ALLELOPATHY: EXPLORING THE FEASIBILITY OF USING NATIVE PLANTS TO SUPPRESS INVASIVE SPECIES

By

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ABSTRACT

Invasive species are a serious and urgent problem worldwide. In California, the impact of invasive species on the ecological environment, economy, and human society has already caused significant losses. Among the methods discussed for controlling invasive species, the "Homeland Security" hypothesis suggests that the effect of inhibiting invasive species can be achieved through the allelopathy of local plants. Here, I selected the native plant *Encelia farinosa* from southern California and the invasive species *Brassica tournefortii* as a study system to test the feasibility of using the allelopathic effects of the native plant to control the invasive species.

Encelia farinosa, or brittlebush, is a shrub that is distributed in the desert areas of the southwestern United States and northern Mexico. In earlier studies, it was identified that the leaves of brittlebush contain toxic plant compounds, namely 3-acetyl-6-methoxybenzaldehyde. Although this compound has been determined to inhibit plant growth, the extent to which these chemicals affect neighboring plants on an ecological scale remains undetermined. To confirm whether *E. farinosa* has allelopathic effects on *B. tournefortii* and whether it remains effective in the ecological environment, I conducted a germination experiment under laboratory conditions and an observational field study.

The germination experiment confirmed that under laboratory conditions, the minimum concentration of the leaf extract of *E. farinosa* was only 2% w/v sufficient to inhibit the germination of the majority of *B. tournefortii* seeds. Subsequently, the observational field study confirmed that the abundance of *B. tournefortii* increased as the distance from *E. farinosa* increased. These results confirm that the leaf extract of *E. farinosa* has a strong inhibitory effect on *B. tournefortii*, and it seems that this pattern also holds true for their distribution in the wild.

However, allelopathy is not necessarily the explanation. More tests are needed to prove that *E. farinosa* can control invasive species under natural conditions.

ACKNOWLEDGEMENTS

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Introduction

An invasive species refers to a non-native species whose population has the ability to sustain itself and spreads from the place of introduction to the surrounding environment (Richardson et al. 2000). Invasive species are one of the main causes of biodiversity loss and ecosystem degradation (Pyšek and Richardson 2010). The losses resulting from these two major issues, as well as the costs incurred in controlling invasive species, have imposed a heavy economic cost on society (Pyšek and Richardson 2010). Successful invasive species can proliferate and spread, thereby altering the local community and ecosystem through mechanisms such as competing for resources and changing the habitat, posing a threat to the local biodiversity (Mack et al 2000). Invasive species have become the sole threat contributing to the extinction of 16% of all species worldwide and have caused 60% of the known species extinctions (Kumschick et al. 2023). Furthermore, invasive plant species can have negative impacts on human health and well-being, such as causing allergic reactions from pollen or direct irritation to the skin (Pyšek and Richardson 2010). However, controlling invasive species is not an easy task. Management efforts are usually long-term and incur multiple costs, which poses a significant burden on the economy. In California, the economic losses caused by invasive plants amount to at least 82 million US dollars each year, and the losses across the entire country could be as high as several billion dollars (California Invasive Plant Council). Therefore, for the global society, finding an effective method to control invasive species has always been a challenging issue that needs to be addressed

One of the ideas for controlling these invasive species was proposed by Cummings, Parker, and Gilbert in 2012, and it is known as the "Homeland Security" hypothesis. This hypothesis posits that invasive species are extremely sensitive to the allelopathic effects of native

species, where allelopathy refers to the phenomenon in which plants influence the germination and growth of adjacent plants by releasing secondary metabolites. They predicted that allelopathy may serve to inhibit invasive species and restore native species. Based on this hypothesis, Cummings, Parker and Gilbert conducted research on local tree species and invasive grass species in the Panama River region in 2012 and observed the inhibitory effect that the local tree species had on the invasive grass species.

In California, *Encelia farinosa* is a native shrub that is widely distributed in arid desert areas, including the Mojave and Sonoran deserts (USDA Forest Service FEIS). It is a major component in a variety of shrub populations as well as in frequently disturbed plant communities (USDA Forest Service FEIS). Usually, under suitable climatic conditions or after a fire, *E. farinosa* forms almost a monotypic stand (USDA Forest Service FEIS). These characteristics, combined with the research history of allelopathy of *E. farinosa*, make *E. farinosa* an ecologically relevant model for evaluating whether the allelopathic effects of local plants can inhibit invasive annual plants. In the arid desert environment where resources are scarce, the impact of allelopathy could be significant. Nonetheless, the allelopathy of *E. farinosa* on the environment has been controversial for a long time. Research on it indicates that this allelopathy still lacks a complete evidence chain and modern experimental verification.

During the 20th century, studies on *E. farinosa* have confirmed the existence of allelopathic effects and identified the chemical substances involved along with their identities and properties. Went (1942) observed that compared to the deceased *E. farinosa*, the annual plants growing on living *E. farinosa* individuals were significantly scarce or absent. He proposed the explanation that the shrubs released specific substances that caused chemical inhibition to the annual plants. Gray and Bonner (1948) confirmed that the toxic substances released by *E.*

farinosa originated from the leaves. Through subsequent separation and structural determination, the allelochemical - 3-acetyl-6-methoxybenzaldehyde (Figure 1) - was identified and synthesized. By conducting inhibition experiments on tomato seedlings, they confirmed that the biological activity of the synthetic sample was consistent with that of the natural sample, providing crucial evidence for the allelopathic effects of *E. farinosa*. However, Gray and Bonner's research merely confirmed the allelopathic substances present in *E. farinosa* leaves and their toxicity in a laboratory setting. They did not conduct any studies on the allelopathy that *E. farinosa* could exert in a natural environment.

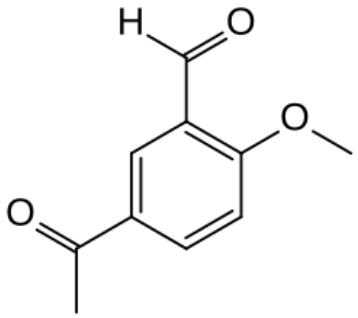

Figure 1. Chemical Structure of 3-acetyl-6-methoxybenzaldehyde

In 1953, Muller re-performed the experiment conducted by Gray & Bonner on tomato seedlings, acknowledging the presence of toxins in the *E. farinosa* leaves. Muller applied the same experimental method to *Franseria dumosa* (now known as *Ambrosia dumosa*) and discovered that *Franseria* was more toxic than *Encelia*. However, he found in the wild that there were many annual plants beneath *Franseria*, but not beneath *Encelia*. Based on this, Muller believed that allelopathic toxins could not explain the shrub-dependence pattern. The toxin effects observed in the laboratory were almost completely counteracted in the natural environment. Halsey (2004) summarized Muller's research process and pointed out the difficulties in isolating the variable of allelopathy during the research. Muller's counterexample

highlights the inconsistency between laboratory inhibition and field patterns, which is the root cause of the long-standing controversy in allelopathy research.

Although current research indicates that allelopathic effects detected in the laboratory do not necessarily produce the same ecological effects in the wild, conducting tests of allelopathy under controlled conditions in the laboratory is still necessary. Isolating interference variables can clearly determine whether a certain species is affected by the allelopathic effects of another species, thereby providing a mechanistic basis for subsequent ecological explanations. Therefore, it is necessary to conduct allelopathy research in laboratory conditions and ecological studies in the field separately. More importantly, each species needs to undergo individualized research into allelopathy because they do not necessarily have the same allelopathic effects.

The existing literature contains almost no data or evaluations regarding the allelopathic effects of *E. farinosa* on invasive annual plants. In California, the invasive species "*Brassica tournefortii*" has caused multiple negative impacts, including increasing the frequency of fires, increasing the load of combustible materials, and depleting soil nutrients (California Invasive Plant Council). Especially for the ecosystems of the Mojave Desert and the Sonoran Desert, the rapid and extensive reproduction and spread of *B. tournefortii* have enabled it to monopolize soil moisture (National Park Service). Using *B. tournefortii* as the receptor species for the allelopathy test enabled us to gain a more detailed understanding of a practical issue: whether the allelopathy of *E. farinosa* could have a positive impact on impeding *B. tournefortii* invasions.

Based on the above ideas, this research explores the inhibitory effect of *E. farinosa* on *B. tournefortii* through allelopathy, as well as its potential as a control measure for *B. tournefortii* in the wild. This research is conducted in two parts. The first part is a leachate experiment, which explores the inhibitory effect of the extract from *E. farinosa* leaves on the germination of *B.*

tournefortii in a laboratory setting. The first hypothesis is that the leaf extract of *E. farinosa* will significantly reduce the seed germination rate of *B. tournefortii*. The second hypothesis is that higher concentrations of the extract solution will result in a stronger inhibitory effect. The second part of the study involved field sampling, which was conducted to explore the impact of *E. farinosa* on the distribution of *B. tournefortii* in the natural environment. If the inhibitory effect in the leachate experiment is clearly present, we hypothesize that the allelopathy of *E. farinosa* will inhibit the spread of *B. tournefortii* under natural conditions.

Methodology

Study System

Encelia farinosa is a shrub found mainly in desert environments in the southwestern United States and northern Mexico. One of the major characteristics of the desert ecosystem is the scarcity of water resources, which leads to water competition among *E. farinosa* individuals (Ehleringer & Driscoll 2022). This competition has a significant impact on the survival rate of *E. farinosa* individuals. That is, the closer the distance to neighboring plants, the stronger the competition for water, and the higher the mortality rate (Ehleringer & Driscoll 2022). Such a mechanism enabled *E. farinosa* to form a clustered distribution (Ehleringer & Driscoll 2022). Such distribution usually occupies a large area, thereby affecting the survival and distribution of other plant species in terms of space and water resources. In addition, allelopathy is another important physiological characteristic exhibited by *E. farinosa* that impacts the distribution of other plant species.

Brassica tournefortii, also known as Saharan mustard or African mustard, is an annual herbaceous plant native to the deserts of northern Africa and the Middle East. This plant germinates in fall or winter, and bears fruit and flowers in winter or spring. *B. tournefortii*

produces a large number of seeds and dies after the seeds set (USDA Forest Service FEIS). Currently, it has been evaluated as an invasive species that is widely distributed in California and causes severe ecological damage to the biological community (California Invasive Plant Council). Berry et al. (2014) systematically researched and summarized the specific ecological invasion hazards brought about by *B. tournefortii*, including its extremely rapid expansion rate, competition for nutrients with local annual plants, alteration of the local ecosystem structure, and increase in fire risk by enhancing the fuel loads.

The field sampling site selected for this research is the hills located in the southeast of the UCR campus. There are many *E. farinosa* and *B. tournefortii* distributed there. The environment on the hills is generally arid, and the surface of the soil is mostly composed of hard materials such as crushed rocks and sand grains. In areas where grass covers a large area, the soil is relatively loose, and many small animal holes can be observed. The slope is quite steep, and *E. farinosa* and *B. tournefortii* are present in the steep areas as well. Since there are no obvious geographical barriers on the hills, pollen and seeds can freely spread. Therefore, all *E. farinosa* and *B. tournefortii* on the hills are considered to belong to the same population.

Leachate Experiment

Firstly, the leaves of *E. farinosa* were collected for the preparation of the extract solution. These leaves all come from mature *E. farinosa* plants, and these individuals are located on the hills in the southeast of the UCR campus. When collecting the leaves, I tried to avoid collecting those that had been bitten by insects or had any disease spots. The leaves I collected were all fresh and had a large surface area. After they were collected, the leaves were quickly washed clean of dust with water and then left to dry at room temperature.

Next, in the laboratory, these leaves were baked in the oven for 3 to 8 hours so that they became very crispy. I cut 5.0 grams of the leaves into small pieces with scissors and then placed them in a mortar. I used a pestle to gently grind the leaves into a powder form. The ground leaves were placed in a beaker, and 50 milliliters of distilled water were added. The solution was left to stand at room temperature for 12 to 24 hours. Subsequently, the solution was filtered through filter paper. This 10% w/v solution was considered to be 100% strength or concentration for the subsequent experiments. Other solutions of different concentrations were prepared by diluting with distilled water according to Table 1. After all the solutions were prepared and labeled, they were stored in a dark environment.

Table 1. Concentration Variation for Leachate Solution

Concentration	**w/v**	**How to prepare**
100%	10%	5.0g of the leaves + 50 mL of distilled water (No dilution)
50.0%	5.0%	15 mL of the 10% w/v solution + 15 mL of distilled water
25.0%	2.5%	10 mL of the 5% w/v solution + 10 mL of distilled water
20.0%	2.0%	3 mL of the 10% w/v solution + 12 mL of distilled water
15.0%	1.5%	2.25 mL of the 10% w/v solution + 12.75 mL of distilled water
10.0%	1.0%	1.5 mL of the 5% w/v solution + 13.5 mL of distilled water
5.00%	0.5%	0.75 mL of the 5% w/v solution + 14.25 mL of distilled water
0.00% (Control)	0.0%	Distilled water

Preliminary Germination Test

The *B. tournefortii* used in the seed germination experiment was stored in a dry environment. Before the experiment began, the seeds were rinsed three times with distilled water to remove any microorganisms that might affect germination on their surfaces. Before the formal germination experiment began, a preliminary test experiment was conducted to ensure that the seeds were capable of germinating. The seeds were divided into four petri dishes, and one dish had 5 seeds. According to the study conducted by Bangle et al. in 2008, the germination method of *B. tournefortii* is as follows:

1. Place filter paper on a petri dish and moisten it with deionized water.
2. Place the seeds on the moist filter paper in the petri dish.
3. Place the petri dish in an environment that is completely dark, like a drawer. Generally, the seeds will germinate within 3 to 12 days.

This research employed the same germination method. The size of the filter paper was designed to be a square with each side measuring two centimeters, and it was placed in a pattern where two sheets were crossed and placed in the center of the petri dish. The volume of water or solution added to each petri dish is 2.5 milliliters. After conducting the test experiments, it was observed that there were signs of successful germination for this batch of seeds, thereby proving the germination ability of the seeds used in the experiments. The first germination occurred in approximately 3 days. Then, after another 3 days, most of the seeds had grown small green leaves.

Germination Experiment

In the formal germination experiments, the 10% w/v solution was diluted to different concentrations according to the recipe in Table 1. Each concentration setting was set as a separate group in order to investigate the inhibitory effects produced by the solution to *B. tournefortii* seeds

at different concentrations. Each group consisted of five petri dishes, and in each petri dish, ten seeds were placed. The first round and the second round of experiments were conducted at different times. In the first round of experiments, the seeds were treated with 10%, 5%, 2.5%, 2.0% and 0.0% w/v concentrations. The treatments in the second round were 1.5%, 1.0%, 0.5% and 0.0% w/v. In the results, there were a total of ten control petri dishes. Leachate solutions with varying concentrations were added to the different groups. The control group was given pure water instead. The volume of solutions added to each petri dish was 2.5 milliliters. If some of the solution evaporates during the experiment, the same treated solution can be added to keep the filter paper moist, but without excessive water accumulation. These petri dishes were kept at 20-25 °C and subjected to a 12:12 light: dark cycle to simulate natural conditions. Observations were made continuously until the control group's germination stabilized. During the observation, the germination status was recorded daily. If the radicle penetrates the seed coat by at least 2 millimeters, it is considered successful germination.

Field Sampling

The objective of the field sampling was to investigate whether the presence of *E. farinosa* in the wild environment could inhibit the distribution and spread of *B. tournefortii*. I chose to go for sampling at noon (around 12 PM) on a hill located in the southeast of the UCR campus. I selected those *E. farinosa* with a radius of approximately 0.5 meters and ensured that their main stems were located at the center. This ensures that the sampled data is not affected by changes in radius and the position of the main stems. The planned number of samples to be collected is 12 to 18 brittlebushes, but the minimum number must not be less than 12. For a sampled brittlebush, I set five directions around it as the center. In each direction, I define four zones. Each zone is a square grid with each side measuring 25 centimeters. Zone 1 consists of a square grid extending

from the center of Brittlebush to 25 centimeters in the direction. The side length range of Zone 2 is from 25 centimeters to 50 centimeters. The side lengths of Zone 3 range from 50 centimeters to 75 centimeters. The side lengths of Zone 4 range from 75 centimeters to 100 centimeters. Figure 2 provides a demonstration of this approach.

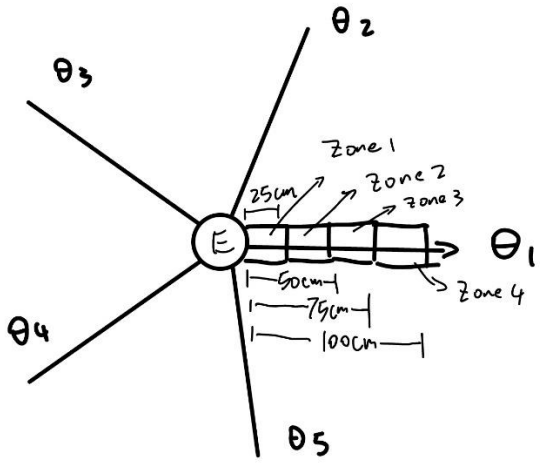

Figure 2. Demonstration of the Directional Approach of Field Sampling

The number of *B. tournefortii* in each area was recorded. I also recorded the approximate radius of each *E. farinosa* sample that was collected. A direction is considered unavailable if another *E. farinosa* occurs within 2 meters along that transect. Since most *E. farinosa* are distributed in clusters, it is very rare to find all five available directions. Therefore, each sample of *E. farinosa* needed to have at least three available directions. Each direction angle is randomly selected. If the direction is unavailable, select randomly again until it is available. In the actual sampling process, the direction angle is provided by the compass, with 0° representing the north direction. I placed a piece of cardboard with a side length of 25 centimeters in the sampling area. After determining the area, I removed the cardboard and then counted the *B. tournefortii*. This can ensure that the sampling area is uniform. A total of 12 *E. farinosa* samples were sampled.

Statistical Analysis

All the data analysis and data graphing were completed using R version 4.5.1 (R Core Team). The distribution of the germination rate of the seeds was tested for normality by the Shapiro-Wilk test using the R package, stats (R Core Team). Because the distribution of germination rate did not show a normal distribution, the non-parametric Kruskal-Wallis test, also from the R package, stats (R Core Team), was used to analyze this data. The response variable was the dish-level germination percentage, and the predictor variable was the leachate concentration treatments. Because the non-parametric Kruskal-Wallis test rejected the null hypothesis, a post-hoc Dunn's test with the Holm method was conducted on the germination rate using the R package, FSA (Ogle et al.).

Another data analysis performed was logistic regression. This analysis is specifically for the analysis of seed-level germination (0 = not germinated, 1 = germinated), treating each seed as an individual data point. The logistic regression was conducted using the function "glmer()" in the R package, lme4 (Douglas et al.). The model specifically employed a binomial generalized linear mixed model. Leachate treatment was included as a fixed effect, and dish was included as a random intercept to account for non-independence of seeds within the same dish. A null model that contained only the dish as a random effect was compared to the full model using a likelihood-ratio test. The model that fits better was adopted.

Because the field sampling data was highly discrete, I employed a generalized linear mixed-effects model with a negative binomial error distribution for the analysis. This model utilized the R package, glmmTMB (Mollie et al.). The response variable was the number of individuals of *Brassica tournefortii*. The fixed effect was the number for "Zone", such that the

farther away from *E. farinosa*, the larger the "Zone" number was. The different individuals of brittlebush were included in the model as a random effect.

Results

Overall, the germination rate of *B. tournefortii* seeds decreases as the leachate concentration increases (Figure 3). Among them, the median germination rate of the control group was the highest. As the leachate concentration increases, the median and interquartile range shifted downward. The leachate concentration values ranging from 5% to 15% indicated a decrease in the germination rate, but it remained within the range of the control group. Subsequently, the median value decreased significantly by 20%. The germination rates of 25% and above leachate concentration were all 0.

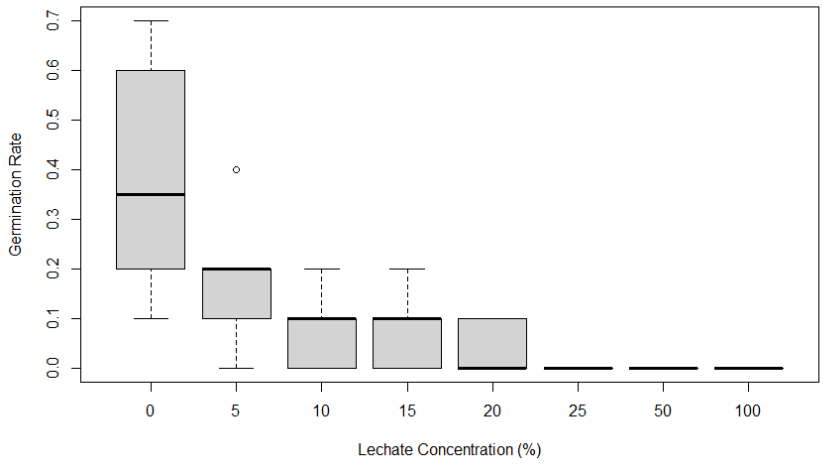

Figure 3. Boxplot of Dish-Level Germination Rate

The result after conducting the Shapiro-Wilk test on the germination rate of the seeds was $W = 0.72$ and $p < 0.001$. This distribution was considered to be significantly deviated from the normal distribution. Therefore, one of the methods for subsequent data analysis was the non-parametric Kruskal-Wallis test. The result of the non-parametric Kruskal–Wallis test conducted on the data of dish-level germination rate was $\chi^2 = 16.78$, $df = 2$, and $p = 0.00023$. Since the p-

value was much less than 0.05, the null hypothesis was rejected, indicating that the germination rate showed significant differences depending on the concentration of the solution (Figure 3). Therefore, a post-hoc Dunn's test with the Holm method was conducted as the subsequent analysis for this non-parametric Kruskal-Wallis test. The results were presented in Table 3.

Table 3. Dunn's Post-Hoc Test with Holm Method

Comparison	Z	P.unadj	P.adj	Interpretation
0 - 10	2.4152813	1.572306e-02	0.377353433	Non-significant
0 - 100	4.0204683	5.808256e-05	0.001626312	Significant
10 - 100	1.3901327	1.644886e-01	1.000000000	Non-significant
0 - 15	2.4152813	1.572306e-02	0.361630374	Non-significant
10 - 15	0.0000000	1.000000e+00	1.000000000	Non-significant
100 - 15	-1.3901327	1.644886e-01	1.000000000	Non-significant
0 - 20	3.0903600	1.999140e-03	0.049978510	Significant
10 - 20	0.5846352	5.587930e-01	1.000000000	Non-significant
100 - 20	-0.8054975	4.205327e-01	1.000000000	Non-significant
15 - 20	0.5846352	5.587930e-01	1.000000000	Non-significant
0 - 25	4.0204683	5.808256e-05	0.001568229	Significant
10 - 25	1.3901327	1.644886e-01	1.000000000	Non-significant
100 - 25	0.0000000	1.000000e+00	1.000000000	Non-significant
15 - 25	1.3901327	1.644886e-01	1.000000000	Non-significant
20 - 25	0.8054975	4.205327e-01	1.000000000	Non-significant
0 - 5	1.3501573	1.769655e-01	1.000000000	Non-significant
10 - 5	-0.9224245	3.563072e-01	1.000000000	Non-significant
100 - 5	-2.3125572	2.074700e-02	0.456433929	Non-significant
15 - 5	-0.9224245	3.563072e-01	1.000000000	Non-significant
20 - 5	-1.5070598	1.317953e-01	1.000000000	Non-significant
25 - 5	-2.3125572	2.074700e-02	0.435686932	Non-significant
0 - 50	4.0204683	5.808256e-05	0.001510147	Significant
10 - 50	1.3901327	1.644886e-01	1.000000000	Non-significant
100 - 50	0.0000000	1.000000e+00	1.000000000	Non-significant
15 - 50	1.3901327	1.644886e-01	1.000000000	Non-significant
20 - 50	0.8054975	4.205327e-01	1.000000000	Non-significant
25 - 50	0.0000000	1.000000e+00	1.000000000	Non-significant
5 - 50	2.3125572	2.074700e-02	0.414939935	Non-significant

The results of Dunn's Test indicated that all the comparisons between the control groups and ≥ 20% leachate were statistically significant, with adjusted p-values of less than 0.05 (Figure 3). This

indicated that more germination occurred within the control group. At lower concentrations (5-15%), the comparisons showed no significance (Figure 3).

In the logistic regression analysis, compared to the null model ($\chi^2 = 89.5$, $df = 7$, $p < 2.2 \times 10^{-16}$), the binomial generalized linear mixed model achieved a better fit ($\chi^2 = 51.30$, $df = 7$, $p = 8.03 \times 10^{-9}$). This result demonstrated a strong statistical significance, indicating that the probability of seed germination had a strong dependence on the leachate treatment (Figure 4). It can be observed that there was a certain number of successfully germinated seeds in the control group. In the range of 5% to 20%, as the concentration increases, the number of successfully germinated seeds also decreases. At 25% and above, there were no seeds that successfully germinated.

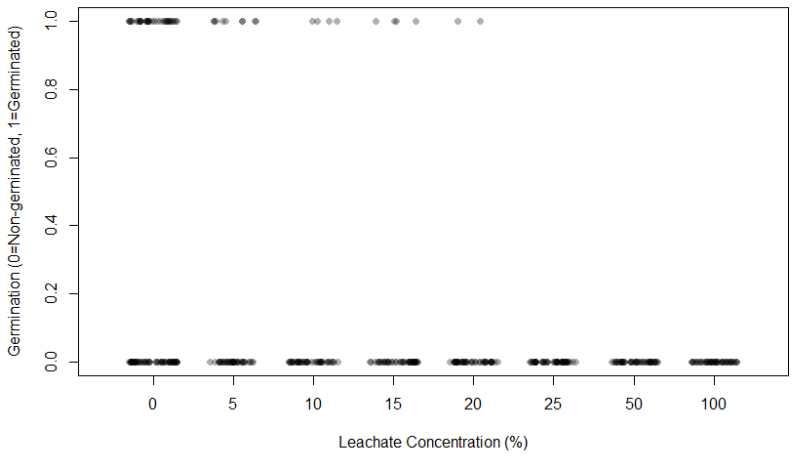

Figure 4. Stripchart of Seed-Level Germination Rate

Field sampling showed that *B. tournefortii* abundance increased across zones, with higher counts observed in Zones 3–4 compared with Zones 1–2 (Figure 5). From Zone 1 to Zone 4, the blue line continued to rise without any reverse trend. This means that from Zone 1 to Zone 4, the total number of *B. tournefortii* has increased.

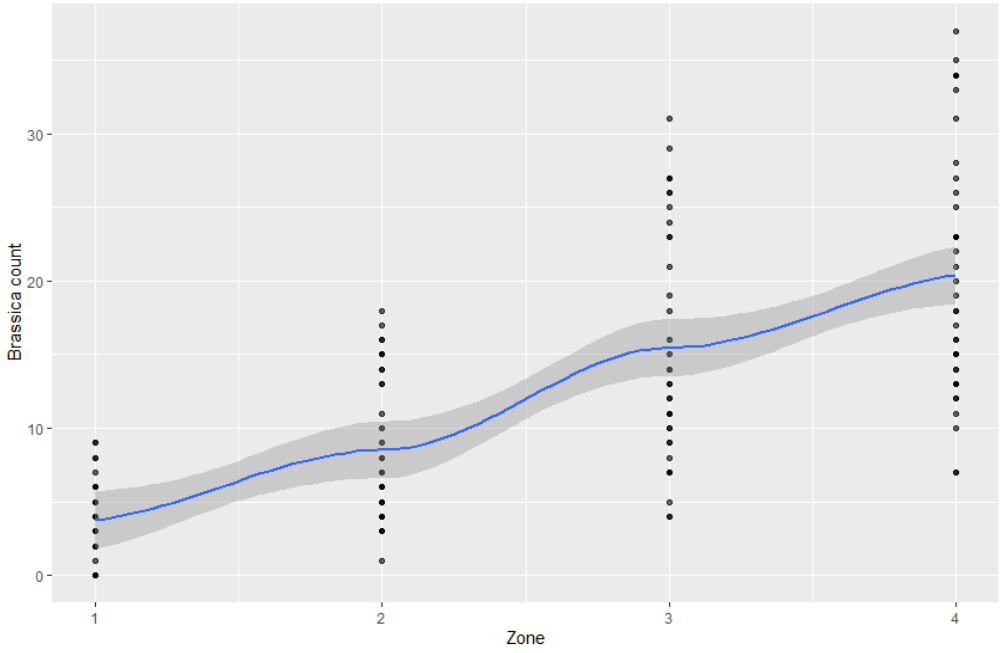

Figure 5. Plot of Field Sampling Result

The *x*-axis represented the Zone number. The *y*-axis represented the number of *B. tournefortii* within each area. The blue line represented the smooth trend, while the gray band represented the confidence interval.

The result of generalized linear mixed-effects model with a negative binomial error distribution analysis was: $\beta = 0.52 \pm 0.03$ SE, $z = 19.77$ and $p < 0.001$. This indicates that the hypothesis that the density of *Brassica* increases as the distance from *Encelia* increases has strong statistical evidence. From $\exp(0.52048) \approx 1.68$, we could observe that for each additional Zone, the expected quantity of *Brassica tournefortii* increases by approximately 68%. The remaining parameters of this model were AIC = 905, logLik = -448.5, and Dispersion parameter = 44.

Discussion

Based on the analysis of seed germination data and multiple charts, the first hypothesis of this study can be verified. The statistical analysis results of the Kruskal–Wallis test indicated that

the leachate solution had an impact on the germination rate of the seeds. The subsequent post-hoc Dunn's test using the Holm method identified the threshold at which the leachate solution affected seed germination. The comparison between the control group and the group with ≥ 20% leachate showed statistically significant results, indicating that concentrations above 20% had a significant impact on the germination of the seeds. According to the chart, there were no seeds that successfully germinated within the 25-100% range. The number of successfully germinated seeds within the 5-20% range decreased as the concentration increased, indicating the toxicity of the components in the leachate solution to the seeds. Therefore, the leaf component extract of *E. farinose* shows significant toxicity towards *B. tournefortii*, and the toxicity becomes more pronounced as the concentration of the extract increases. The toxicity threshold at which the *B. tournefortii* seeds can germinate and survive is 20-25%. There is a 25% or higher chance of no germination.

The results obtained from the data analysis of the field samples are in complete accordance with the expectations in the hypothesis, that is, the abundance of *B. tournefortii* increases with increasing distance from *E. farinosa*. *B. tournefortii* shows a high sensitivity to the spatial distribution of *E. farinosa*, and this sensitivity is manifested as a significant increase in release as the distance increases. This is evidence that brittlebush can also exert significant allelopathic effects on *B. tournefortii* in its natural environment.

Therefore, based on the significant inhibitory effect of brittlebush on *B. tournefortii* under both laboratory conditions and natural environments, increasing the number and distribution of brittlebush might be a possible and feasible way to control the invasion of *B. tournefortii*. Among the options for controlling the distribution of *B. tournefortii*, *E. farinosa* can be considered as one of the potential solutions.

Limitations

This research has several limitations. Firstly, this research only examined the allelopathic effects of *E. farinosa* on *B. tournefortii* but did not test the allelopathic effects of *E. farinosa* on other annual plants. Although 3-acetyl-6-methoxybenzaldehyde in the leaves of *E. farinosa* was confirmed by Gray and Bonner in 1948 to have an inhibitory effect on plants, their experiment was only conducted on tomato seedlings. At present, there is no strong evidence to prove that the allelopathy of *E. farinosa* is universal for annual plants. Therefore, regarding whether the allelochemicals of *E. farinosa* can effectively inhibit *B. tournefortii*, this research provides data and evidence to support this claim. However, this research does not address whether the allelopathy of *E. farinosa* also has an effective inhibitory effect on other non-native plant species, local plant species in California, and even non-annual plants.

Secondly, the *E. farinosa* leaf samples collected in this research, as well as the locations of the field samples, were all in the hills located in the southeast of the UCR campus. The data obtained all come from the same *E. farinosa* and *B. tournefortii* population. This study did not investigate whether the conclusion reached would still be effective in other field locations and among different populations.

Thirdly, this study did not have the opportunity to test the effects of variables other than leachate concentration on the allelopathic properties of *E. farinosa*. This is also one of the difficulties in the research on the underlying principles of allelopathy, as in the wild environment, it is difficult to explore and study the impact of a certain variable on allelopathy by controlling all other variables. Different soil compositions, the presence of other plants around *E. farinosa* individuals, as well as the interference from microorganisms, all may affect the inhibitory effect of allelopathy on annual plants in the field. For *B. tournefortii*, the fact that it

appears to be inhibited by *E. farinosa* may be influenced by other factors. This research did not investigate whether the germination of *B. tournefortii* is sensitive to factors such as water source and light. Therefore, allelopathy does not necessarily have to be the sole explanation for the data obtained in this experiment.

Finally, this research cannot determine whether the goal of controlling *B. tournefortii* through extensive cultivation of *E. farinosa* would be counterproductive and cause harm to the local ecosystem due to the excessive presence of *E. farinosa* itself. In addition, it would be necessary to determine the extent to which the allelopathy of *E. farinosa* affects local plants. Therefore, this research emphasizes that although the data support this approach, it remains a potential option.

Future Research Directions

One of the important future research directions is to investigate whether excessive *E. farinosa* might instead have a negative impact on the local ecosystem. Not only does this study focus on allelopathy, but the high-water resource competition ability of *E. farinosa* is also an aspect worthy of attention. Clarifying this point is necessary to determine the practical feasibility of the scheme of using the allelopathic effects of *E. farinosa* to control *B. tournefortii*. Another future research direction could be to explore the mechanism of the allelopathic effects of *E. farinosa* at both the macroscopic and molecular levels. On a macroscopic level, if possible, we can explore the standard conditions under which *E. farinosa*'s allelopathic effects can be exerted by simulating different natural conditions. At the molecular level, by integrating multi-omics and systems biology approaches, we can investigate whether there are other chemical substances that assist in the allelopathic effects of *E. farinosa*. These research directions will further help us

understand the role of allelopathy in ecological systems and the feasibility of using it as a tool for controlling invasive species.

Conclusion

Based on all the experimental results and data analysis, we can conclude that under laboratory conditions, the leaf extract of *E. farinosa* has a strong allelopathic effect on *B. tournefortii*. The data observed and collected in the field also conform to this pattern, showing that the abundance of *B. tournefortii* is higher the farther it is from *E. farinosa*. However, because the data collected in the field were merely observational, it is not definitive proof that this pattern was caused by allelopathic effects. More experiments on other natural factors are needed to explore the role of the allelopathic effect of *E. farinosa* in ecosystems and to evaluate whether *E. farinosa* can contribute to invasive plant management under natural conditions.

References

"About Invasive Species In California." *California Department of Fish and Wildlife*, wildlife.ca.gov/Conservation/Invasives/About. Accessed 9 Feb. 2026.

Anypodetos. *Chemical structure of 3-acetyl-6-methoxybenzaldehyde*. 12 Apr. 2016. *Wikipedia*, https://en.wikipedia.org/wiki/3-Acetyl-6-methoxybenzaldehyde#/media/File:3-Acetyl-6-methoxybenzaldehyde.svg. Accessed 9 Feb. 2026.

Bangle, Dianne N., et al. "Seed germination of the invasive plant brassica tournefortii (Sahara mustard) in the Mojave Desert." *Western North American Naturalist*, vol. 68, no. 3, Sept. 2008, pp. 334–342, https://doi.org/10.3398/1527-0904(2008)68[334:sgotip]2.0.co;2.

Berry, Kristin H., et al. "Models of invasion and establishment for African mustard (*brassica tournefortii*)." *Invasive Plant Science and Management*, vol. 7, no. 4, Dec. 2014, pp. 599–616, https://doi.org/10.1614/ipsm-d-14-00023.1.

Brahmsteadt, Taryn R. "Encelia Farinosa, White Brittlebush." *Fire Effects Information System*, U.S. Department of Agriculture, 2024, www.fs.usda.gov/database/feis/plants/shrub/encfar/all.pdf.

"Brassica Tournefortii." *California Invasive Plant Council*, www.cal-ipc.org/plants/profile/brassica-tournefortii-profile/. Accessed 5 Feb. 2026.

"The Cost of Invasive Plants in California." *California Invasive Plant Council*, www.cal-ipc.org/solutions/research/cost/. Accessed 5 Feb. 2026.

Cummings, Justin A., et al. "Allelopathy: A tool for Weed Management in forest restoration." *Plant Ecology*, vol. 213, no. 12, Dec. 2012, pp. 1975–1989, https://doi.org/10.1007/s11258-012-0154-x.

Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Ehleringer, James R., and Avery W. Driscoll. "Intrinsic water-use efficiency influences establishment in Encelia farinosa." *Oecologia*, vol. 199, no. 3, July 2022, pp. 563–578, https://doi.org/10.1007/s00442-022-05217-5.

Gray, Reed, and James Bonner. "Structure determination and synthesis of a plant growth inhibitor, 3-acetyl-6-methoxybenzaldehyde, found in the leaves of Encelia farinosa." *Journal of the American Chemical Society*, vol. 70, no. 3, 1 Mar. 1948, pp. 1249–1253, https://doi.org/10.1021/ja01183a114.

Halsey, Richard W. "In search of allelopathy: An eco-historical view of the investigation of chemical inhibition in California coastal sage scrub and Chamise Chaparral." *Journal of the Torrey Botanical Society*, vol. 131, no. 4, Oct. 2004, p. 343, https://doi.org/10.2307/4126940.

Innes, Robin J. "Brassica Tournefortii, Sahara Mustard." *Fire Effects Information System*, U.S. Department of Agriculture, 2023, www.fs.usda.gov/database/feis/plants/forb/bratou/all.pdf.

Kumschick, Sabrina, et al. "Using the IUCN Environmental Impact Classification for alien taxa to inform decision-making." *Conservation Biology*, vol. 38, no. 2, 5 Dec. 2023, https://doi.org/10.1111/cobi.14214.

Mack, Richard N., et al. "Biotic invasions: Causes, epidemiology, Global Consequences, and Control." Ecological Applications, vol. 10, no. 3, June 2000, pp. 689–710, https://doi.org/10.1890/1051-0761(2000)010[0689:bicegc]2.0.co;2.

McGillycuddy M, Warton DI, Popovic G, Bolker BM (2025). “Parsimoniously Fitting Large Multivariate Random Effects in glmmTMB.” _Journal of Statistical Software_, *112*(1), 1-19. doi:10.18637/jss.v112.i01<https://doi.org/10.18637/jss.v112.i01>.

Mollie E. Brooks, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400. doi:10.32614/RJ-2017-066.

Muller, Cornelius H. “The Association of Desert Annuals with shrubs.” *American Journal of Botany*, vol. 40, no. 2, Feb. 1953, pp. 53–60, https://doi.org/10.1002/j.1537-2197.1953.tb06449.x.

Ogle DH, Doll JC, Wheeler AP, Dinno A (2026). _FSA: Simple Fisheries Stock Assessment Methods. doi:10.32614/CRAN.package.FSA<https://doi.org/10.32614/CRAN.package.FSA>, R package version 0.10.1, <https://CRAN.R-project.org/package=FSA>.

Pyšek, Petr, and David M. Richardson. “Invasive species, environmental change and management, and health.” *Annual Review of Environment and Resources*, vol. 35, no. 1, 21 Nov. 2010, pp. 25–55, https://doi.org/10.1146/annurev-environ-033009-095548.

R Core Team (2025). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

“Research Needs.” *National Parks Service*, U.S. Department of the Interior, 21 June 2024, www.nps.gov/moja/learn/nature/researchneeds.htm.

Richardson, David M., et al. “Naturalization and invasion of alien plants: Concepts and definitions.” Diversity and Distributions, vol. 6, no. 2, Mar. 2000, pp. 93–107, https://doi.org/10.1046/j.1472-4642.2000.00083.x.

Went, F. W. “The dependence of certain annual plants on shrubs in southern Californi deserts.” *Bulletin of the Torrey Botanical Club*, vol. 69, no. 2, Feb. 1942, p. 100, https://doi.org/10.2307/2481445.