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Living on leftovers: biomass management in annual grasslands may shift functional group dominance

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ABSTRACT

Livestock grazing in North American rangelands has the capacity both to promote and control the spread of undesirable plant species. Within California annual grasslands, desirable forage peaks in spring and supports considerable livestock grazing. However, spring grazing appears to promote the invasion and spread of two late-season and unpalatable non-native annual grasses, Aegilops triuncialis and Elymus caput-medusae. We tested the hypothesis that grazing reduces the leaf area and water use of early-spring annuals, thus increasing residual soil water availability for the late-season species. We used grazing-exclosure experiments to examine the interactive effects of simulated grazing (i.e., clipping) and competition on soil moisture availability, and on physiological, phenological, and demographic responses. When compared to unclipped controls, spring clipping significantly increased late-season volumetric soil moisture by 13-24% in the top 7 cm of soil, and 8–11% in the top 20 cm of soil (p < 0.05, all sites), which supported significantly higher rates of stomatal conductance (73-100% increase) in both late-season invading species (p < 0.01, all sites). Flowering was significantly delayed in clipped plots for both invader species suggesting these species experienced a longer growing period (p < 0.0001 in all cases). In competition plots, the effects of clipping on the demographic response depended on neighborhood composition. When invaders were grown together, no significant effect of clipping on survival or reproduction was detected in either invader. However, when growing in mixtures with early-spring forage annuals or native species, clipping increased survival and reproductive output in late-season invader species by 3-fold. We suggest that strategies for arresting or reversing the dominance of these late-season invasive annuals must recognize the influence of current biomass management strategies on late-season resource availability.

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Introduction

Predicting invasive behavior in non-native plant species is hampered by the wide range of variables that may affect establishment and spread in new environments (Vanderhoeven et al. 2010; Pyšek et al. 2015). Ecologists have focused on factors that directly affect the capacity for invasion, such as habitat disturbance, competitive ability, genetic variation, genome size, and reproductive systems (Foxcroft, Pickett, and Cadenasso 2011). However, it has been more difficult to predict invasive dynamics in response to subtle interactions within new environments that include resource heterogeneity, soil feedback, and indirect effects that influence resource availability (e.g., White, Wilson, and Clarke 2006). Indeed, most invasions are a consequence of human redistribution of propagules into environments that have been disturbed in some way by human activities. These activities interact with an unknown array of factors that may influence the invasion process at different spatial and temporal scales (Davis, Grime, and Thompson 2000).

Low-elevation grasslands in central California make up a large and complex system that has been completely transformed by disturbance and invasion and is now referred to as the California Annual Type (Heady 1977) – an explicit acknowledgment of the transformational consequences of the invasion and naturalization of annual grasses and forbs from the Mediterranean Basin. The transformation began as early as 1545 with Hernando Cortez, but the shift in dominance was greatly accelerated by a century of very heavy livestock grazing beginning in 1769 (Burcham 1957). Today, there is no part of low-elevation California that does not exhibit strong dominance by non-native grasses except in soils with specific (typically harsh) abiotic conditions such as ultra-mafic serpentines (Harrison, Rice, and Maron 2001).

The dominance of these grasslands by highly aggressive and fecund generalist species reduces the success of later-arriving species unless they take advantage of unfilled niche space or are highly competitive for the ephemeral seasonal resources typical of the Mediterranean-type climate (e.g., Enloe et al. 2004). In the western United States, the ability of early-season annuals to germinate at high densities in the fall, mature quickly as temperatures increase in the spring, and rapidly deplete soil resources in the late spring has resulted in a vegetation type that has defied recent restoration efforts aimed at using native perennial species to improve and extend the grazing season for livestock (Dyer and Rice 1999. Marty, Collinge, and Rice 2005). These widespread early-season annual grass genera (e.g., *Avena, Bromus, Festuca,* and *Hordeum*) are valued in rangelands for their high quality, albeit short-lived, forage value (Bartolome, Stroud, and Heady 1980). They can be physically larger and competitively superior to most native and some recently introduced exotic species, and their fall germination confers early access to soil moisture and nutrient resources.

Despite long-term dominance by early-season annual grasses, additional species have invaded that represent a different functional group. Late-season annual grasses have germination patterns similar to early-season annuals, but aboveground biomass remains low until later in the season. These species typically remain green and flower after the early-season annuals have senesced (Malmstrom et al. 2017). Several late-season species are less desirable than early-season annual grasses due to their lower forage quality. In particular, *Aegilops triuncialis* and *Elymus caput-medusae*, have dramatically extended their ranges in the past 50 years, especially in areas where spring grazing

of the dominant early-season annuals is common. Although unpalatable plant species can dominate pastures and rangelands because of avoidance by livestock, the mechanism by which late-season annual grasses can wrest dominance from early-season annual grasses is not well understood. One assumption is that the shift must be associated with variation in resource ability related to vegetation management (Pearson et al. 2016).

To investigate the potential mechanism(s) governing the invasion of late-season annual grasses into grasslands already thoroughly invaded by early-season annual grasses, we tested several related predictions. First, reduction of leaf area of the annual grassland community by grazing should reduce soil water extraction and increase soil water availability later in the season. In this way, the soil moisture is increased for those species not negatively affected by the defoliation process or late-spring growing conditions.

Second, when competition with early-spring annuals is reduced by grazing, late-season annuals will exhibit higher photosynthetic rates earlier in the spring as they either recover from biomass removal or avoid such losses by being of smaller stature than early-spring annuals. Thus, late-season species will experience a longer growing season because of greater residual soil moisture and this will be reflected in extended vegetative growth that delays the onset of flowering.

Third, late-season species will show higher biomass production and greater seed production in areas where biomass reduction occurs compared to areas where it does not. Effects of biomass removal on late-season performance (e.g., photosynthetic rate, survival, and reproduction) may depend on the functional group composition of the competitive neighborhoods. This effect could be due either to differential removal of early-season biomass *vs.* late-season biomass or to differences in within and among functional group competitive strength.

Methods

Target species

Aegilops triuncialis L. is a cleistogamous annual grass native to Eurasia that was introduced about 1914 into the Sierra Nevada foothills of California, USA (Kennedy 1928) and again about 1940 in the northern Coast Range of California (Gomola 2014). While it was considered a local nuisance for grazers, A. triuncialis was not considered an aggressive invader after introduction. However, since about 1990, A. triuncialis has spread rapidly in the coastal and interior foothills of northern California (Peters and Johnson 1996) and has now moved into southern Oregon and western Nevada and scattered populations can be found as far south in California as San Diego County (Dyer 2017).

E. caput-medusae (L., formerly, *Taeniatherum caput-medusae* Nevski) is a cleistogamous annual grass, native to Eurasia and North Africa, that was introduced to Oregon about 1887 (Young 1992) with an estimated six additional introductions up to 1988 (Novak 2004). Since about 1960, *E. caput-medusae* has become a widespread nuisance species in both California and the intermountain West (Kyser et al. 2014). It is particularly problematic in rangelands because the foliage contains a high silica content that deters grazing and slows decomposition, and the dead thatch inhibits germination of more desirable species.

Both species grow slowly in the spring months and are relatively small-statured plants. They often flower after other spring annuals have begun to senesce in late spring and they complete their life cycle as much as a month later; these phenological differences can be observed across landscapes with remote sensing (Malmstrom et al. 2017). Both species produce low quality forage that substantially reduces rangeland productivity. *E. caput-medusae* now dominates millions of acres of semi-arid rangeland in the Pacific Northwest. It has achieved noxious weed status in five Western states (California, Colorado, Nevada, Oregon, and Utah) (Kyser et al. 2014), and can reduce forage production by 50% and livestock production by up to 25% (James et al. 2022). *A. triuncialis* is a federally- and state-listed noxious weed that threatens western rangelands and native habitats. It is unpalatable to livestock under many conditions and can reduce rangeland productivity by 50–75% (Jacobson 1929).

This study took place in the Central Valley of California, where a Mediterranean-type climate is characterized by hot dry summers and cool wet winters. Mean annual precipitation (1982–2024) is 47.1 with 11.7 cm occurring on average during the March–June growing period (California Irrigation Management System; https://cimis.water.ca.gov/). During our study, total annual rainfall in 2008, 2009, and 2010 was 42.5, 38.3, and 42.2 cm, respectively (calculated as water year to correspond with California growing seasons, from October of the previous year through September of the water year). Spring rainfall (long-term average of 11.7 cm) was much reduced in 2008 (3.3 cm - 28% of average), somewhat reduced in 2009 (10.6 cm - 90% of average), and average in 2010 (11.8 cm). Research farm plots were resampled in spring 2014, in the third year of a multi-year drought, with very low annual precipitation (23.6 cm), and spring rainfall of 8.6 cm (74% of average).

Rangeland sites

The rangeland field experiments were conducted on two working ranches with a mixture of oak woodland and grasslands to capture diverse responses in heterogeneous environments. One set was located on a commercial cattle ranch (Cattle T) within a mosaic of open annual grassland and blue oak (*Quercus douglasii* Hook. and Arn.) savanna, *E. caput-medusae* was common at the site, but not *A. triuncialis*. This site was chosen to evaluate responses on deeper, more fertile soils composed of Tehama loam characterized by fine-silty, mixed, superactive, thermic Typic Haploxeralfs (USDAWeb Soil Survey, http://websoilsurvey.sc.egov.usda.gov). At this site, experimental plots were all within one large beef cattle exclosure, with 30 replicate blocks of treatments.

The second set of plots was designed to capture responses on a range of shallower, less productive soils on a working sheep ranch (Sheep R). Twenty replicate blocks of treatments were each individually fenced (each 4.9 m \times 6.7 m) across 102 ha, crossing multiple soil types including Corning gravely loam (fine, mixed, semiactive, thermic Typic Palexeralfs) and the Sehorn-Balcomb complex (fine, montmorillonitic, thermic Entic Chromoxererts) (USDAWeb Soil Survey, http://websoilsurvey.sc.egov.usda.gov). At this site, the vegetation was open annual grassland with established *A. triuncialis*,

E. caput-medusae, introduced forage grasses, and some scattered native perennial grasses. The field sites were approximately 5 km apart at 38°N and -122°W , and 20-30 km from the UC Davis Farm site (the exact locations are protected for confidentiality).

At both Cattle T and Sheep R, grazing exclosures were built in autumn 2007 (Table 1). We established unclipped control plots and spring-clipped plots that were $1.5 \text{ m} \times 1.5 \text{ m}$ with 0.5 m buffers, laid out using a randomized, complete block design. The spring-clipped treatment was manually clipped twice in March in all years of the experiment. To match the high grazing intensity outside the exclosures, vegetation within clipped plots was clipped to a height of 2 cm and all clipped material was removed from the plot. During the winter in 2007, two of the plots at Cattle T and one exclosure at Sheep R were damaged by animal activity and so could not be used in subsequent analyses.

Soil volumetric water content was measured on 1 May 2009 at 7 and 20 cm soil depths using a time domain reflectometry soil probe (Field Scout TDR Soil Moisture Meter, Spectrum Technologies, Inc., Aurora, IL). Due to logistic constraints, soil volumetric water content was measured on a random subset of treatment blocks at each field site. A total of 15 blocks were measured at Sheep R and 12 blocks were measured at Cattle T. At each field site, clipping effects on soil volumetric water content were measured separately for 7 and 20 cm soil depths and were analyzed using a Restricted Maximum Likelihood Estimation (ReML) analysis of variance approach with clipping as a fixed factor and block as a random factor.

As a surrogate for photosynthetic activity, we measured stomatal conductance in both *A. triuncialis* and *E. caput-medusae* on 4–5 May 2008 and 2–3 May 2009 using a steady-state leaf porometer (Model SC-1; Decagon Devices, Pullman, WA). To estimate maximal rates of conductance, measurements were taken only between 1000 and 1300 h to avoid water stress and were obtained from non-senescent, fully opened flag leaves subtending the inflorescences of both species. When possible, two plants within each plot were selected for conductance measurements; these subsamples were then averaged for each plot. For each field site, clipping effects on conductance were analyzed using a ReML analysis of variance approach with clipping as a fixed factor and block as a random factor.

To examine the effect of clipping on time to flowering, plots were sampled on 1 May 2009 and 5 May 2010, at times when these late-season grasses were flowering across the landscape. Four 10 cm by 10 cm quadrats were equally spaced within each plot and the percent of flowering individuals were measured within each quadrat. Individuals were considered to be flowering if the spike had fully emerged from the leaf sheath. Percent flowering within each of the quadrat subsamples were then

Sheep R/ Cattle T	Plot treatments: Plot measurements:	Established	Clipped <i>Conductance</i>	Clipped Conductance Flowering Soil moisture	Clipped				
					Flowering				N
		2007	2008	2009	2010	2011	2012	2013	2014
UCD farm	Plot treatments: Plot measurements:	Established	Clipped Seed production Plant density Conductance	Clipped	Clipped	Clipped	Clipped	Clipped	Clipped Seed production

Table 1. Timeline for the creation of plots and exclosures and the application of treatments.

averaged for each plot. For each field site, clipping effects on time to flowering were analyzed using a ReML analysis of variance approach with clipping, species, and clipping by species interactions as fixed factors and block as a random factor.

Research farm site

To examine whether effects of spring defoliation on A. triuncialis and E. caput-medusae performance might depend on the composition of the local competitive neighborhood, a field experiment that manipulated botanical composition was established in autumn 2007 on a former agricultural field near the UC-Davis campus in Yolo County, California, USA (38°32'46"N, 121°47' 05"W). The site was an agricultural field until 1985 and left fallow until the establishment of this experiment in 2007 (Table 1). This location was slightly drier than the ranch sites with a mean annual precipitation of 48.5 cm. The site was essentially level (0-2% slope). Soils were primarily the Reiff series (75%, coarse-loamy, mixed, superactive nonacid, thermic Mollic Xerofluvents) with a lesser amount of the Brentwood soil series (25%, fine, smectitic, thermic Typic Haploxerepts) (USDA Web Soil Survey, http://websoilsurvey.sc.egov.usda.gov). To deplete any resident seedbank, the site was irrigated prior to seeding, and plants that germinated were treated with glyphosate. Non-planted species were weeded periodically, but seeded species were allowed to vary in abundance. In addition to a mixture of late-season annual species (A. triuncialis and E. caput-medusae), competitive neighborhood treatments focused on two other types of species mixtures intended to represent typical grassland functional groups. A native species mix contained (mostly perennial) species native to California grasslands: Bromus carinatus, Elymus glaucus, Elymus triticoides, Acmispon americanus, Lupinus bicolor, Stipa pulchra, Poa secunda, and Festuca microstachys. An early-season annual species mix contained naturalized exotic annuals: Avena fatua, Bromus hordeaceus, Festuca perennis, and Trifolium subterraneum. Naturalized exotic plants are defined as those that have been present in California grasslands since the mid- to late-1800s and are now ubiquitous on the landscape.

Within each of eight replicate blocks, three different competitive neighborhoods were planted in 1.5 by 1.5 m treatment plots, the same plot-size used in the rangeland work. Plots were separated by a 1 m buffer. The competitive neighborhood treatments were: (1) A mix of late-season annuals (A. triuncialis and E. caput-medusae); (2) the A. triuncialis/E. caput-medusae mixture added to an early-season annual species mix; and (3) the A. triuncialis/E. caput-medusae mixture added to the early-season annual species mix plus the native species mix. These treatments simulate the primary types of botanical communities currently found in California grasslands; pure native grassland communities are essentially non-existent in the grasslands of California (D'Antonio et al. 2007). Plant neighborhoods were established by adding 139g of seed to each 1.5×1.5 plot. For neighborhood mixtures with different groups of species (early-season annuals, late-season annuals, native species), seeds were added at an equal proportion (by seed weight) of each group type. Within each group type, individual species were added at an equal proportion (by seed weight) of the component species. Crossed with the neighborhood treatments was a clipping treatment where half of the neighborhood treatment plots in each replicate block were clipped to a height of 5 cm every spring, starting April 2008 (the first growing season of the experiment). The timing of clipping was targeted at peak aboveground growth of grasses, but before peak biomass (which usually occurs as soils dry), resulting in annual clipping in mid-March to mid-April, depending on the rainfall for each growing season. This design resulted in six treatment combinations within each of the eight replicate blocks.

We measured stomatal conductance in both *A. triuncialis* and *E. caput-medusae* using a steady-state leaf porometer on 2–3 May 2008 on randomly selected plants of each species within each treatment plot. Similar to the procedures followed at the ranch sites, measurements were taken only between 1000 and 1300h to avoid water stress and were obtained from non-senescent, fully opened flag leaves subtending the inflorescences. To examine the interactive effects of neighborhood composition and clipping on plant survival and reproduction, four 10 by 10 cm quadrats were placed at equal spacing within each treatment plot and all plant material removed from within the quadrat and bagged. Within each of these quadrat samples, we counted the number of plants and the number of seeds for both *A. triuncialis* and *E. caput-medusae*. Estimates of adult survival and reproduction from each of the four quadrat subsamples were then averaged for each treatment plot. The interactive effects of neighborhood composition and clipping on stomatal conductance, plant survival, and reproduction were analyzed using a ReML analysis of variance approach with clipping, neighborhood composition, and clipping by neighborhood interactions as fixed factors and block as a random factor.

To examine longer-term effects (i.e., six years) of competitive neighborhood and annual spring clipping on demography, treatment plots were resampled for reproduction on 25–26 May 2014. Four 10 by 10 cm quadrats were placed at equal spacing within each treatment plot and all plant material removed from within the quadrat and bagged. Within each of these quadrat samples, we counted the number of spikes for both *A. triuncialis* and *E. caput-medusae*. Although we did not count seed number directly, spike number is highly correlated with seed number in both *A. triuncialis* (r = 0.99, p < 0.0001) and *E. caput-medusae* (r = 0.98, p < 0.0001). The interactive effects of neighborhood composition and clipping on spike number in both *A. triuncialis* and *E. caput-medusae* were analyzed using a ReML analysis of variance approach with clipping, neighborhood composition, and clipping by neighborhood interactions as fixed factors and block as a random factor.

Analyses of variance (ReML) of data from the ranch sites and the UC-Davis field site were conducted using JMP version 11 software (SAS Institute, Inc., Cary, NC). To conform to parametric data assumptions of the analyses, flowering data were arcsine square root transformed while conductance and demographic data were natural log-transformed before analyses. Untransformed values are presented in the text and figures.

Results

Rangeland sites

Spring clipping and aboveground biomass removal in annual grass plots significantly and consistently increased May soil volumetric water content both on deep fertile soils and on shallower, less-fertile ones. On Sheep R, soil volumetric water content (mean



Figure 1. Spring clipping increases volumetric soil water content in May 2009. Measurements at 7 cm soil depth at (A) Sheep R: p = 0.010; $R^2 = 0.95$; F = 9.01 and (B) Cattle T: p < 0.001; $R^2 = .88$; F = 35.73, at 20 cm soil depth at (C) Sheep R: p = 0.017; $R^2 = 0.98$; F = 7.64 and (D) Cattle T: p = 0.007; $R^2 = 0.93$; F = 11.13. Error bars represent 1 SE. There were 14 replicate treatment blocks at Sheep R and 12 replicate treatment blocks at Cattle T.

 \pm 1 standard error) rose 13% at 7-cm depth (Figure 1(A)), from 16.0 \pm 1.6% to 18.1 \pm 1.7% (p = 0.010, r^2 = 0.95), and 11% at 20 cm (Figure 1(C)), from 23.4 \pm 3.0% to 26.0 \pm 3.3% (p = 0.017, r^2 = 0.98). On the deeper, more fertile soils at Cattle T, overall soil moisture levels were greater, but the same phenomenon was observed. Soil water content in May 2009 increased 24% at 7 cm (Figure 1(B)) from 29.4 \pm 1.6% to 36.6 \pm 1.5% (p < 0.001, r^2 = 0.88), and 8% at 20 cm (Figure 1(D)), from 40.3 \pm 2.2% to 43.7 \pm 1.6% (p = 0.007, r^2 = 0.93).

Stomatal conductance in both A. triuncialis and E. caput-medusae increased in May with spring clipping. These measurements were conducted in 2 years that differed in



Figure 2. Spring clipping increases leaf-level conductance rates. Measurements on *A. triuncialis* at Sheep R in (A) May 2008: p < 0.001; $R^2 = 0.70$; F = 16.60 and B) May 2009: p < 0.001; $R^2 = 0.86$; F = 32.62. Measurements on *E. caput-medusae* at Cattle T in (C) May 2008: p < 0.0001; $R^2 = 0.85$; F = 77.89. and (D) May 2009: p < 0.001; $R^2 = .67$; F = 47.78. Error bars represent 1 S.E. There were 19 replicate treatment blocks at Sheep R in 2008 and 2009. There were 28 replicate treatment blocks at Cattle T in 2008 and 2009.

spring rainfall amounts: 2008, in which spring was dry; and 2009, when spring was wetter. A. triuncialis conductance was measured at Sheep R and E. caput-medusae conductance was measured at Cattle T. In 2008 (Figure 2(A)), conductance in A. triuncialis (Sheep R) doubled under spring clipping, from 38.6 ± 6.7 to 76.6 ± 11.9 mmol H₂O m⁻² s⁻¹ (p = 0.0013, $r^2 = 0.70$). In 2009 (Figure 2(B)), when spring conditions were wetter, spring clipping still increased A. triuncialis conductance by 73%, from 114.1 ± 16.8 to 197.4 ± 22.8 mmol H₂O m⁻² s⁻¹ (p < 0.0001, $r^2 = 0.86$). Similarly, spring clipping more than doubled conductance in E. caput-medusae (Cattle T) in 2008, when



Figure 3. Spring clipping reduces percent flowering in 2009 and 2010 of *A. triuncialis* (p < 0.0001) and *E. caput-medusae* (p < 0.0001) at Sheep R. (A) May 2009: $R^2 = 0.66$; interaction p = 0.216. (B) May 2010: $R^2 = 0.86$; interaction p = 0.576. Error bars represent 1 S.E. There were 19 replicate treatment blocks at Sheep R in 2009 and 2010.

it rose from 50.0 \pm 7.5 to 103.5 \pm 17.0 mmol H₂O m⁻² s⁻¹ (p < 0.0001, $r^2 = 0.85$, Figure 2(C)). In wetter 2009, clipping increased *E. caput-medusae* conductance by 83%, from 107.1 \pm 10.8 to 196.0 \pm 11.2 mmol H₂O m⁻² s⁻¹ (p < 0.0001, $r^2 = 0.67$, Figure 2(D)).

The time to flowering (a surrogate for the length of the vegetative growing season) significantly increased in both *A. triuncialis* and *E. caput-medusae* at Sheep R and in *E. caput-medusae* at Cattle T in 2009 and 2010 (*A. triuncialis* was not established at Cattle T). Differences in time to flowering were estimated by measuring the percentage of plants flowering at a given census. Lower percent flowering at a given census was interpreted as an indication of an increase in time to flowering and thus an increase in the length of the vegetative growing season. Under spring clipping in 2009 (Figure 3(A)), the percent of *A. triuncialis* plants flowering at census at Sheep R fell by more than half, declining from 76.7 \pm 5.8% to 30 \pm 5.0% (p < 0.0001) and the percent of *E. caput-medusae* plants flowering decreased 35%, from 85.7 \pm 9.1% to 55 \pm 2.6% (p < 0.0001). The pattern at Sheep R was similar in 2010 (Figure 3(B)); the percent of *A. triuncialis* plants flowering at census decreased by about half with



Figure 4. Spring clipping reduces percent flowering in *E. caput-medusae* at Cattle T in (A) May 2009: p < 0.0001, $R^2 = 0.65$. (B) May 2010: p < 0.0001, $R^2 = 0.93$. Error bars represent 1S.E. There were 28 replicate treatment blocks at Cattle T in 2009 and 2010.

spring-clipping, from 93.8 \pm 8.8% to 48.3 \pm 7.7% (p < 0.0001) and in *E. caput-medusae* decreased about 58%, from 84.6 \pm 8.9% to 35.4 \pm 6.5% (p < 0.0001). At Cattle T, likewise, the percent of *E. caput-medusae* plants flowering at census decreased 43% in 2009, from 85.5 \pm 1.8% to 48.9 \pm 5.2% (p < 0.0001, $r^2 = 0.65$, Figure 4(A)) and decreased 38% in 2010, from 93.2 \pm 2.6% to 57.1 \pm 6.1% (p < 0.0001, $r^2 = 0.93$, Figure 4(B)). Thus, for both species in both years, clipping appears to prolong the opportunity for vegetative growth before flowering.

Research farm site

Without clipping, stomatal conductance in *E. caput-medusae* was significantly higher (interaction p = 0.013, F = 4.96, Figure 5) in late-season annual plots compared to plots in which late-season annuals were grown with early-season annuals only or in neighborhoods of early-season annual and native species. However, with spring



Figure 5. Interactive effects of clipping treatment and competitive neighborhood on stomatal conductance (p=0.013) measured for *E. caput-medusae* plants within farm plots (May 2008). Letters indicate significant differences (p<0.05; HSD) among treatment combinations. Error bars represent 1 S.E. There were eight replicate treatment blocks at the farm in 2008. AETR = *A. triuncialis*; ELCM = *E. caput-medusae*.

clipping, stomatal conductance in *E. caput-medusae* did not differ significantly among competitive neighborhoods. Only the main treatment of clipping significantly affected conductance in *A. triuncialis*: rates of leaf conductance were significantly higher in clipped plots (p < 0.0001, F = 35.25) when averaged across neighborhood treatments. Conductance increased from 31.4 ± 6.3 mmols H₂O m⁻² s⁻¹ in unclipped plots to 84.8 ± 6.2 mmols H₂O m⁻² s⁻¹ in clipped plots. In general, spring clipping appeared to have little effect on conductance of *A. triuncialis* and *E. caput-medusae* when these species were growing in their own late-season neighborhood.

Adult survival of A. triuncialis and E. caput-medusae was significantly higher when grown in their own late-season neighborhood, regardless of clipping treatment (Figure 6(A): A. triuncialis interaction term p = 0.0115; Figure 6(B): E. caput-medusae interaction p < 0.0001). Spring clipping increased survival of both species (E. caput-medusae not significantly) when they were grown in neighborhoods of early season annuals and native species suggesting that competitive suppression by these other functional groups was alleviated by the clipping treatment.

Without spring clipping, both species had significantly higher reproductive output when grown in their own late-season neighborhood, although the clipping effect was more pronounced for *E. caput-medusae* than for *A. triuncialis* (Figure 7(A): *A. triuncialis* interaction p = 0.0134; Figure 7(B): *E. caput-medusae* interaction p < 0.0001). For *A. triuncialis*, the presence of early season annuals and native perennials suppressed *A. triuncialis* reproduction regardless of the clipping treatment while suppression of *E. caput-medusae* reproduction by early annuals and native perennials was not significant under spring clipping.

Six years after plot establishment, interaction terms between neighborhood composition and clipping treatment were not significant for either A. triuncialis or E. caput-medusae spike production. However, averaged across neighborhood treatments, both A. triuncialis and E. caput-medusae produced significantly more reproductive spikes under spring clipping (Figure 8(A): A. triuncialis p = 0.001, E. caput-medusae



Figure 6. Interactive effects of clipping treatment and competitive neighborhood on adult survival in (A) *A. triuncialis* (p = 0.012) and (B) *E. caput-medusae* (p < 0.001) measured within farm plots (May 2008). Letters indicate significant differences (p < 0.05; HSD) among treatment combinations. Error bars represent 1 S.E. There were eight replicate treatment blocks at the farm in 2008. AETR = *A. triuncialis*; ELCM = *E. caput-medusae*.

p = 0.020). Averaged across clipped and unclipped plots, both *A. triuncialis* (p = 0.0048) and *E. caput-medusae* (p = 0.0019) produced significantly more reproductive spikes when growing in their own late-season neighborhood (Figure 8(B)).

Discussion

Management of unwanted plant species in highly invaded grassland ecosystems is typically accomplished with some form of biomass removal. Grazing is a favored technique for several reasons. First, other biomass removal methods, such as prescribed fire and herbicides, may be impractical for logistical reasons (e.g., not viable at large scales), economic reasons (e.g., loss of usable forage), and safety reasons (e.g., wildfire hazard, toxicity to wildlife). Second, grazing is a natural process in grasslands, it is cost-effective, and easily



Figure 7. Interactive effects of clipping treatment and competitive neighborhood on reproduction in (A) *A. triuncialis* (p=0.013) and (B) *E. caput-medusae* (p<0.0001) sampled from farm plots (May 2008). Letters indicate significant differences (p<0.05; HSD) among treatment combinations. Error bars represent 1 S.E. There were eight replicate treatment blocks at the farm in 2008. AETR = *A. triuncialis*; ELCM = *E. caput-medusae*.

applied and manipulated. Third, grazing can be used to favor native species over invasive species and is often used to maintain native populations and to promote habitat restoration while reducing or controlling the abundance of non-native species (e.g., Beck et al. 2015). In California rangelands, grazing by cattle and sheep is used both to reduce non-native biomass (e.g., Weiss 1999) and to take advantage of a high-quality winter and spring forage provided by those species. However, long-term observation suggests that the use of grazing at peak growth of the dominant early-season annual functional group may favor a second functional group of undesirable late-season annuals.

From this study, we conclude that the removal of leaf area from early-season annual grasses during the peak of the growing season changes soil resource availability in



A. triuncialis E. caput-medusae

Figure 8. Main effects in the farm plots (May 2014) of (A) clipping treatment and (B) competitive neighborhood on reproduction in *A. triuncialis* (p < 0.001) and *E. caput-medusae* (p = 0.020) sampled within farm plots 6 years after initial planting. In Figure B, the letters indicate significant differences (p < 0.05; HSD) among competitive neighborhoods separated by species. Error bars represent 1 S.E. There were eight replicate treatment blocks at the farm in 2014. AETR = *A. triuncialis*; ELCM = *E. caput-medusae*.

favor of late-season annual grasses, and these effects were robust across soil types and annual precipitation. Specifically, late-season annual grasses avoid defoliation by having relatively less biomass exposed to grazing in early spring. A delay in biomass production until most grazing has concluded allows the late-season grasses avoid the negative effects of defoliation on reproductive output. In addition, by removing leaf area of early-season annuals before depletion of soil resources, grazing appears to extend the growing season in favor of late-season annuals, which further promotes biomass production and reproductive output in these species.

Increased stomatal conductance under defoliation treatments indicated lower water stress and therefore higher photosynthetic activity in both *A. triuncialis* and *E. caput-medusae*. The reduced water stress was also reflected in the delayed onset of reproduction and a lengthening of the growing season, which has also been correlated with increased seed mass in *A. triuncialis* (Dyer 2017). This longer growing season, 16 👄 A. R. DYER ET AL.

higher survival, and increased seed production in the A. triuncialis and E. caput-medusae plots suggests a release from competitive suppression by dominant early spring annuals.

A change in soil moisture appears to be the proximal mechanism underlying the shift in late-season species performance. As a result, the defoliation treatments had a strong indirect effect on community composition. That is, seed contributions to the short-term soil seed bank of the dominant species were reduced while seed contributions of the inferior competitors were increased, and this shift in relative seed density appears to have long-term consequences for these grasslands. While these annual grasses do not produce long-term seed banks (Talbot, Biswell, and Hormay 1939; Russi, Cocks, and Roberts 1992), the resource dominance exhibited by annual grasses in these systems will continue and may even be enhanced by a shift in abundance of late-season annuals. If the conditions favoring late-season annuals persist (i.e., spring grazing occurs annually), then the shift in community composition could be cumulative over time.

Several mechanisms may influence the interaction between resource availability and species traits. First, invasive species may be characterized by high phenotypic plasticity and tolerance of stressful conditions in relation to their original habitats. However, phenotypic plasticity is not a necessary condition if the invasive species are merely taking advantage of open or underutilized niche space. In California, the niche space previously occupied by perennial grass species has not been occupied by ecological replacements, and subsequent invasions by species, such as *A. triuncialis* and *E. caput-medusae* may be predictable. For example, Dyer, Hardison, and Rice (2012) found that *Bromus tectorum* exhibited an opportunistic strategy to late season resource availability. Such a strategy is a combination of phenological plasticity, niche range and tolerance, and can be highly variable across populations.

Second, competitive ability, opportunistic growth, and palatability are interactive factors in grazing systems. Typically, grazing intensity is greatest when the most palatable species are present, and reduced or absent when the forage becomes less favorable. This pattern will favor species with lower palatability. Management systems that rely on a single type of grazer will also tend to select for plant species that are avoided by the grazing animals, unless stocking densities and rotations are managed to prevent this. Those less-palatable species will experience higher resource availability and an extended growing season. Without further study, the resulting shifts in community composition cannot be attributed to competitive superiority alone.

Third, California rangelands have been subjected to intense disturbances such that entire community assemblages have shifted, and naturalized annuals are ubiquitous and dominant members. The more recent introduction of species such as *A. triuncialis* and *E. caput-medusae* will be marked by slower expansion because of the high densities of ecologically similar and highly competitive resident species. The slow expansion is likely influenced by climate variability, and habitat suitability may periodically shift for all species. The recent expansion of these two late-season annual species could be an inexorable process and not strictly related to changes in resource supply.

We do not know whether the shifts in community composition we are attempting to understand are driven by changes in soil resources due to grazing or to climate or both. However, the consequences for western grasslands should not be underestimated. The overall shift in functional diversity from a diverse assemblage of annuals and perennials to one dominated primarily by annual species has been well described. The invasion of species such as *A. triuncialis* and *E. caput-medusae* threaten further conversion to a community dominated by fewer annuals species in dense monospecific stands of low palatability and low economic value. From an ecological perspective, this should be treated as a serious threat.

From an economic perspective, the western rangelands dominated by annual grasses are a natural resource valued in the billions of dollars annually for cattle grazing. However, the production of non-palatable annual biomass in these ecosystems reduces forage value and creates a much greater risk from residual flammable fuels that normally would have been reduced by grazing (Balch et al. 2013). Thus, the shifts toward dominance by late-season annual grasses could have important consequences for the future use, value, and ecological stability of these rangelands.

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18 👄 A. R. DYER ET AL.

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