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Effects of fennel (*Foeniculum vulgare* L.) interference on germination of introduced and native plant species

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ABSTRACT

Allelopathy was proposed as one mechanism that allows introduced species to become invasive. With this examination being the first of a three-part series, we evaluated this concept for the invasive fennel plant (*Foeniculum vulgare*) whose allelopathic potential is recognized. Since the late 1980s, fennel has invaded grassland and soft chaparral vegetation communities on Santa Cruz Island in Channel Islands National Park. Using a rapid bioassay technique, we evaluated the germination response of forb and grass functional groups from different centres of origin. The response of 34 California native and introduced Mediterranean species to water soluble fennel leaf leachate was determined in the laboratory between April 2005 and August 2006. In general, germination of native species was significantly inhibited at fennel leachate concentrations above 2.0%. For introduced species, there was no significant effect on germination with most species able to germinate in leachate concentrations of 5.0%. Native species were negatively impacted at the most critical stage in their development, whereas introduced species were able to germinate even at the highest treatment concentration of fennel leachate used in bioassay.

Key Words: Bioassay, fennel, *Foeniculum vulgare*, germination, interference, native, non-native invasive plant.

INTRODUCTION

To utilize allelopathic interference successfully in weed management, it is necessary to find naturally occurring chemical compounds that inhibit seed germination and plant growth, or prevent propagule or fruit production (17). Since allelochemicals are generally produced in small amounts and probably exert their effects in concert with other allelochemicals, it is desirable that the selected bioassay be extremely sensitive and that some indication of mechanism of action of allelochemical(s) be determined (12,28). This is a very important point that must be considered in the application of allelopathy in agricultural management (2). One of the complementary courses that many allelopathic studies have followed over the past thirty years is to make sure that allelopathy research contributes to biological conservation (19,35), since temporal dominance of some species during stages of succession resulted from allelopathic mechanisms (44). Allelopathy provides an explanation for the ability of invasive species to persist beyond the initial stages of secondary succession by forming monospecific stands and/or influencing patterns

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of species in natural ecosystems (16,43). Coevolution is the common explanation for coexistence between species that utilize allelopathy, with molecules that are commonly released into the environment losing effectiveness against target plants as they genetically adapt tolerance to the continuous presence of compounds (14,32,33). Recently, support for coevolution was demonstrated for diffuse knapweed (*Centaurea diffusa* Lam.) and spotted knapweed (*Centaurea maculosa* Lam.) invasion into North America (3,6).

Bioassays assess the inhibitory or stimulatory potential of a compound through its application-induced response to the target species (20,29). In allelopathy, bioassays are necessary in each step of the isolation, purification, and identification processes of active compounds (37,30). Since initial pioneering work in the 1940s and 1950s (31), numerous inexpensive and easy-to-use bioassays have been used to check activity of putative allelopathic compounds. The most widely used bioassay is seed germination, carried out in Petri dishes, with filter paper as the most common seedbed (27). If population-level consequences of allelopathic interactions are of interest, interactions should be studied during the life history stages that are likely to have the largest demographic effects; and this has focussed research efforts on the sensitivity of seeds or seedlings to allelochemicals (28,36). Past research examined four germination bioassay indices and determined that each index led to different interpretations of allelochemical effects on seed germination (8). Two aspects of germination were discussed: germination capacity and germination rate. Germination capacity was calculated by means of the maximum germination percentage, which is a widely used index (5,22). The maximum germination percentage ignored slack times in germination and only gave a global interpretation of germination capacity - inhibition, stimulation or no action (8). The germination rate indices have an important edge over germination capacity because they are more sensitive as an indicator of allelopathic effects and better at revealing what occurred during the germination process (1); however, none of the indices were superior to each other at describing germination progress (38). Some researchers claim that germination capacity could be useful to obtain ecological information in plant succession, but it is not sensitive enough to study and validate allelochemical effects on a physiological process such as germination (24,25,45). Based on this assumption, we expect that there will be no differences in germination capacity between species of introduced and native origin nor between functional groups when subjected to the water-soluble leachate from the invasive plant fennel- *Foeniculum vulgare*.

MATERIALS AND METHODS

Thirty-two target species were obtained from commercial sources for evaluation, except for *Calandrinia ciliata* (Ruiz & Pav.) DC. and *F. vulgare*. *C. ciliata* was obtained from Santa Cruz Island, CA. *F. vulgare* seeds were collected in 1994 by B. Dash, and W. Colvin collected *F. vulgare* seeds in 1995 from the Central Valley of Santa Cruz Island, California (9). *C. ciliata* seeds were collected by W. Colvin in 2002 during a weed seed bank analysis of the Central Valley of Santa Cruz Island, California (9). The target species had to occur in one or both of the vegetation communities most heavily impacted by fennel- grassland and coastal sage scrub (26). While none of the introduced species required special treatment to break seed dormancy, several of the native species had to be

manipulated (Table 1). *Calystegia macrostegia* (Greene) Brummitt, *Lupinus bicolor* Lindl., *L. Microcarpus* Sims, and *L. succulentus* W.D.J. Koch were scarified between two sheets of 60 grit aluminum oxide sandpaper (3M model #346U) using 1.13 Kg of mass (a telephone directory) for 30, 50, 120, and 130 clockwise rotations, respectively. Stratification was based on the literature (13), personal communication (42) and germination trials. Wild collected seed germination rates may be as low as 20% (18). Therefore, species with germination rates < 10% during germination tests were not used for experimental comparisons. Due to concerns of test paper toxicity (42), species exhibiting germination rates < 40% with Whatman #1 filter paper were re-evaluated with Schleicher and Schuell #597 seed test papers. For introduced species, only *F. vulgare* was re-evaluated, while the following native species were re-evaluated: *Asclepias fascicularis* Decne., *C. ciliata, C. macrostegia, Castilleja exserta* (A. Heller) Chuang & Heckard, *Clarkia unguiculata* Lindl., *Eriophyllum confertiflorum* (DC.) A. Gray, *Layia platyglossa* (Fisch. & C.A. Mey.) A. Gray, *L. bicolor, L. microcarpus, L. succulentus, Sisyrinchium bellum* S. Watson, *Leymus triticoides* (Buckley) Pilg., *Melica imperfecta* Trin. and *Nassella lepida* (Hitchc.) Barkworth. Commercial seed sources were: Elkhorn Native Plant Nursery, P.O. Box 270, Moss Landing, CA 95039, USA; Peaceful Valley Farm & Garden Supply, P.O. Box 2209, Grass Valley, CA 95945, USA; S&S Seeds, Inc., P.O. Box 1275, Carpinteria, CA 93014, USA; and Theodore Payne Foundation, 10459 Tuxford Street, Sun Valley, CA 91352, USA.

Allelopathy bioassays were done as per the following methods (15). This method of allelochemical collection caused the least disruption in the natural mode of release (23). Leachates were made using the following procedure. First, 2.5 g of dried fennel leaves were soaked in 100 ml distilled water for 2-h at 25°C to make the 2.50% concentration. Next, this extract was filtered under vacuum to obtain a "2.50% leachate". Finally, the 1.25%, 3.75% and 5.00% leachates were made using 1.25, 3.75, and 5.00 g of dried fennel leaves, respectively, following the above technique. For each species, 500 seeds were divided into five groups of 100 seeds each and were subjected to one of the following treatments: Imbibition of seeds for 1 h in (a) fennel leaf leachate concentrations (1.25%, 2.5%, 3.75% and 5.0%) or (b) Control (distilled water).

Germination chambers were constructed in the following manner. First, 45 g of clean, 30-mesh graded, kiln-dried sand were added to 15 PYREX® 100 x 15 mm Petri dishes. Next, the sand was levelled and a 90-mm filter paper was placed on top of the sand. Then, the dish was irrigated with 10 ml of distilled water or leachate of appropriate concentration. Five replicates of each treatment were created by placing 20 seeds in each dish, one cm in from the edge with the hypocotyl end of the seed facing the centre of the dish. Then, another piece of filter paper was dipped into distilled water, or leachate of appropriate concentration, before being placed over the seeds, and the Petri dishes were sealed with Parafilm. Finally, sealed germination chambers were placed in darkness in an incubator at 25.0°C. Chambers were removed from the incubator at maximum germination rate and stored in the darkness of a refrigerator set at 2.0°C to suspend growth until root and stem lengths were recorded (10,11). During germination tests, the incubation time determined to achieve the maximum germination capacity for introduced species was 120 h, except for *Brassica* sp. L., *Lotus corniculatus* L., *Medicago sativa* L., *Melilotus alba*

Table 1. Methods used to break seed dormancy in test plant spp.

Introduced Forbs		**Introduced Grasses**	
Plant spp.	Methods to break seed dormancy	Plant spp.	Methods to break seed dormancy
Brassica sp.	None	*Avena fatua*	None
Foeniculum vulgare	Stratification [7 days at 2.0°C]	*Bromus hordeaceus*	None
Lotus corniculatus	None	*Festuca arundinacea*	None
Medicago sativa	None	*Lolium multiflorum*	None
Melilotus alba	None	*Lolium perenne*	None
Raphanus sativus	None	*Vulpia myuros*	None
Vicia sativa	None		
Native Forbs		**Native Grasses**	
Plant spp.	Methods to break seed dormancy	Plant spp.	Methods to break seed dormancy
Achillea millefolium	None (E)	*Bromus carinatus*	None
Asclepias fascicularis	None (E)	*Hordeum brachyantherum*	None (E)
Calandrinia ciliata	Stratification [7 days at 2.0°C]	*Leymus triticoides*	Stratification [21 days @ 2.0°C]
Calystegia macrostegia	Scarification + stratification [10 days at 2.0°C]	*Melica imperfecta*	Stratification [19 days @ 2.0°C]
Castilleja exserta	Stratification [21 days at 2.0°C] (RSM)	*Nassella cernua*	None (E)
Clarkia unguiculata	Stratification [21 days at 2.0°C] (RSM)	*Nassella lepida*	Stratification [7 days @ 2.0°C]
Eriophyllum confertifolium	Stratification [5 minutes at 120.0°C (E)]	*Nassella pulchra*	None (E)
Eschscholzia californica	Stratification [10 days at 2.0°C (RSM)]		
Lasthenia californica	Stratification [14 days at 2.0°C (RSM)]		
Layia platyglossa	Stratification [8 days at 2.0°C]		
Lupinus bicolor	Scarification + stratification [18 days at 2.0°C (E)]		
Lupinus microcarpus	Scarification + stratification [18 days at 2.0°C]		
Lupinus succulentus	Scarification + stratification [18 days at 2.0°C (E,RSM)]		
Sisyrinchium bellum	Stratification [90 days at 2.0°C (E,RSM)]		

* Seed manipulations based on: (E) = Emery (1988), and/or (RSL) = Ransom Seed Laboratory

Medik., and *Raphanus sativus* L., which germinated in 72 h. During germination tests for native species, the incubation time determined to achieve maximum germination was 168 h, except for *Nassella cernua* (Stebbins & Love) Barkworth that achieved maximum germination in 240 h.

Differences in germination between leachate concentrations for each species to potential allelopathic interference from fennel were evaluated with Pearson's χ^2 cross-tabulation. Percent inhibition or stimulation was determined according to established procedures (18), and the mean inhibition was determined for forbs and grasses according to centre of origin for each leachate concentration. Osmotic concentration of leachate treatments was ascertained by freezing-point depression with an Osmette S Automatic Osmometer model 4002 by Precision Systems, Inc., Sudbury, MA, for the 1.25%, 2.5%, 3.75% and 5.0% fennel leaf concentrations (10).

RESULTS

C. ciliata, C. exerta, E. confertifolium, F. vulgare, L. triticoides, L. bicolor, L. succulentus and *S. bellum* did not germinate under the test conditions (25°C, darkness), while *A. fasciculatis, L. platyglossa* and *Lasthenia californica* Lindl. had germination capacities of 3.0, 1.0 and 2.0%, respectively. Therefore, these species did not undergo further experimental work.

As the concentration of fennel leaf leachate increased, allelopathic interference significantly inhibited the germination of *L. corniculatus* ($\chi^2 = 10.59$, $df = 4$, $p = 0.0316$) and *M. sativa* ($\chi^2 = 21.53$, $df = 4$, $p < 0.001$) (Table 2). For the other 4-introduced forb species, allelopathic interference was insignificant with no effect on germination capacity. Germination capacity of *Avena fatua* ($\chi^2 = 17.56$, $df = 4$, $p < 0.001$), *Festuca arundinacea*. ($\chi^2 = 130.45$, $df = 4$, $p < 0.001$), *Lolium multiflorum* ($\chi^2 = 29.50$, $df = 4$, $p < 0.001$) and *Vulpia myuros* ($\chi^2 = 241.35$, $df = 4$, $p < 0.001$) was significantly inhibited as the concentration of fennel leaf leachate increased on 6-introduced grasses. Increasing the concentration of fennel leaf leachate significantly inhibited the germination capacity of 5-native forbs: [*C. macrostegia* ($\chi^2 = 16.37$, $df = 4$, $p = 0.0026$), *Achillea millefolium* L. ($\chi^2 = 273.31$, $df = 4$, $p < 0.001$), *C. unguiculata* ($\chi^2 = 136.06$, $df = 4$, $p < 0.001$), *Eschscholzia californica* ($\chi^2 = 94.42$, $df = 4$, $p < 0.001$), and *Lupinus microcarpus* ($\chi^2 = 32.00$, $df = 4$, $p < 0.001$)]. As the concentration of fennel leaf leachate increased, allelopathic interference significantly inhibited the germination capacity of 4-native grasses [*Hordeum brachyantherum* ($\chi^2 = 55.89$, $df = 4$, $p < 0.001$), *Melica imperfecta* ($\chi^2 = 124.91$, $df = 4$, $p < 0.001$), *Nassella. cernua* ($\chi^2 = 18.93$, $df = 4$, $p < 0.001$) and *N. lepida* ($\chi^2 = 189.71$, $df = 4$, $p < 0.001$)]. For *Nassella pulchra,* interference was not significant; yet the germination of *Bromus carinatus* ($\chi^2 = 19.95$, $df = 4$, $p < 0.001$) was significantly stimulated.

The mean inhibition (%) in the germination of forbs with a native centre of origin was greater than for introduced forbs, even though mean inhibition (%) increased positively with increasing *F. vulgare* leachate concentrations on forbs from both centres of origin (Figure 1). The mean inhibition (%) on the germination of grasses with a native centre of origin was greater than for introduced grasses, even though mean inhibition (%) increased positively with increasing *F. vulgare* leachate concentrations on grasses from both centres of origin (Figure 2).

Table 2. Stimulatory or Inhibitory effects of *F. vulgare* leachate concentrations on germination of test plant spp.

Introduced Forbs				**Introduced Grasses**			
Plant spp.	Leachate (%)	Germination Capacity	Stimulation or Inhibition (%)	Plant spp.	Leachate (%)	Germination Capacity	Stimulation or Inhibition (%)
Brassica sp.	Distilled Water	91	0	*Avena fatua*	Distilled Water	98	0
	1.25%	91	0		1.25%	98	0
	2.5%	88	- 3.3		2.5%	95	- 3.1
	3.75%	83	- 8.8		3.75%	86	- 12.2
	5.0%	92	- 1.1		5.0%	91	- 7.1
Lotus corniculatus	Distilled Water	82	0	*Bromus hordeaceus*	Distilled Water	93	0
	1.25%	74	- 9.8		1.25%	91	- 2.2
	2.5%	78	- 4.9		2.5%	92	- 1.1
	3.75%	72	- 12.2		3.75%	93	0
	5.0%	63	- 23.2		5.0%	84	- 9.7
Medicago sativa	Distilled Water	74	0	*Festuca arundinacea*	Distilled Water	86	0
	1.25%	71	- 4.1		1.25%	73	- 15.1
	2.5%	66	- 10.8		2.5%	52	- 39.5
	3.75%	50	- 32.4		3.75%	68	- 20.9
	5.0%	51	- 31.1		5.0%	13	- 84.9
Melilotus alba	Distilled Water	89	0	*Lolium multiflorum*	Distilled Water	84	0
	1.25%	84	- 5.6		1.25%	78	- 7.1
	2.5%	79	- 11.2		2.5%	63	- 25.0
	3.75%	87	- 2.2		3.75%	62	- 26.2
	5.0%	80	- 10.1		5.0%	53	- 36.9
Raphanus sativus	Distilled Water	97	0	*Lolium perenne*	Distilled Water	92	0
	1.25%	91	- 6.2		1.25%	90	- 2.2
	2.5%	86	- 11.3		2.5%	88	- 4.3
	3.75%	88	- 9.3		3.75%	92	0
	5.0%	86	- 11.3		5.0%	83	- 9.8
Vicia sativa	Distilled Water	91	0	*Vulpia myuros*	Distilled Water	86	0
	1.25%	95	- 4.4		1.25%	25	- 70.9
	2.5%	96	- 5.5		2.5%	16	- 81.4
	3.75%	94	- 3.3		3.75%	7	- 91.9
	5.0%	94	- 3.3		5.0%	0	- 100.0
Native Forbs				**Native Grasses**			
Achillea millefolium	Distilled Water	74	0	*Bromus carinatus*	Distilled Water	70	0
	1.25%	13	- 82.4		1.25%	76	+ 8.6
	2.5%	3	- 95.9		2.5%	82	+ 17.1
	3.75%	0	- 100.0		3.75%	79	+ 12.9
	5.0%	0	- 100.0		5.0%	94	+ 34.3

Calystegia macrostegia	Distilled Water	36	0	*Hordeum brachyantherum*	Distilled Water	37	0
	1.25%	25	- 30.6		1.25%	21	- 32.3
	2.5%	23	- 36.1		2.5%	14	- 62.2
	3.75%	17	- 52.8		3.75%	8	- 78.4
	5.0%	14	- 61.1		5.0%	1	- 97.3
Clarkia unguiculata	Distilled Water	54	0	*Melica imperfecta*	Distilled Water	34	0
	1.25%	24	- 55.6		1.25%	3	- 91.2
	2.5%	9	- 83.3		2.5%	1	- 97.1
	3.75%	1	- 98.1		3.75%	0	- 100.0
	5.0%	1	- 98.1		5.0%	0	- 100.0
Eschscholzia californica	Distilled Water	83	0	*Nassella cernua*	Distilled Water	53	0
	1.25%	72	- 13.3		1.25%	68	+ 28.3
	2.5%	70	- 15.7		2.5%	57	+ 7.5
	3.75%	53	- 36.1		3.75%	57	+ 7.5
	5.0%	22	-73.5		5.0%	38	- 44.1
Lupinus microcarpus	Distilled Water	20	0	*Nassella lepida*	Distilled Water	50	0
	1.25%	1	- 95.0		1.25%	3	- 94.0
	2.5%	11	- 45.0		2.5%	1	- 98.0
	3.75%	1	- 95.0		3.75%	0	- 100.0
	5.0%	11	- 45.0		5.0%	2	- 96.0
				Nassella pulchra	Distilled Water	51	0
					1.25%	48	- 5.9
					2.5%	45	- 11.8
					3.75%	40	- 21.6
					5.0%	43	- 15.7

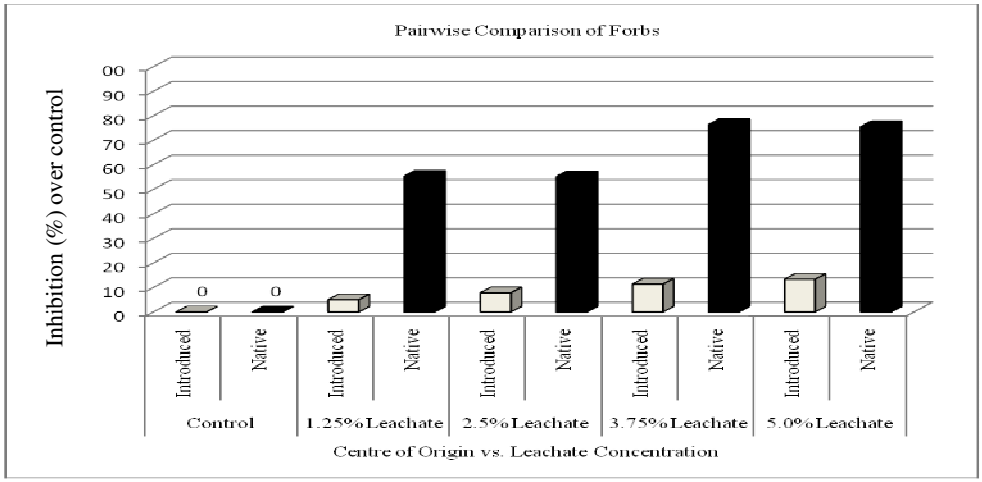

Figure 1. Pair-wise comparison of mean inhibition (%) on germination of forbs grouped by centre of origin and % *F. vulgare* leachate concentration used during bioassays.

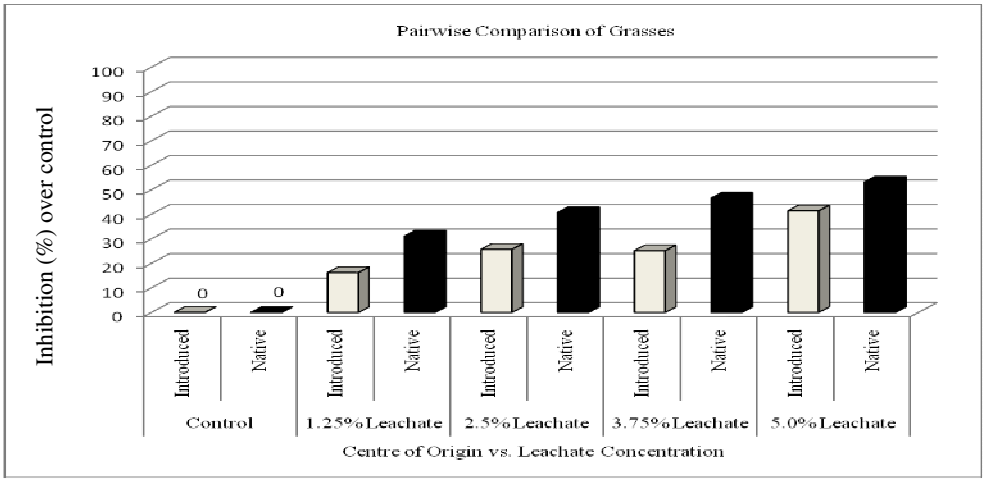

Figure 2. Pair-wise comparison of mean inhibition (%) on germination of grasses grouped by centre of origin and % *F. vulgare* leachate concentration used during bioassays.

DISCUSSION

We did not do viability tests on 8 species (*C. ciliata, C. exerta, E. confertifolium, F. vulgare, L. triticoides, L. bicolor, L. succulentus* and *S. bellum*) that did not germinate. *C. ciliata* were 4-year-old seeds stored *ex situ* and their age may have negatively affected their germination capacity. Ten- and eleven-years-old *F. vulgare* seeds stored *ex situ* did not germinate for use in this experiment. Viability tests were not done for *F. vulgare*, although 1-, 3- and 5-years-old fennel seeds stored *ex situ* had 89%, 62% and 53% germination, respectively (40,41). S&S Seeds, Inc. reported that *L. succulentus* and *S. bellum* have 10 to 20% and 70 to 80% germination, respectively, but the seeds remained dormant. Thus these seeds were non-viable; the methods used to break seed dormancy were ineffective and/or the conditions provided were insufficient to give experimental results. *A. fascicularis* seeds were purchased in 2000 for pilot study work and their age at the time of bioassay may have reduced their germination capacity < 10%.

Using more than one index to reflect the germination process more accurately was recommended, since the behaviour of a seed population with respect to germination has several quantitative aspects that must be considered, and quantification obviously should not be limited to one parameter, such as maximum germination percentage or germination rate (4). Yet, while others contend that germination capacity was not sensitive enough to study and validate allelochemical effects on a physiological process such as germination (24,25,45), our results indicate that significant differences in germination capacity between species of introduced and native centres of origin as well as functional group were discernable when subjected to the water soluble leachate from the invasive plant fennel- *F. vulgare*. This study served as the first of a three-part series examining rapid allelopathy bioassay investigations into the potential interference effects of *F. vulgare* on plant succession. The potential allelopathic effects of *F. vulgare* on the root and shoot growth of introduced and native forb and grass species from different centres of

origin are discussed elsewhere in relation to their ecological impacts on grassland and coastal sage scrub vegetation communities on Santa Cruz Island, California (10,11).

There was little impact of treatments on germination of introduced species. The germination of only 2 of the 6 introduced forb species was inhibited. While for introduced grasses, the germination of 4 of the 6 grass species was inhibited, indicating that these grasses experienced more negative effects from allelopathic interference than forbs. However, all introduced species (grasses or forbs) germinated with greater capacity at 5.0% fennel leaf leachate concentration as well as had a shorter incubation time than native species.

The potential allelopathic interference of fennel on native species was different than on introduced species. All native forbs showed significant inhibition to their germination capacity. In native grasses, germination of all spp. was inhibited except in *B. carinatus* (stimulation). Most of the native species showed a marked decline in germination when fennel leaf leachate concentration reached 1.25% and had a longer incubation time than introduced species. This response suggests that germination capacity is the critical difference in the mode of action from fennel allelochemicals on species from introduced or native centres of origin.

For this comparison, we preferred commercial sources of seed over seed collected locally from Santa Cruz Island, California, to minimize the micro-evolutionary processes (34,39) that could confound the interpretation of these results and prevent them from remaining focused on answering macro-evolutionary questions (7,21). Overall, germination capacity was inhibited for 50% (6 of 12) of the introduced species compared to 75% (9 of 12) of the native species in this bioassay. For forbs, only 33% (2 of 6) of the introduced species compared to 100% (6 of 6) of the native species had their germination capacity significantly inhibited by fennel. For grasses, there was no difference in germination capacity with 67% (4 of 6) of the introduced and native species having their germination capacity significantly inhibited, while 17% (1 of 6) of the native grasses had their germination capacity significantly stimulated. These findings suggest that California grassland and coastal sage scrub vegetation communities may have community-level consequences to their spatial structure that could be a result of coevolution between fennel and the introduced species examined here. Our results assert that germination capacity adequately reflects the allelochemical effects on the physiological process of germination.

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