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Interactions among habitat, management, and demography for an invasive annual grass

Elise S. Gornish · Jeremy J. James

Abstract Effective long-term management of noxious plant species depends on our ability to identify and manage ecological processes-driving invasion and to use site-specific information to design realistic management strategies and goals. However, there is a surprising lack of research that investigates relationships among habitat characteristics, weed demography, and management efforts. We investigated the interactions among these factors using the invasive annual grass medusahead (*Elymus caput-medusae*). In Yuba County, California, we seeded medusahead in densities from 0 to 50,000 seeds/m^2 in open grassland and oak woodland habitats. We also exposed plots to defoliation none, once, or twice in a season and captured how medusahead germination, establishment, and persistence responded to experimental treatments. We found that medusahead establishment was higher in the grassland, compared to the woodland habitat, likely due, in part, to the presence of litter under oak canopies. After a single defoliation event, medusahead persistence was higher in the oak, but not the grassland plots. We also found that defoliation once or twice reduced medusahead density. However, a single clipping treatment actually resulted in increased seed production. This was likely a compensatory response by a younger cohort, and provides an explanation for why single control efforts do not generally result in successful long-term outcomes. This work highlights the complex relationships between density-dependent and density-independent processes that may influence invasion dynamics.

Introduction

One of the most critical aspects of rapidly changing climatic conditions is the increase in invasion by non-native plant species into ecological systems worldwide (Hellmann et al. 2008; Thomas 2010; Bradley et al. 2012). This massive increase in the incidence and impact of invasive plants highlights the need for the development of more effective weed management tools (e.g., Pauchard et al. 2015). Recently, studies have demonstrated the dominant role of underlying abiotic factors, such as precipitation and soil conditions, for mediating control efforts (e.g., Davy et al. 2015). This is largely driven by effects on plant demography and competitive ability (Gillespie and

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Allen 2004; Young and Mangold 2008), which subsequently mediate the effectiveness of control efforts (e.g., Ramula et al. 2008). This suggests that understanding the interactions among weed demography, habitat factors, and management efforts should be a priority for applied research initiatives. For example, an understanding of how particular life stages of an invasive plant might respond to control efforts across habitats could ultimately provide optimal management recommendations, based on seasonality and site-specific characteristics.

Managers have long understood the importance of considering demography for control efforts. For example, many plants have life stages that are disproportionately susceptible to the effects of control efforts (Buckley et al. 2003; Davis et al. 2004). Moreover, since vital rates can vary across sites (Jongejans et al. 2010), considerations of how habitat characteristics and demography interact to affect management outcomes is important for designing and deploying effective invasive plant control. And, managers have acknowledged the context dependency associated with management outcomes, where invasion dynamics can differ across sites depending on, for example, the functional identities of the extant community (Sheley and James 2010), the presence of litter (Elgersma et al. 2012), or the timing of control (e.g., Emery and Gross 2004). However, how these factors might interact to ultimately affect control efforts has received much less attention in applied and theoretical research. Such understanding is critical if progress is to be made on limiting the range expansion of invasive species. This is particularly important for heterogeneous landscapes that are characterized by the dominance of aggressive invasive plant species, such as grassland ecosystems in the western United States.

In this study, we investigated interactions among habitat type, management, and demography of an invasive annual grass, medusahead (*Elymus caput-medusae* [L.] Nevski). Medusahead is a cool season grass that was inadvertently introduced to the U.S. several times from the Mediterranean region of Europe and has since been documented in over 17 Western states (Skaar 2015). Ecological consequences of medusahead infestation on annual and intermountain grassland habitats are considerable, and can include modifications of the fire cycle (D'Antonio and Vitousek 1992; Young 1992), reductions in wildlife habitat suitability (Nafus and Davies 2014), and declines in native biodiversity

(Kyser et al. 2014). The substantial thatch layer that characterizes medusahead infestation can also have extensive economic implications. For example, the low palatability of medusahead has been estimated to reduce livestock production by up to 80 % (Hironaka 1961; DiTomaso 2000).

In response to the widespread negative outcome of medusahead invasion, managers have employed a variety of methods to control the weed, including managed grazing (e.g., DiTomaso et al. 2008; Davy et al. 2015), herbicide (Kyser et al. 2012), and prescribed fire (Kyser et al. 2008). Despite the promise of these strategies, medusahead continues to expand its range across the western U.S. A recent meta-analysis of medusahead control outcomes in annual grassland and intermountain regions identified large variance associated with management efficiency (James et al. 2015). This suggests that underlying abiotic (habitat characteristics) and biotic (demography) variables might mediate control efforts. For example, studies have demonstrated how medusahead invasion can depend on the presence of a conspecific seedbank (Davies 2008), a plant litter dynamics (Evans and Young 1970), and tiller densities (Murphy and Turner 1959).

We conducted an experiment in the Sierra Nevada foothills of California to investigate how habitat characteristics (type and shade and litter presence), medusahead demography, and a management approach (defoliation) interact to ultimately affect medusahead invasion. Research on other invasive plants suggests that differences in habitat type are important for mediating demography and management outcomes (Buckley et al. 2003; Lehtila et al. 2006). We expected the presence of litter to be, in part, responsible for these differences because thatch has been shown to inhibit medusahead in certain environments (Cherr 2009). Further, because seedbank density can affect demographic dynamics (Davies 2008), which ultimately drive response to biotic and abiotic factors (e.g., Keammerer and Hacker 2013), we expected significant relationships between seed density and management efforts.

Methods

Installation

The experiment was deployed at the University of California Sierra Foothills Research and Extension

Center (SFREC). SFREC is located in the low-elevation Sierra Nevada foothills of Yuba County, CA. Soil at the site is a moderately deep and well-drained complex of approximately 40 % Sobrante gravelly loam and 35 % Timbuctoo gravelly loam (Lytle 1998). Average long-term precipitation at the site is 720 mm with an average annual high temperature of 12 °C and average annual low temperature of −0.5 °C.

The experiment was deployed in areas of SFREC highly infested with medusahead (>95 % cover in open grassland habitat; <1 % cover in oak woodland habitat). Eighty permanent plots (1 m^2) were erected in open grassland habitat (0 % tree cover) and paired oak woodland habitat (40–50 % tree cover of mostly blue oak, *Quercus douglasii*, and interior live oak, *Q. wislizeni*). Plots were separated by 2 m. The two habitats differed in the identity of dominant herbaceous species and the presence of leaf litter (Gornish et al. 2015). The two habitats also differed in soil temperature and soil moisture, as demonstrated by data collected from 12-bit Smart Sensors (Onset Computer Corporation, Bourne MA) installed in the upper 5 cm of experimental plots in the open grassland and oak woodland plots (Fig. 5A, B in Appendix). T-tests indicated that shallow soil temperatures ($t = -26.61$, $p < 0.001$) and soil moisture ($t = -43.88, p < 0.001$) were significantly lower in oak woodland plots (by almost 3.7 °C, on average) compared to open grassland plots during the day and the night. This was likely due to relatively low herbaceous vegetative cover providing shade to the soil surface under oak canopies compared to open grassland habitat.

Site preparation included the removal of standing biomass by mowing all plots in early Fall 2014. The soil was then watered and solarized via clear 4 mm thick polyethylene tarps, which covered the plots at the soil surface for approximately 14 days in order to encourage depletion of the seedbank. Finally, 1 % Glyphosate (Roundup) was applied to kill germinated plants. In October 2014, 'multi-density' plots were hand seeded with one of five densities of field-collected medusahead (0, 100, 1000, 10,000, and 50,000 seeds/m^2; see Marañón and Bartolome 1989 for seedbank values), mixed in with 500 grams of medusahead thatch. Immediately following the addition of medusahead seed, 6000 seeds each of neighboring grass species (annual rye and Blando brome) and 4000 seeds of a clover mix (rose, Persian, and park subclover; Peaceful Valley Farm & Garden Supply, Grass Valley CA) were added—for a total of 16,000 neighbor seeds—to maintain a realistic competitive environment (Marañón 1998; E. Gornish, *unpublished data*). Organza drawstring germination bags were also added to each plot in November 2014. Each bag contained 50 locally collected medusahead seeds, and the bags were installed within the NW quadrant of each plot.

A defoliation treatment was applied to the plots in April 2015. This treatment was intended to simulate a typical mowing or grazing regime used in a management program. All standing biomass in defoliation treatment plots were clipped. Defoliation was applied with electronic shears positioned approximately 15 cm above the soil surface (a clipping intensity of about 70 %, which is expected to reduce root growth of invasive annual grasses [Arredondo and Johnson 1998]). Shears were then used to disturb the clipped thatch twice (two swipes across the plot) to simulate movement of a mower. This tended to displace approximately half of the clipped thatch to the exterior of the plot. The defoliation treatment was applied when 75 % of the medusahead tillers were in the 'boot' stage within a plot, because this life stage is particularly vulnerable to the effects of grazing (Hempy-Mayer and Pyke 2008). Half the plots were clipped, and half remained intact. Treatments were randomly assigned to plots within habitat-level quadrats (Fig. 6 in Appendix). Main factors were replicated four times for a total of 80 plots (two habitats × five seeding densities × two defoliation treatments × four replicates).

Additional high density seed plots (50,000 seeds added) were installed in the open grassland sites in October 2014 in order to facilitate additional experimental investigations. In one sub-study, treatments were deployed in order to simulate environmental factors associated with the oak woodland habitat. These included the presence of shading, the presence of oak litter, and both shading and litter. Shading was applied via 50 % shade cloth attached to 1.5 m tall PVC pipes erected at the corners of each treatment plot. Litter was applied by collecting 500 g of litter (the average weight of litter found in a m^2 area under oak canopies at our site) from under proximate oak canopies and distributing it evenly over treatment plots. Litter was almost entirely composed of oak leaves and small oak twigs. Medusahead seeds were

introduced to plots after the litter treatment was applied.

In a second sub-study, a more complex defoliation treatment was applied in April 2015 to the newly added high density (50,000 seed) plots. The defoliation treatment was the same as described above, with one additional level. The defoliation treatment was either not applied (no clipping), applied once (plots clipped in late April 2015), or applied twice (plots clipped in late April 2015, and then clipped again 3 weeks later).

Data collection

Upon germination in early winter of 2014, 20 medusahead seedlings were marked in each of the multi-density plots (Ramula and Buckley 2009). Individuals were identified by throwing a bi-colored toothpick into the plot and marking the seedling closest to the colored tip. Individuals were marked first by a colored rubber band gently secured at the base of the plant. A numbered pin flag was installed next to the plant. Once plants matured, a metal numbered tag replaced the rubber band and flags were removed. Medusahead stages were described at the tiller level as it was infeasible to identify individuals once plants matured (adult plants can be composed on up to 100 tillers). We followed the 20 marked seedlings throughout the growing season. When a tiller died during the experiment, the tag was removed from the plot and a new tiller was randomly chosen and marked with a unique numbered tag in order to maintain (when possible) a total of 20 tillers followed per plot. Marked tillers were censused several times in 2015 for survival and spikelet production. Marked seedlings were surveyed for survival in March 2015 for estimates of percent establishment. A month following the clipping treatment (May 2015), marked tillers were surveyed for survival to derive estimates of percent persistence. In June 2015, the total density of medusahead tillers in all plots was estimated. At this time we also collected intact seed heads from ten individual reproductive spikes per plot for estimates of seed production. Percent germination was assessed by collecting all germination bags in February 2015 and counting the number of germinated seeds.

Data analysis

For the multi-density study, we used ANOVA to understand how explanatory factors of habitat type (open grassland or oak woodland), and seed density (100, 1000, 10,000, and 50,000) affected percent germination and establishment. The defoliation treatment (clipped or not clipped) was not included as an explanatory factor in these models because this treatment occurred after germination and establishment were complete. We also used ANOVA to describe how explanatory factors of habitat type, seed density, and the presence of the defoliation treatment affected medusahead persistence, seed number per reproductive spike, and density. In both cases, replicate was included as a random factor. Response variables were log transformed to accommodate ANOVA assumptions when appropriate. Tukey post hoc tests were used when appropriate to identify contributions of treatment levels.

For the single-density sub-experiments, we also used ANOVA for analysis. For the oak habitat simulation experiment, percent germination, establishment, and persistence were response variables and explanatory factors included treatment (control, shade only, litter only, and shade + litter) and a random variable for replicate. In the defoliation experiment, density and seed number per reproductive spike were the response variables and explanatory variables that included clipping number (zero, once, and twice) and a random variable for replicate.

Results

Although medusahead germination was unaffected by treatments (Fig. 1A; Table 1 in Appendix), seedling establishment was, on average, 1.5 times higher in the open grassland, compared to the oak woodland habitat ($F = 13.38$, $p < 0.001$; Fig. 1B).

In the oak woodland habitat, defoliation resulted in the persistence of medusahead tillers that was more than twice as high as those not exposed to defoliation (Fig. 2A; $F = 21.43$, $p < 0.001$), although this did not subsequently result in higher densities in the clipped plots. In the open grassland, however, there was no difference in defoliation effects on persistence (Fig. 2B). Density of medusahead tillers across plots
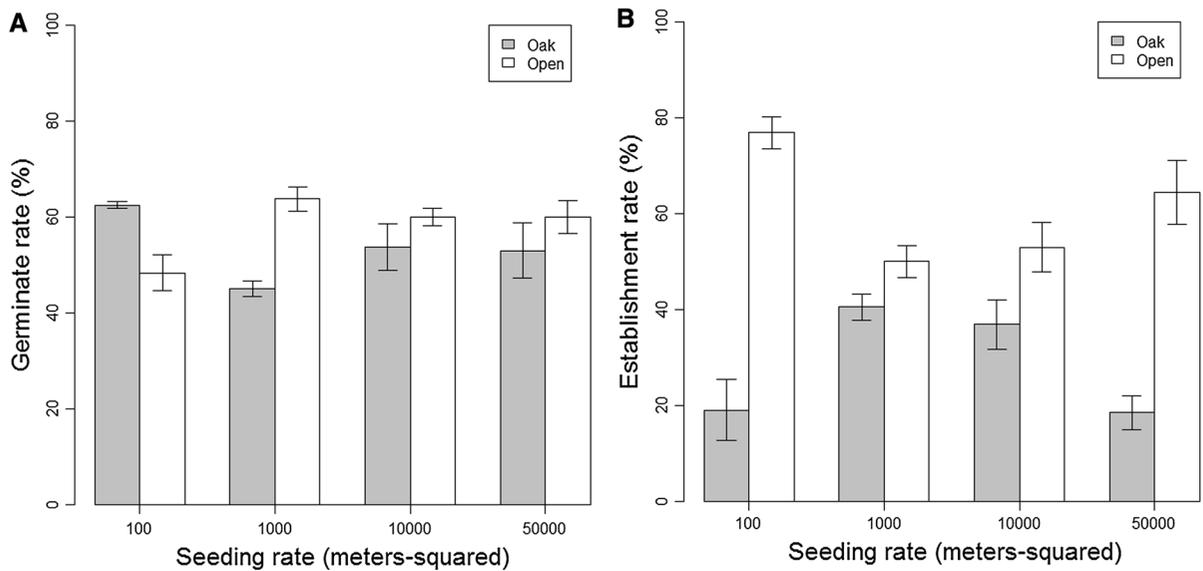
Fig. 1 Means $\pm$ SE of **A** percent germination and **B** percent establishment of medusahead across seeding rates in both oak woodland (*gray bars*) and open grassland (*white bars*)

(Fig. 2C, D) was significantly lower in the oak habitat (average = 11 tillers per plot), compared to the open grassland (average = 250 tillers per plot; $F = 31.46$, $p < 0.001$). There was no effect of defoliation on medusahead density in the oak habitat (Fig. 2C), but in the grassland habitat, density was almost twice as high in the plots that were not exposed to defoliation (Fig. 2D; $F = 3.3$, $p = 0.05$).

The treatments simulating abiotic characteristics of the oak woodland habitat in the grassland habitat did not affect medusahead germination (Fig. 3A; Table 2 in Appendix). However, the treatments did contribute to significant differences in establishment ($F = 5.051$, $p = 0.02$, Fig. 3B). Specifically, the litter treatment resulted in a reduction of establishment compared to control ($p = 0.01$) and the shade treatment ($p = 0.007$) by 88 and 89 %, respectively. The treatments also contributed to significant differences in persistence ($F = 9.25$, $p = 0.008$, Fig. 3C), where the litter treatment resulted in an average of 0 % establishment, compared to an average of 79 % establishment in the shade treatment ($p = 0.003$).

Finally, we found that defoliation treatment application number significantly affected medusahead density ($F = 12.09$, $p < 0.001$, Fig. 4A). Clipping twice reduced density by 70 % compared to control (post hoc $p < 0.001$), and by 60 % by clipping once

(post hoc $p = 0.03$). Seed production per reproductive spike was also affected by the defoliation treatment number ($F = 7.38$, $p = 0.002$, Fig. 4B). Clipping medusahead once results in 42 % more seeds per spike compared to control plots ($p = 0.03$) and plots that were clipped twice ($p = 0.01$).

Discussion

Although environmental variables are clearly important drivers of population growth rate (Lehtila et al. 2006; Jacquemyn et al. 2010), there is a surprising lack of research that investigates the relationship among habitat characteristics, vital rates, and invasion (Ramula 2014). This understanding is critical for leveraging demographic contributions for invasive plant control (Wooton and Pfister 2013). We investigated the potential relationships among these factors using the noxious annual grass medusahead.
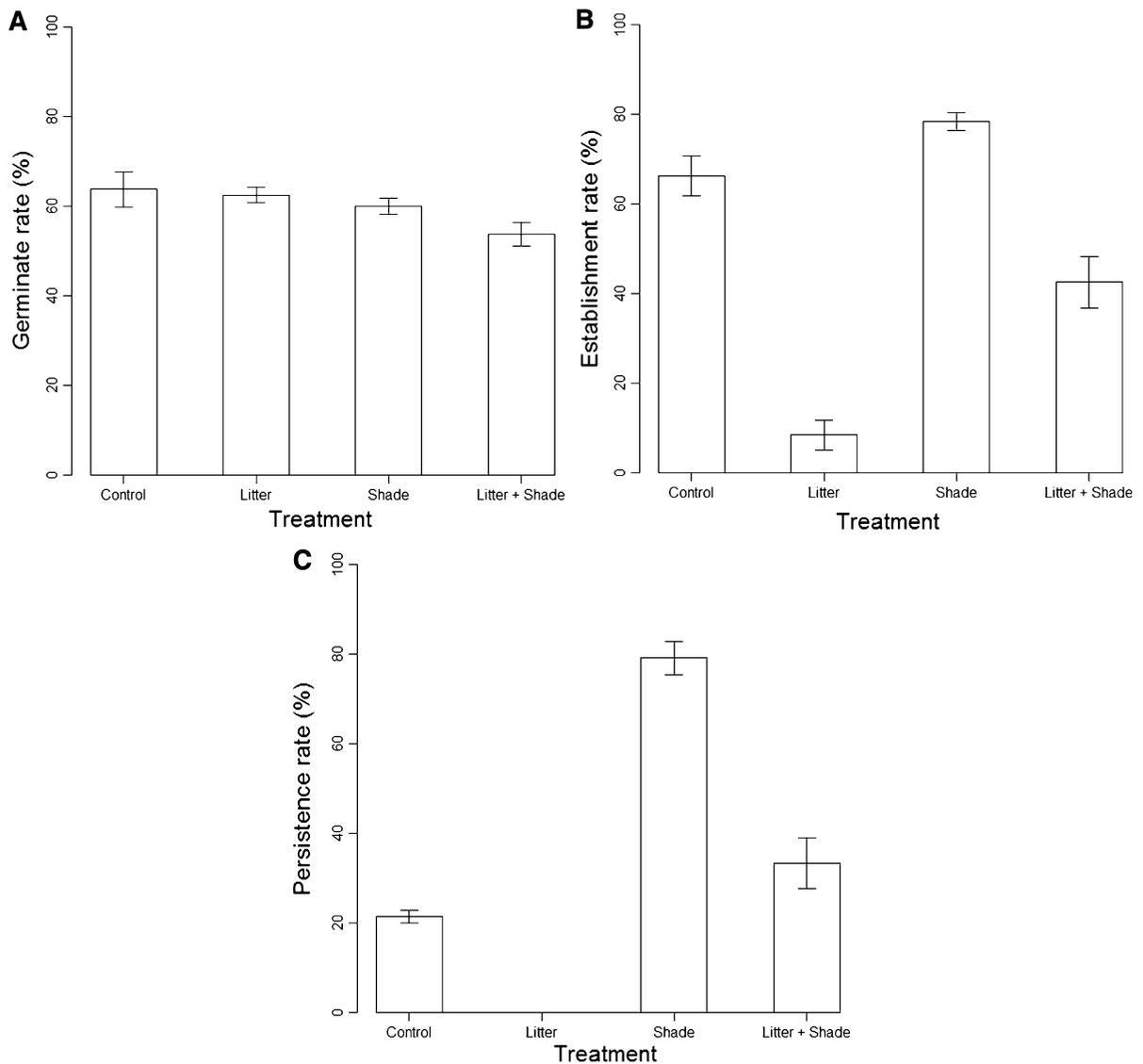
Establishment and persistence of medusahead were higher in open grassland plots compared to oak woodland plots, ultimately resulting in higher overall density in the grassland habitat. This suggests that maintenance of oak corridors can be useful for isolating patches of medusahead (Gornish et al. 2015). Although grass litter (Evans and Young 1970,
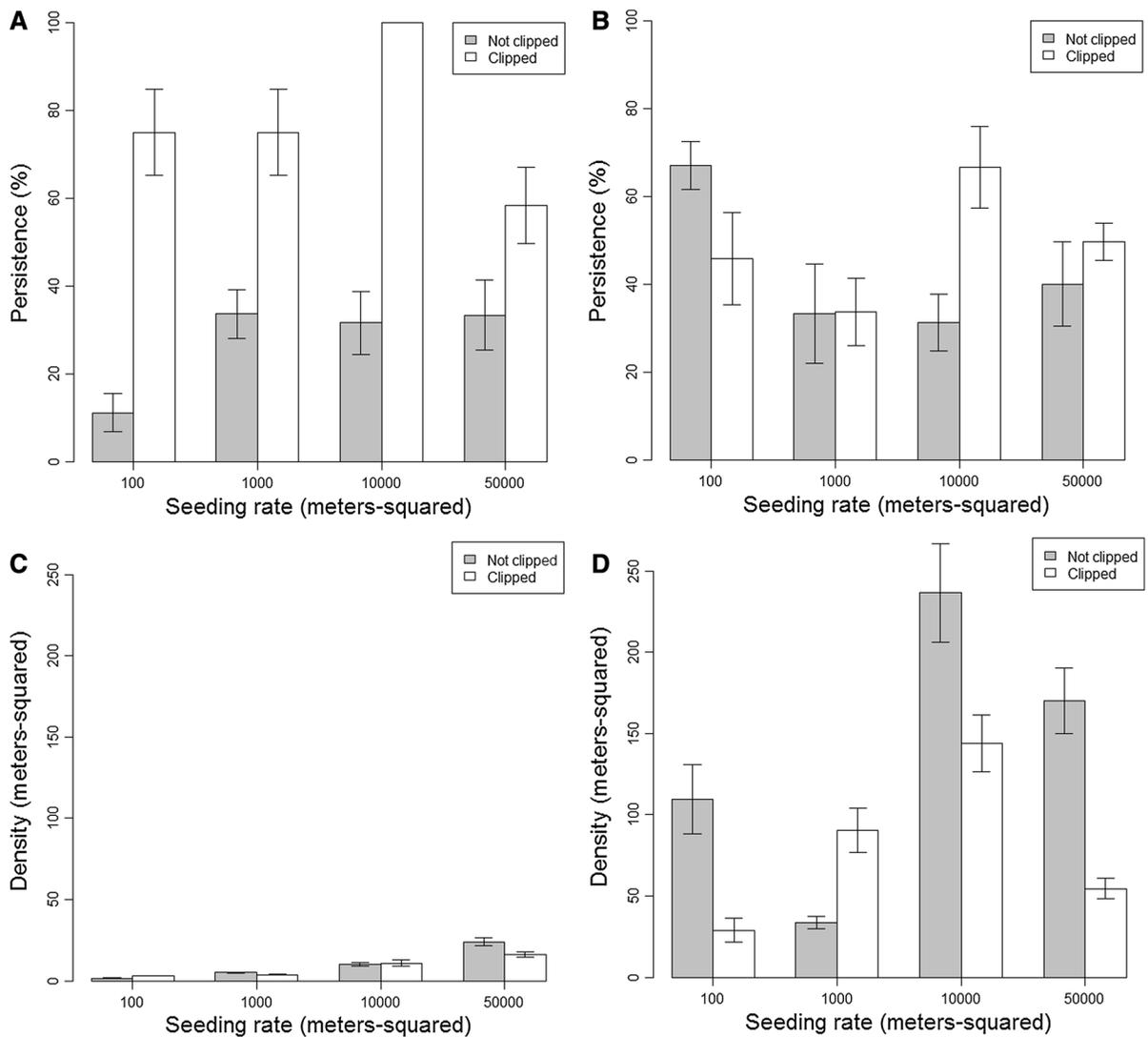
Fig. 2 Means ± SE of persistence of medusahead tillers in **A** oak and **B** open grassland habitat and total density of medusahead tillers in **C** oak and **D** open grassland habitat across seeding rates in unclipped (*gray bars*) and clipped (*white bars*) plots

but see Amatangelo et al. 2008) and sometimes oak litter (Donath and Eckstein 2008) are generally regarded as beneficial to invasive annual plant species due to the associated enhancement of soil moisture in rangeland habitat, we found that experimental addition of oak litter was responsible for limiting medusahead establishment and persistence. The presence of desiccated germinated seedlings on top of the litter layer suggests that the litter was acting as a physical barrier to medusahead establishment (Facelli and Pickett

1999; Schramm and Ehrenfeld 2010). For the few seedlings that were able to penetrate the litter layer to establish, persistence was likely limited by a chemical barrier. Tree litter is known to affect vegetation due to the low rate of decomposition (Xiong and Nilsson 1999) and the litter of oak trees particularly is known to negatively affect herbaceous species due to chemical leaching of phenolic compounds (Kuiters and Sarink 1986). Persistence of medusahead could have been limited by both chemical means as well as

Fig. 3 Means ± SE of **A** percent germination **B** percent establishment and **C** percent persistence of medusahead across treatments simulating factors associated with oak woodland systems

through antagonistic interactions with a soil microbiome cultivated by the oak litter (e.g., Madritch and Hunter 2005). Although using oak litter to manage medusahead on large scales is infeasible, these results suggest that other potential factors restricting medusahead from oak canopies (such as soil microbial communities or competition) could be useful for identifying applied research priorities.

In the multi-density experiment, we found that habitat interacted with the defoliation treatment, but seeding density did not (Fig. 2A; $p < 0.001$). This is

not entirely unexpected as survival of annual plants can be insensitive to density (Goldberg et al. 2001; Ramula and Buckley 2010). The defoliation treatment was effective in reducing overall density, despite an increase in persistence of tillers in the oak woodland plots. Heterospecifics in these plots, which comprised many species functionally dissimilar to medusahead, including western poison oak (*Toxicodendron diversilobum*), miner's lettuce (*Claytonia perfoliata*), and prickly lettuce (*Lactuca serriola*), were likely competitively dominant to medusahead. In the presence of
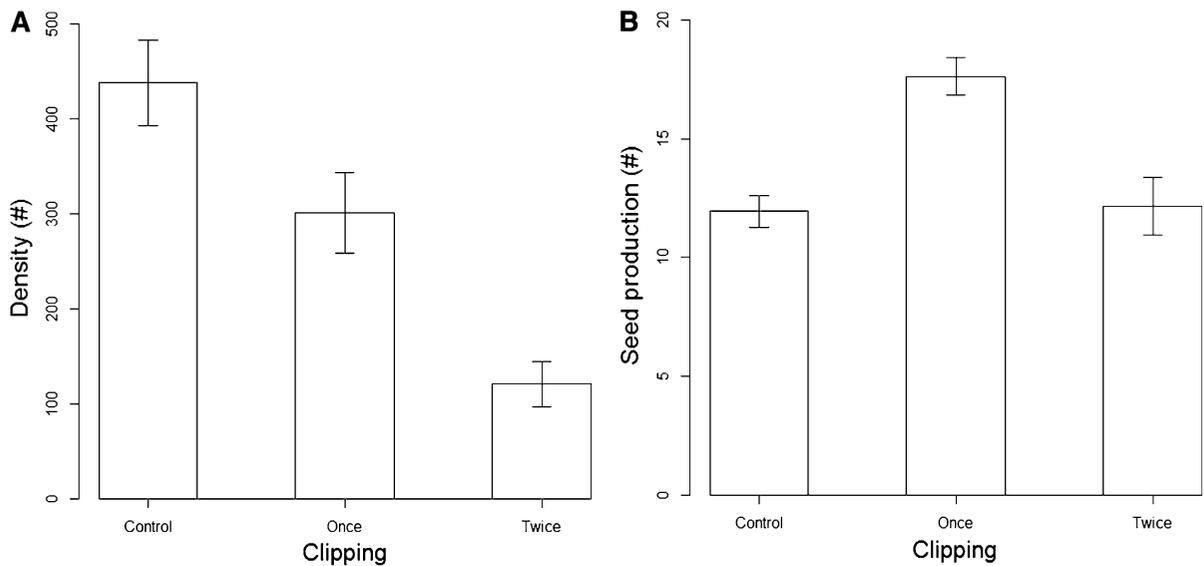
Fig. 4 Means $\pm$ SE of **A** density and **B** seed production per reproductive tiller of medusahead across clipping treatments

the defoliation treatment, the competitive pressure from heterospecifics may have been reduced and medusahead tillers that escaped the treatment may have had better access to resources, ultimately being more likely to persist (e.g., Benayas et al. 2005; Williams et al. 2007).

Perhaps the most compelling results of this study are from the defoliation sub-experiment where we identified not only a significant effect of multiple management efforts compared to a single management effort, but also evidence for a compensatory response by the single clipped plots (e.g., Turner et al. 2016). Seeds of invasive annual grasses are known to produce several cohorts, which germinate at different times during the winter (e.g., Mack and Pyke 1983). Younger (and smaller) seedlings from a later germinating cohort largely escape a single defoliation event. As a result of the reduction of competitive pressure, resources become more plentiful and surviving individuals explode in seed production. This compensatory behavior may explain why reductions in density that occur after a single management effort do not often translate into reductions in density the following year. The second clipping treatment essentially targeted this additional cohort. This result advocates for multiple control efforts for medusahead within a single

season to address the potential reproductive compensatory response of younger cohorts.

Sustainable, long-term management of invasive plants fundamentally depends on our ability to identify and manage the ecological processes driving invasion and to use site-specific information to design realistic management strategies and goals (Sheley et al. 2011). While medusahead management in annual grassland systems has long been a central research interest (e.g., Lusk et al. 1961), up until now there was little understanding of how density-dependent and density-independent processes may influence common management efforts associated with defoliation or how these responses may vary based on habitat type. Based on the results here, while seedbank density may play a modest role in determining how medusahead populations respond to management, variation in cohort phenology appears to be the largest driver in influencing how medusahead populations change through time following management. Future work that focuses on being able to forecast the phenological distribution and variation among medusahead cohorts at a particular site and year will likely be critical in efforts to increasing the efficacy of common management tools and for our understanding of how the distribution and abundance of this species changes through time and under common land management activities such as grazing.
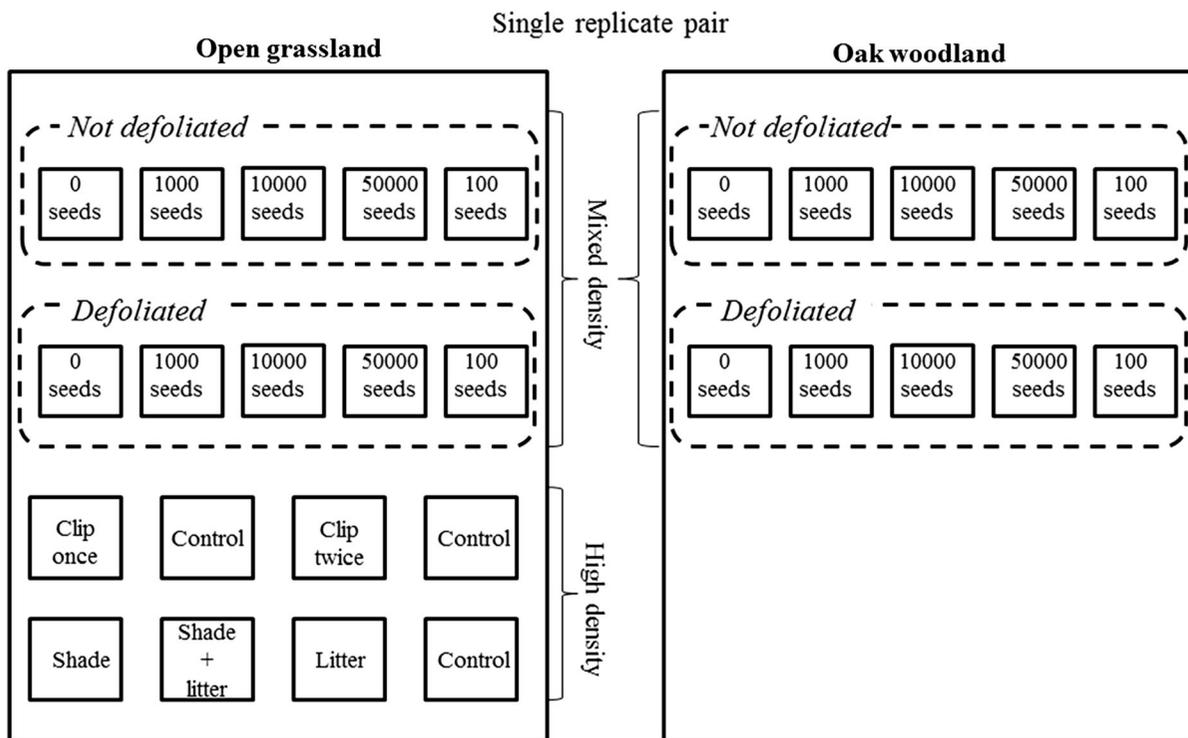
Appendix

See Figs. 5, 6 and Tables 1, 2
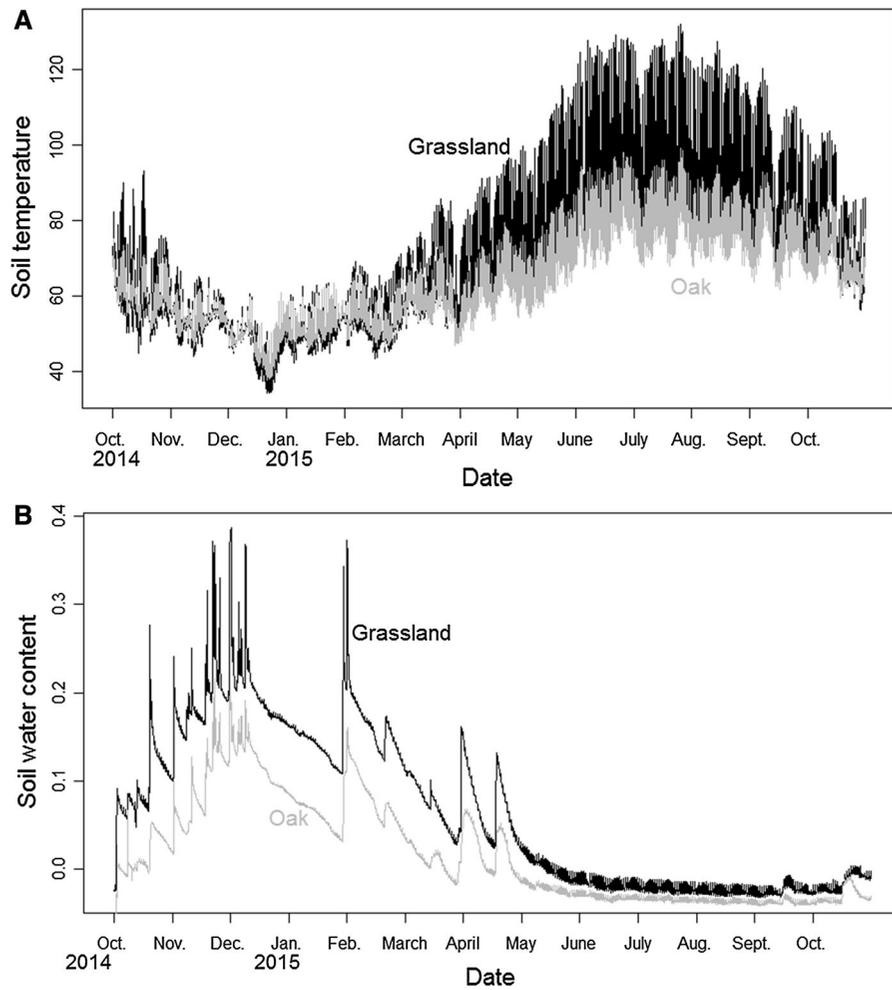
Fig. 5 A soil temperature (°F) and **B** soil moisture during the final year of the experiment in open grassland (*black lines*) and oak woodland (*gray lines*) plots

Fig. 6 Example of a single replicate plot layout

Table 1 ANOVA output for the multi-density study

Habitat	Response	Explanatory factor	Sum Sq.	F value	P value
Oak woodland	Germination	Seeding rate	27.6	1.18	0.19
	Establishment	Seeding rate	1080	1.58	0.22
	Persistence	Seeding rate	402	0.37	0.55
		Defoliation	23,403	21.43	<0.001
		Seeding rate × defoliation	2318	2.12	0.16
	Density	Seeding rate	11.87	29.84	<0.001
		Defoliation	0.00	0.00	0.97
		Seeding rate × defoliation	0.47	1.20	0.28
	Seed number	Seeding rate	248	4.32	0.04
		Defoliation	63.1	1.10	0.30
		Seeding rate × defoliation	32.7	0.57	0.45
Open grassland	Germination	Seeding rate	100,413	0.52	0.48
	Establishment	Seeding rate	16,937	5.52	<0.001
	Persistence	Seeding rate	69	0.04	0.84
		Defoliation	287	0.17	0.68
		Seeding rate × defoliation	290	0.17	0.68
	Density	Seeding rate	6276	0.55	0.46
		Defoliation	37,290	3.31	0.05
		Seeding rate × defoliation	9722	0.86	0.36
	Seed number	Seeding rate	46.9	1.48	0.23
		Defoliation	2.5	0.08	0.78
		Seeding rate × defoliation	19.7	0.62	0.43

Table 2 ANOVA output for the single-density (50,000 seeds) study

Experiment	Response	Explanatory factor	Sum Sq.	F value	P value
Habitat simulation	Germination	Treatment	418	0.25	0.86
	Establishment	Treatment	9870	5.51	0.02
	Persistence	Treatment	9902	9.25	0.008
Defoliation	Density	Defoliation	489	12.09	<0.001
	Seed number	Defoliation	326.7	7.38	0.002

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