



Evidence for Allelopathic Interference in an Exotic Invasive Grass, Medusahead (*Taeniatherum caput-medusae*)

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Introduction

Medusahead (Mh), one of the most problematic invasive annual weeds in North America, has spread from its original introduction near Roseburg, Oregon to its current range of roughly 1 million hectares spanning the western United States. This wave of Mh invasion is causing declines in both native and agriculturally-desirable species, and up to an 80% reduction in forage for livestock and wildlife. The success of invasive grasses like Mh has been attributed to several factors including fast growth rate, high productive potentials, adaptive nature and, above all, interference by resource depletion and allelopathy. Allelopathy, defined as any direct or indirect effect (commonly negative) of one plant on another mediated through the production and release of chemical compounds, is thought to be a primary mechanism driving the successful establishment of invasive weeds. Commonly cited effects of allelopathy include reduced seed germination and seedling growth. However the importance of allelopathy to invasive success is still under debate, and its effects are likely to be species-specific, having negative effects on some species and neutral effects on others. A better understanding of the role of allelopathy in invasive interactions is needed to clarify the mechanisms governing invasive success and inform the management of future invasive outbreaks.

Objective

Currently it is not known whether this physical competitive barrier (thatch) is augmented by allelopathic interference from Mh seeds, awns, and litter. To address this gap in knowledge, we conducted a series of controlled laboratory experiments investigating allelopathy in Mh and its effects on six grassland species. Specifically, we measured seed germination and seedling growth in the absence and presence of Mh awns, litter, and germinating seeds. Given the overwhelming and rapid success of Mh in its introduced range, we hypothesized that Mh will have negative allelopathic effects on seed germination and seedling growth in its competitors.

Methods and Materials

Seed germination and growth experiments were conducted using 6 species, hereafter referred to as “target” species that are common to the annual grasslands of California and often found growing next to Mh. Seeds from all species, except purple needlegrass, were collected from Bobcat ranch (38° 30'54" N, 122° 1'44" W), CA, USA in May and June of 2003. Purple needlegrass seeds were collected from potted plants grown in May of 2000 and 2001. Plants were grown from seeds collected in May 1997 from the Sierra Foothill Research & Extension Center, Yuba Co., CA (39° 15'03" N, 121° 18'47" W). Seeds were stored until used in the experiment in either plastic or paper bags envelopes in a dark cupboard at room temperature.

Germination Trial 1. The first experiment examined whether seed germination and growth of target species are inhibited in the presence of Mh seeds, awns, and litter. Seeds were germinated in 10-cm diameter plastic Petri dishes lined with four layers of paper towel, moistened twice daily. Twenty seeds of each target species were sown under each of the following treatments: 1) No Mh seeds, awns, inflorescences or straw (Control); 2) 10, 20, or 40 Mh seeds; 3) 20 Mh awns cut into small pieces (ca. 0.0067 g); 4) 10 Mh inflorescences (ca. 0.119 g); 5) 10 Mh straws (ca. 0.112 g); 6) 10 inflorescences and 10 straws (ca. 0.445 g). “Inflorescences” consisted of the remains of the spikes without the culm after seeds disarticulated. “Straws” were the culms that supported the spikes. Each treatment was replicated four times (four Petri dishes), which yielded a total of 32 dishes for each of the 6 species tested (Table 1). Figure 1a illustrates the experimental set-up within Petri dishes. Germination was monitored from 25 December 2006 - 10 January 2007, starting at day 4 after seeds were placed in the dishes. The experiment terminated when the number of germinating seeds had reached an asymptote. Shoot dry mass of 10 randomly selected seedlings in each Petri dish were measured at the end of the germination trial.

Germination Trial 2. A second experiment was conducted to determine if Mh’s effect on competitors is mediated by released chemical substances. The general set-up and protocol used was the same as described in Trail 1. Trial 2 consisted of the following treatments: 1) No Mh seeds or awns (Control), 2) 10, 20, or 40 Mh seeds, and 3) 20 Mh awns (ca. 0.0067 g).

Each treatment included 4 replicates requiring a total of 20 Petri dishes for each of the 6 species tested (Table 1). In Trial 2, Mh seeds or awns were placed in the dishes and watered first and then removed 4 days later, after seeds had germinated. After removal of all Mh tissues, 20 seeds of a target species were sown in the same Petri dish (Fig. 1b). The trial began on 24 February 2007 and ended on 14 March 2007, when the number of germinating seeds reached an asymptote.

Analysis: Germination was analyzed as a survival or time to “failure” process using an interval-censored approach where the response variable was the time to germination (“failure”) and the frequency was the number of seeds germinated during the 24 hours between observations. All seeds that did not germinate by the end of the experiment were right-censored (SAS Institute Inc. 2005). We tested the Weibull, exponential and lognormal distributions. Residuals were tested with quantile plots. The best fit and distribution of residuals were achieved with the lognormal distribution, so we chose it for the final analyses. Treatment effects were tested by likelihood ratios at the 1% level. Estimated parameters of significant effects were used to generate predicted curves for cumulative germination and 95% simultaneous confidence bands as a function of time (Meeker and Escobar 1998 pp. 60-62). This constitutes a conservative approach to comparing germination curves across treatments.

Comparisons among species are of exploratory nature, since no a priori hypotheses were posed in this regard. Shoot masses were averaged for each Petri dish, and the averages were analyzed with a simple linear model with effects for species, medusahead treatment and their interaction. The model implies a completely randomized design where each treatment had four replications. Box-Cox transformations were used as necessary to achieve homogeneity of variance in the residuals. We separated means using Tukey’s HSD.

Results

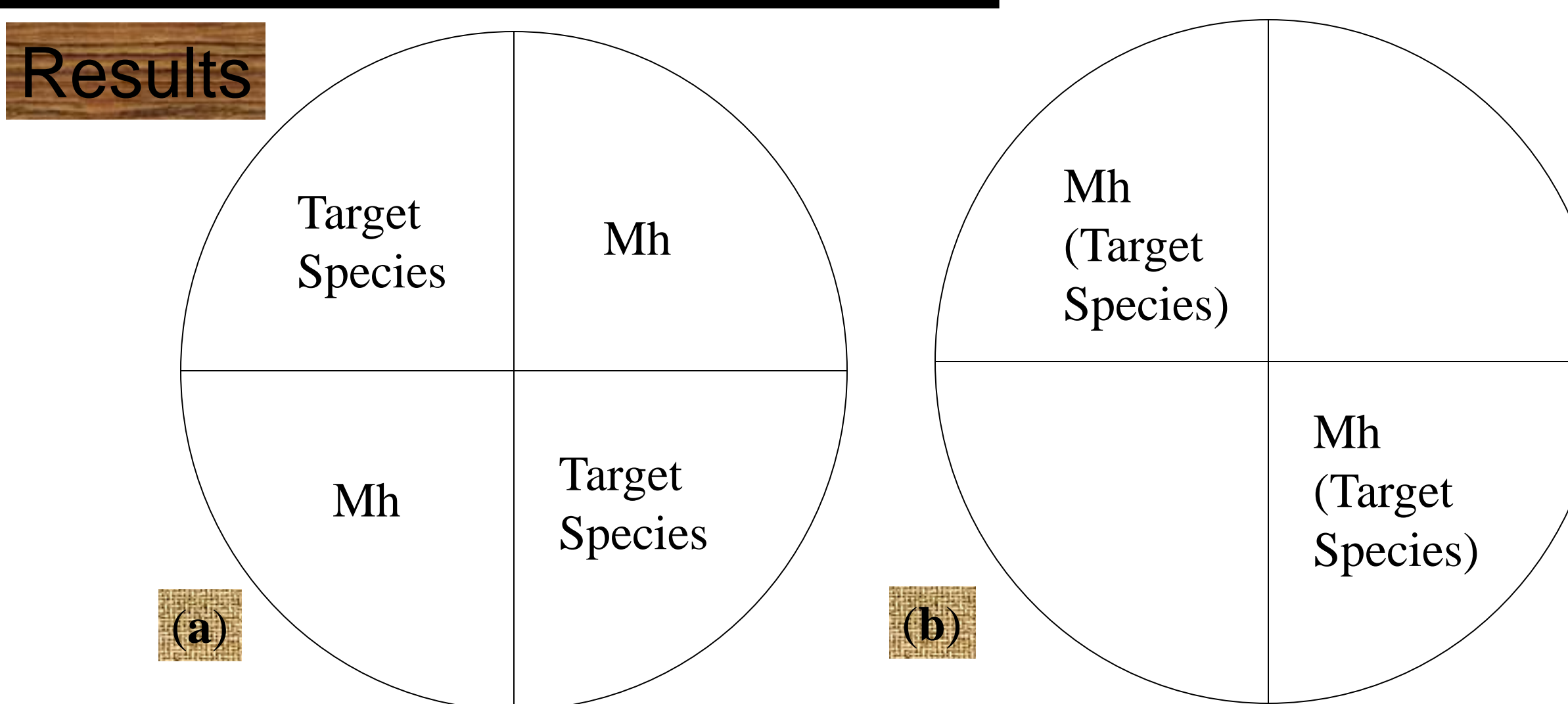


Figure 1. Experimental arrangement of Mh seeds, awns, inflorescence, inflorescence + straw, and straw together with the six desirable species in germination Trial 1 (a) and following Mh removal in Trial 2 (b).

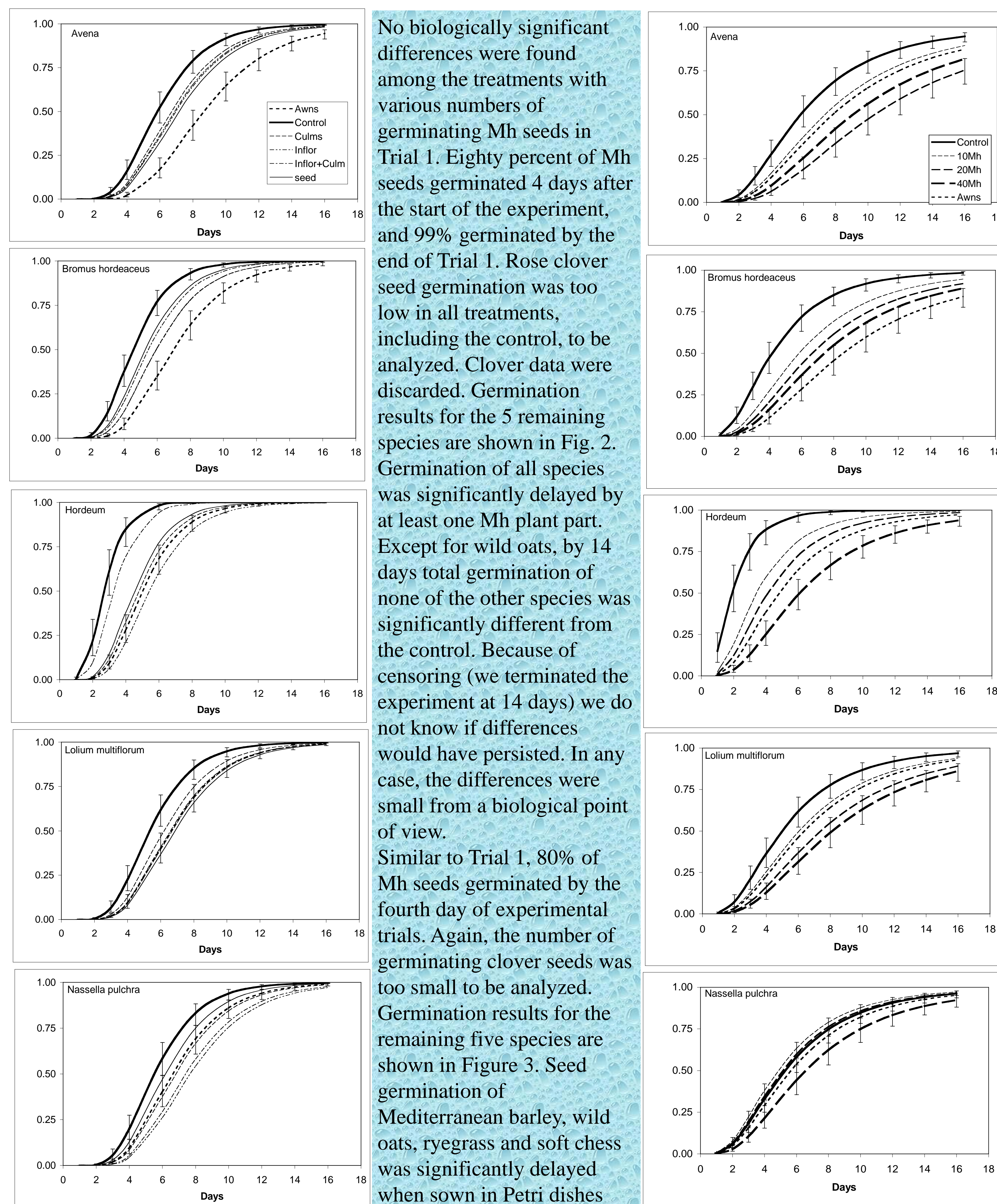


Figure 2. Graphical results from Germination Trial 1. For clarity of presentation and interpretation, only the 95% confidence intervals for controls and awn treatments are shown for each of the 5 desirable species that germinated.

Figure 3. Graphical results of Germination Trial 2 for each of the 5 desirable species that germinated. For clarity, 95% confidence intervals for control and awn treatments are presented.

purple needlegrass. In both trials, time to germination was affected by species. The presence of Mh tissue or germinating seeds generally slowed germination of all species. Overall, germination was slower in Trial 2. Species that germinated faster tended to exhibit greater impacts of treatments. Although increasing the number of germinating Mh seeds did not have an effect in Trial 1, it did in Trial 2. In general, there was a “dose response” whereby increasing number of Mh seeds reduced germination rate. However, the impact of the number of seeds was not fully explained by a quadratic model where number of seeds was a continuous explanatory variable. Germination of purple needlegrass was slowed down by the presence of previous season’s Mh culms and seedhead “skeletons” consisting of the remains of the spike after florets have disarticulated. After 4-8 days of germination time, the total number of seeds germinated in the treatments with awns or culms and old inflorescences was about half of that observed for controls.

Conclusions

Medusahead had the most pronounced and persistent effects on seed germination and seedling growth of wild oats. These results are consistent with, and may account for, the distribution of Mh and wild oats observed at Bobcat Ranch, where a few patches of pure wild oats can be found adjoining Mh patches, but seldom growing within Mh-dominated patches. These observations support the hypothesis that if allelopathy is an important determinant of the germination and growth of neighboring individuals under natural conditions, there should be a relationship between the chemical interactions among species and the small-scale distribution patterns of those species