increases in aboveground activity. This indicates that *A. fasciculatum* activity

FIGURE 4. Oxygen isotope composition ($\delta^{18}O$) from four water sources (n = 6), rainwater collected in February, well water to represent groundwater collected in February, *Adenostoma fasciculatum* stems collected during the rainy (February) season and dry (June) season. Dots are outliers. Significance at *p* < 0.005 is denoted by ***. Summary statistics can be found in Appendix S5.

increased and were longer than the roots of *E. calycina* at the onset of the summer drought at shallow depths in the soil profile (0–10 cm), indicating that *A. fasciculatum* is extracting remaining moisture from the last rain events. Under conditions where *A. fasciculatum* has an exotic grass understory, the grass might have an overlapping resource depletion zone with native shrubs resulting in direct competition for water (Chakraborty and Li, 2009). Yet since this study was conducted in monospecific stands, further observations of potential root overlap in mixed stands are needed.

During the dry season, the $\delta^{18}O$ signature of the stem water indicates that *Adenostoma fasciculatum* is taking up enriched water. There are a few potential explanations for this, one being that *A. fasciculatum* is accessing a third source of water that we did not sample. However, if *A. fasciculatum* is primarily using remaining surface water in June, the surface soil water may be heavier in ^{18}O due to evaporative enrichment after precipitation ceases. The enriched $\delta^{18}O$ signature could also suggest that *A. fasciculatum* is using a mix of water from deep and surface sources because the roots are still active at both depths. April soil moisture values for *A. fasciculatum* plots were higher than those for *Ehrharta calycina* but not higher than those for bare ground plots, which suggests that processes other than hydraulic redistribution is driving differences in soil moisture between native and invasive vegetation. One possibility is that *A. fasciculatum* transpires less than *E. calycina*, which is a pattern that has been seen in other comparisons of invasive and native water-use (Williamson et al., 2004b; Cavaleri and Sack, 2010). Also, differences in root length, especially at shallow depths, between the vegetation types could be driving differences in soil moisture. It is also important to note that previous studies corroborate that *A. fasciculatum* produces roots much deeper (>1 m deep) than our observation zone (Kummerow, 1983; Schenk and Jackson, 2002; Williamson et al., 2004a). As the technology to study roots develops, future research in the chaparral should make efforts to monitor roots below 40 cm.

CONCLUSIONS

Using a combination of intensive measurements of individual plants during the growing season and NDVI to assess phenology at the landscape scale, we measured differences in soil moisture associated with vegetation type, which could be driven by differences in rooting strategies. While our intensive studies did not allow us to measure additional plant species, they are supported by other observations of moisture depletion by invasive grasses (Davis and Mooney, 1985; Eliason and Allen, 1997; Williamson et al., 2004a, b). The depletion of soil moisture earlier in the season by *Ehrharta calycina* provides support for our hypothesis that *E. calycina* can deplete soil moisture rapidly. We also found support for our hypothesis that *E. calycina* would produce more, longer roots at shallower depths earlier in the growing season than *Adenostoma fasciculatum* (Frazer and Davis, 1988). Subsequently, these invasive grasses have the potential to accelerate the onset of the summer drought and decrease deep soil water recharge, which could inhibit the re-establishment of native shrubs and further increase vulnerability to invasion. Potentially, native shrubs may redistribute water between deep and shallow depths sustaining continued root activity (Querejeta et al., 2003, 2007, 2009; Kitajima et al., 2013), however we did not find evidence that *A. fasciculatum*

is accessing deeper water sources at the onset of the summer drought compared to the rainy season. These results suggest that in a mixed stand, native chaparral shrubs and invasive grasses would have overlapping resource depletion zones (Chakraborty and Li, 2009). Competition for water is one mechanism that has been cited as a cause of persistence of invasive grasses in desert shrublands (DeFalco et al., 2007). Although we did not measure direct competition for water in this study, the overlapping depletion zone indicates that an invasive understory would directly compete with a native overstory; this may explain why native shrubs have not been able to recolonize and the invasive grass stand has been stable for over six decades.

DECLARATION OF AUTHORSHIP

M.L.P., B.E.M., and E.B.A. conceived and designed the experiments. M.L.P. and B.E.M. performed the experiments. M.L.P. and B.E.M. analyzed the data. M.L.P., B.E.M., M.F.A., and E.B.A. wrote the manuscript.

DATA AVAILABILITY

All data and analyses used to generate these results are publicly available as a redistributable R package, website: https://github.com/bmcnellis/SDEF.analysis/releases/tag/v1.1.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. *P*-values and *F*-values (in parenthesis) for Repeated Measures ANOVAs. Significant values ($P < 0.05$) in bold.

APPENDIX S2. Outputs from estimated marginal means (least-squares means), testing for an effect of vegetation types at the different month levels, with soil VWC the response variable.

APPENDIX S3. *P*-values and *F*-values (in parenthesis) for Repeated Measures ANOVAs with root length as the response variable. Significant values (*P* < 0.05) in bold.

APPENDIX S4. Outputs from estimated marginal means (least-squares means), testing for an effect of vegetation types at depth levels for the different months, with root length as the response variable.

APPENDIX S5. *P*-values for Tukey's pairwise comparison for δ¹⁸O sources. Significant values (*P* < 0.05) in bold.

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