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Short title: Competition limits Stinkwort

Association with roadsides reflects escape from competition in *Dittrichia graveolens*

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Abstract

Invasive plants commonly establish and spread along roadsides, and understanding the mechanisms underlying this pattern is essential for risk assessment and effective management. Stinkwort, *Dittrichia graveolens* (L.) Greuter, a recent California invader, primarily inhabits roadsides but is beginning to spread into nearby plant communities. We tested whether *D. graveolens* grows best along roadsides due to a preference for soil conditions or is limited to these disturbed environments by plant competition. Lab and greenhouse experiments showed no germination advantage in engineered fill (simulating roadside soils), and *D. graveolens* grew slightly better in field topsoil. Competition trials with two annual grasses (soft brome, *Bromus hordeaceus* (L.) and Italian rye grass, *Festuca perennis* (L.) Columbus & J.P. Sm.) showed strong growth suppression of *D. graveolens* by both grasses, but competition was stronger in field topsoil than engineered fill. Engineered fill limited growth for all species, suggesting that roadside soils may provide a refuge from competition. In two years of field experiments, we examined mechanisms of competition by comparing responses to (1) removal of thatch, aboveground biomass, and above- and belowground biomass, (2) shading, and (3) water and nutrient addition and protection from belowground competition via trenching. Belowground competition in particular strongly affected *D. graveolens* performance. Our findings suggest that competition confines *D. graveolens* to disturbed roadsides; management should prioritize reducing bare, disturbed areas and enhancing plant competition in areas vulnerable to invasion.

Keywords: Asteraceae, competition, disturbance, invasive, roadside, stinkwort

Management Implications

Stinkwort, *Dittrichia graveolens* (L.) Greuter, is an emerging invader in California, characterized as a species of concern because of its high invasive potential and high potential impact. Currently, stinkwort is most often found along roadsides and other disturbed areas in western North America, but the nature of this association is unresolved. Our research shows that this species is strongly limited by competition from other plants, especially by belowground competition. While stinkwort can establish when plant competition is limited by disturbance, it struggles to persist in dense, competitive vegetation and therefore finds refuge along roadsides and in disturbed sites where competition is low.

This means managers can best reduce the risk of stinkwort invasion by promoting robust plant cover in vulnerable areas, especially trails, construction zones, or (where feasible) roads. Practices that reduce competition, especially belowground disturbances that expose soil, are likely to increase vulnerability to invasion and should be timed or managed carefully.

Given that the wind-dispersed seeds of stinkwort can travel far into established vegetation, early detection and spot treatments of outbreaks in disturbed patches are particularly important. The control of roadside populations as seed sources combined with strengthening plant communities to enhance competition offers a proactive strategy that could reduce the need for repeated control efforts over time.

Introduction

Disturbance is a critical process in many ecosystems, providing heterogeneity and influencing diversity at both the patch-level and landscape scale (Greipsson 2011; Hobbs and Huenneke 1992). Disturbance reduces competition and frees up space and resources, which colonizing species can exploit (Catford et al. 2012; Hobbs and Huenneke 1992). Thus, disturbance also plays an important role in the invasion process for many non-native species (Catford et al. 2012; Hobbs and Huenneke 1992; Minchinton and Bertness 2003; Pimm 1989). Roadsides, transportation corridors, and other disturbed environments facilitate primary spread of non-native species (Baker 1974; McDougall et al. 2018; Tyser and Worley 1992). The movement of species away from roadside edges and into established vegetation (secondary spread) is a critical phase in the invasion process (Ward et al. 2020).

Roadside soil is often disturbed from the initial construction and ongoing road maintenance, characterized by distinct texture and mineral composition, increased compaction, and erosion (Lázaro-Lobo and Ervin 2019; Mills et al. 2020). Road runoff increases soil salinity and can contain vehicle contaminants (Lázaro-Lobo and Ervin 2019; Trombulak and Frissell 2000), and roadsides often have lower nutrient availability (Liu et al. 2021). Due to maintenance regimes and physical impacts from vehicle traffic, roadsides have high disturbance rates and lower plant cover (Christen and Matlack 2006).

A classic question in ecology is whether species distributions reflect an affinity for certain environmental conditions or rather competitive exclusion from higher-quality habitats. Some plant species are more successful in specific abiotic conditions (Gioria et al. 2023; Wamelink et al. 2018) leading to strong patterns of association with these soils or environmental conditions. In contrast, species may be widely distributed, but biotic interactions with more competitive plant species, herbivores, or pathogens may limit their range (Hutchinson 1959; Gioria et al. 2023). Understanding the nature of an association with roadsides is crucial for effective management. If a species has an affinity for disturbed soils, then land managers should focus early detection on those areas. If biotic interactions, such as escape from competitive pressure, limit the distribution of a species then land managers can focus on reducing disturbance and promoting competition.

We investigated abiotic soil conditions and reduced plant competition (resulting from disturbance) as two potential factors causing stinkwort [*Dittrichia graveolens* (L.) Greuter; Figure 1], to grow along roadsides. This annual herb was introduced to California in the early 1980s and was originally found in disturbed areas along railroad tracks and roads in the County of Santa Clara (Brownsey et al. 2013; Preston 1997). Native to the Mediterranean Basin in Europe, *D. graveolens* is often found in bare, disturbed habitats, including roadsides, agricultural lands, gravel riparian areas, and ruderal zones associated with annual or biennial weeds (Brullo and de Marco 2000; Rameau et al. 2008; Šajna 2017). Since its initial detection in 1984, *D. graveolens* has spread across California, now occupying over 83% of counties, with a range extending > 400 km north, > 200 km east, and > 690 km south of its original point of introduction (Calflora 2024; Lustenhouwer and Parker 2022).

In California, *D. graveolens* has been observed spreading into wildlands and rangelands away from roads (Brownsey et al. 2013; Melen et al. 2024). These observations highlight the spread potential of *D. graveolens* and the invasion risk this species poses. However, little is known about this invasion process and what conditions enable *D. graveolens* to spread away from roadsides into more intact plant communities. Here we studied whether *D. graveolens* populations preferentially grow along roadsides because of beneficial soil conditions or if they are limited to growing along roadsides due to competition. We characterized germination and growth responses to engineered fill and field soil in lab and greenhouse experiments. Then in four separate field experiments over two years, we manipulated competition, disturbance, and shading in an established grassland to determine the effects of above- and belowground competition on growth and survival to reproduction.

Materials and Methods

Study sites

The County of Santa Clara (37.36°N 121.97°W) is located at the southern end of the San Francisco Bay in California, USA. The county encompasses the Santa Clara Valley, bordered by the Diablo Mountain Range to the east, the Santa Cruz Mountains to the southwest, and San Francisco Bay to the northwest. The valley experiences a mild Mediterranean climate with warm, dry weather much of the year (Grossinger et al. 2007) due to its proximity to the

moderating effects of the San Francisco Bay. The rainy season is predominantly from November to April with 375 ± 125 mm SD of annual precipitation (McKee et al. 2003), and the average daily mean temperature in the San Jose region ranges from 27.9°C to below-freezing (Hanson et al. 2004).

Soil sources

We compared the response of both seeds and plants to field topsoil and to engineered fill as a proxy for the physical microenvironment of roadside soils. Field topsoil was collected from a woodland site, and engineered fill was taken from a nearby construction project at UC Santa Cruz; several cubic tons of these soils were in storage at a central campus location, and we subsampled several buckets of each soil type for our experiments (Figure 2).

Seed germination in roadside and field soil

In September and October 2020, we collected *D. graveolens* seeds from 16 populations in the County of Santa Clara. These sites represent a mix of roadside and vegetated habitat (Table S1 in Melen et al. 2024). For each population, we collected from ≥ 10 individuals at 3 m intervals along a randomly-placed transect, and combined seeds into a single sample.

In June and July 2021, we compared germination behavior of seeds on the two substrates, placing 10 seeds in each of 80 Petri dishes for each substrate (engineered fill and field topsoil). We visually inspected each seed beforehand to ensure we used only fully developed seeds. Petri dishes were sealed with Parafilm M™ and placed in a randomized block design in an incubation chamber with a 16-hour day and 23 °C/19 °C day/night temperature cycle. Each day we scored germination until no further germination was observed, then for 7 more days (engineered fill = 12 d, field topsoil = 11 d). When scoring for germination, we looked for the first emergence of the root radical or the cotyledon and removed any germinated seeds. We kept soil moist by misting with DI water.

We used R version 4.3.1 (2023-06-16; R Core Team 2023) for all statistical analyses. Our general approach for each response variable was to run mixed effects models with, at a minimum, fixed effects for soil and block as a random effect.

We compared the germination rate on two substrates (engineered fill and field topsoil) using a mixed-effects Cox proportional hazards model (coxme and survival packages; Therneau 2022, 2023), with soil type as a fixed effect, and dish (N = 5 replicates) nested within population (N = 16) as random effects. We evaluated the main effect of soil type using a Type II partial-likelihood-ratio test (car package; Fox and Weisberg 2019).

Plant growth response to disturbed soil

We assessed the response of *D. graveolens* to competition and abiotic soil conditions in the same two substrates with three competition treatments: *D. graveolens* grown alone, with *Bromus hordeaceus*, or with *Festuca perennis*. These non-native European annual grasses were selected because they are commonly found in California's annual grasslands (Dawson et al. 2007; HilleRisLambers et al. 2010; Seabloom et al. 2003), including at our field site described below (Melen et al. 2024). We collected *B. hordeaceus* seeds from Blue Oak Ranch Reserve (37.38° N 121.74°W) and *F. perennis* seeds from Younger Lagoon Reserve (36.96°N 122.07°W) on the UC Santa Cruz Coastal Science Campus.

We germinated *D. graveolens* seeds in the conditions described above (see *Seed germination*). We germinated grasses in potting mix trays under fluorescent light banks with 16-hour days. We filled D16 Deepots (5 cm diameter, 18 cm height) with engineered fill and field topsoil and then transplanted seedlings in sets of three (one for each treatment) after radicles and cotyledons emerged. We randomized pots into a blocked design with each block consisting of 2 *D. graveolens* seedlings from each of the 16 seed-source sites for each of the 3 competition treatments, N = 96 per block × 8 blocks (768 total). We grew plants in a greenhouse for 4 months before harvesting. We clipped *D. graveolens* aboveground biomass at the crown and dried it in a 60 °C oven for 3 days before weighing.

We fitted a Generalized Linear Model (GLM) to analyze the effect of competition on *D. graveolens* biomass (car package; Fox and Weisberg 2019). The model used a Gamma distribution with a log link function; fixed effects were competition and soil. We initially used population and block as random effects (lme4 package; Bates et al. 2015), but both prevented model convergence. Because AIC scores showed that the random effects did not contribute

importantly to the model, they were not included. We evaluated the main and interaction effects using Type II likelihood ratio tests (car package; Fox and Weisberg 2019). We conducted post-hoc pairwise comparisons using estimated marginal means, comparing them using Welch t statistics with Satterthwaite degrees of freedom, and a Bonferroni adjustment for multiple comparisons (emmeans package; Lenth 2024).

Field experiment Year 1: response to competition and disturbance

To assess the response of *D. graveolens* to competition in a field setting, we conducted an experiment at Blue Oak Ranch Reserve, part of the University of California Natural Reserve System. Blue Oak Ranch Reserve is located on the western slopes of Mount Hamilton in the Diablo Range, just east of San Jose, California, United States (37°22'54.89"N, 121°44'10.55"W). The reserve is a former rangeland, representing a key habitat type threatened by the invasion of *D. graveolens*. We established a 10 × 26 m fenced field site in a non-native grassland with a mixture of annual grasses and forbs. A subset of treatments from this experiment, combined with a separate study focused on local adaptation among seed sources, was the focus of an earlier paper (Melen et al. 2024). Here, we focus on the response to competition and disturbance.

We quantified *D. graveolens*' response to four competition treatments: (1) control, which was the grassland including the year's plant growth as well as the previous year's thatch; (2) thatch removal, which involved raking and removing the previous year's thatch; (3) aboveground removal, where we used a string trimmer to trim grassland vegetation to 8 - 13 cm above the ground; (4) and above+below removal, where we tilled the soil to completely remove above- and belowground biomass.

In January 2021, we germinated *D. graveolens* seeds in the conditions described above and transplanted them into D16 Deepots (5 cm diameter × 18 cm height) with field topsoil collected from Blue Oak Ranch Reserve in December 2020. We grew the seedlings in the greenhouse for about eight weeks until the first true leaves had emerged and lengthened for all plants. We did not directly seed *D. graveolens* into the field site due to biosafety concerns about this noxious weed.

We used a randomized block design with 10 blocks of 1.5 m² plots (Figure S1). From 27 February - 24 March 2021, we planted 16 *D. graveolens* seedlings into each plot using dibblers (640 seedlings; 40 plots total). Seedlings were planted in a 4 × 4 grid centered on the plot. The distance between plants within plots was 33 cm, and plots were separated from each other by a 25 cm buffer. We surveyed plants weekly to assess *D. graveolens* survival and replaced any dead plants during the first month. We assessed bud development as a key phenology stage for terminating plants to ensure no seeds were released into the site. Weekly plant surveys continued until all plants had either produced buds or perished.

We measured height and dried and weighed aboveground biomass after harvest. Height and biomass were correlated ($r = 0.58$, $N = 213$), and results for the response variables were similar. Therefore, we present only the results for final aboveground biomass as our measure of performance and proxy for reproductive output.

For all statistical models, competition treatment was the fixed effect and population and block were included as random effects. Here we describe the structures of the models.

We analyzed survival in two ways. The probability of surviving to reproduction (budding) was compared across competition treatments with a GLMM using a binomial family with a logit link function (lme4 package; Bates et al. 2015). We evaluated the main effect of competition treatment using a Type II Wald Chi-Square tests (car package; Fox and Weisberg 2019). Second, time to death was analyzed using a mixed-effects Cox proportional hazards model (coxme and survival packages; Therneau 2022, 2023). We evaluated the main effect of competition treatment using likelihood ratio tests (car package; Fox and Weisberg 2019).

We analyzed biomass at reproduction using a linear mixed-effects model (lme4 package; Bates et al. 2015). The significance of the competition treatment was assessed using Type III Wald F test with Kenward-Roger degrees of freedom (car package; Fox and Weisberg 2019). We did post-hoc comparisons using the differences among estimated marginal means (emmeans package; Lenth 2024), using the Bonferroni method.

Field experiments Year 2: response to disturbance--aboveground vs. belowground competition

In January 2022, we germinated *D. graveolens* seeds in the conditions described above and transplanted them into 10.16 cm height \times 8.89 cm width injection molded pots with potting media (ProMix[®] HP[®] BioFungicide[™] + Mycorrhizae[™]), where they grew for about eight weeks until the first true leaves had emerged and lengthened for all plants. We conducted three experiments related to above and belowground competition using a subset of the same 1.5 m² plots as the previous year (Figure S2).

Aboveground and belowground competition: In year 2 we replicated our test of the relative effect of above and belowground competition on *D. graveolens*, with 54 planting locations randomly assigned to three treatments: (1) control, which was the grassland including the year's plant growth as well as the previous year's thatch; (2) aboveground removal, where we clipped grassland vegetation to 1 - 3 cm high, (3) above+below removal, where we dug holes to a depth of 45 cm to completely remove above- and belowground biomass. We did not include a thatch removal experiment in year 2. We planted two *D. graveolens* seedlings in each planting location (N = 108) and maintained clipping treatments weekly, recording survival for nine weeks. Because no plants survived to flower (see results), we did not measure biomass.

We analyzed seedling survival using a mixed-effects Cox proportional hazards model (coxme and survival packages; Therneau 2022, 2023), with treatment (control, clipping, belowground competitor removal) as a fixed effect, and a random effect of plot. We assessed the significance of the treatment using Type II likelihood ratio tests (car package; Fox and Weisberg 2019).

Aboveground shading: To separate the effects of shading from other aboveground interactions, we used an artificial shading experiment with 11 plots, which were each hoed to remove above and belowground competition. The plots were divided into four quadrants; four bamboo stakes were placed in the corners of each quadrant and were randomly assigned a treatment of control (no shade cloth) or shade cloth (GCI Landscaper's Choice Premium 5-ounce Woven Landscape Fabric 500 Series). Shade cloth was attached to the bamboo stakes and maintained for the duration of the experiment. On 17 March 2022, we planted two *D. graveolens* seedlings per quadrant (N = 88 plants total, 4 seedlings per treatment per plot). We weeded the plots weekly and recorded *D. graveolens* survival for nine weeks.

We analyzed seedling survival using a mixed-effects Cox proportional hazards model (coxme and survival packages; Therneau 2022, 2023), with treatment (no shade and shade) as a fixed effect, and a random effect of plot. We assessed the significance of the shading treatment using Type II likelihood ratio tests (car package; Fox and Weisberg 2019).

Mechanisms of belowground competition: To investigate the mechanisms involved in belowground interactions, we used a two-factor factorial design with trenching and resource addition treatments in 28 grassland plots. In each plot, we dug six holes, each 15 cm in diameter and 45 cm deep; three were lined with weed cloth fabric (GCI Landscaper's Choice Premium 5oz Woven Landscape Fabric 500 Series), and the other three were left unlined. We placed PVC collars, each 15 cm in diameter and 12 cm deep, into all holes, positioning them with a 2-cm lip above the soil surface to prevent runoff and inserting them to a depth of 10 cm. The original soil was then replaced. We planted two *D. graveolens* seedlings in each treatment site. To release plants from the effects of belowground competition for water and nutrients, we used three resource addition treatments: control, the addition of 283.49 grams of water, and the addition of 283.49 grams of water plus 5 grams of fertilizer (Osmocote 14-14-14). The soil surface was scratched using a fork in all treatments to encourage infiltration. We maintained treatments weekly and recorded *D. graveolens* survival for nine weeks.

We analyzed seedling survival using a mixed-effects Cox proportional hazards model (coxme and survival packages; Therneau 2022, 2023), with treatment (control, water, water + nutrients) and competition (weed cloth, no weed cloth) as fixed effects, and a random effect of plot. We assessed the significance of the interaction and main effects by comparing models using likelihood ratio tests.

Results and Discussion

Seed germination in roadside and field soil

The proportion of germinated seeds was high in both soil types (engineered fill = 81 %, field topsoil = 84 %), with seeds showing a slightly higher chance of germinating in field topsoil than in engineered fill (5 % higher; relative risk of 1.05 ± 0.06 SE; $X^2_1 = 105.57$, $P < 0.001$; Figure 3).

Plant growth response to disturbed soil

When we grew *D. graveolens* in competition with non-native annual grasses, they were significantly smaller than those growing alone ($X^2_2 = 48.03$, $P < 0.001$), and *D. graveolens* grew much smaller in engineered fill ($X^2_1 = 431.87$, $P < 0.001$, Figure 4). In addition, we saw a significant interaction between competition and soil ($X^2_2 = 470.32$, $P < 0.001$). When grown with *B. hordeaceus*, competition reduced *D. graveolens* biomass by 14 fold in field topsoil ($\bar{X}_{\text{alone}} / \bar{X}_{\text{competitor}} = 14.3$, $t = 25.47$, $P < 0.001$) compared to only a 77 % reduction in biomass in engineered fill ($\bar{X}_{\text{alone}} / \bar{X}_{\text{competitor}} = 1.77$, $t = 5.45$, $P < 0.001$). Similarly, competition with *F. perennis* caused a 55-fold reduction in *D. graveolens* biomass in field topsoil ($\bar{X}_{\text{alone}} / \bar{X}_{\text{competitor}} = 54.6$, $t = 38.16$, $P < 0.001$) and only a 91 % reduction in engineered fill ($\bar{X}_{\text{alone}} / \bar{X}_{\text{competitor}} = 1.91$, $t = 6.18$, $P < 0.001$).

Field experiment Year 1: response to competition and disturbance

Overall survival to reproduction was strongly affected by treatment ($X^2_3 = 136.01$, $P < 0.001$), with about a 50 % absolute increase in overall survival in the above+below removal treatment compared to the control. Surprisingly, survival in the thatch removal treatment was 15 percentage points lower than in the control (Figure 5a). Likewise, survival analysis showed variation in the timing of mortality, with an 84 % reduction in mortality risk in the above+below removal treatment ($X^2_3 = 200.1$, $P < 0.001$; Figure 5b).

Aboveground biomass was also significantly different across the treatments ($F_{3, 203.6} = 154.57$, $P < 0.001$; Figure 6). The post hoc pairwise comparison revealed that plants in the control treatment were significantly (almost 19-fold) smaller than in the above+below removal treatment ($\bar{X}_1 - \bar{X}_2 = 0.18$, $P < 0.0001$), but did not differ in size from the aboveground removal ($\bar{X}_1 - \bar{X}_2 = 0.14$, $P = 1.00$) or thatch removal ($\bar{X}_1 - \bar{X}_2 = 2.9$, $P = 1.00$) treatments.

Field experiment Year 2: response to disturbance – aboveground vs. belowground competition

In the second year of experiments, the above and belowground treatment (control, clipping, belowground competitor removal) had a significant effect on the survival of *D. graveolens* ($X^2_2 = 15.18$, $P < 0.001$; Figure 7a). Clipping marginally significantly increased survival by 32 % over the control ($Z = 1.64$, $P = 0.100$), and belowground competitor removal increased survival by 61

% ($Z = 3.85$, $P < 0.001$). Shading treatment reduced survival by almost 4-fold ($X^2_1 = 46.161$, $P < 0.001$; Figure 7b). In the trenching experiment, controlling belowground competition increased survival by 33% ($X^2_1 = 10.37$, $P = 0.0013$; Figure 8). However, there was no significant effect of the watering and nutrient treatments ($X^2_2 = 2.94$, $P = 0.23$) or the interaction between trenching and water + nutrients ($X^2_2 = 1.11$, $P = 0.58$). We did not harvest biomass because all the plants died before reaching reproduction. Plants in Year 2 died after 56 days on average (± 0.67 SE), representing around one-third of their lifespan (until bolting) compared to plants in Year 1 (mean age 157 ± 2.60 SE). We are unable to explain the cause of this sudden mortality in Year 2, which might have reflected a combination of herbivory, temperature, and precipitation patterns, and the fact that seedlings were established slightly later than in Year 1.

Taken together, our results suggest that *D. graveolens*' spread is limited by competition and that its association with roadsides reflects reduced competition, rather than an affinity for the roadside soil conditions. Competition strongly reduced *D. graveolens* performance in two greenhouse and multiple field experiments conducted over two years with contrasting weather patterns, lending generality to the findings. Restoration practitioners can use this information to prioritize managing soil disturbances and promoting competition close to transportation corridors, and aggressively controlling roadside populations before they have the chance to spread.

Other studies concur with our conclusion that *D. graveolens* is a poor competitor. Brownsey et al. (2014) found that *D. graveolens* develops shallow roots early, with significant growth starting in May, after most resident species are established. In contrast, *Bromus hordeaceus* initiates root growth by March and shoot growth by April, enabling it to outcompete *D. graveolens* by exploiting winter rains before senescing in summer. This delayed root development limits the ability of *D. graveolens* to compete with graminoids that capitalize on California's winter rains and senesce during the dry summer months. Similarly, Brinkmann (2020) observed that *D. graveolens* struggled to establish in straw mulching experiments when germinating alongside forbs. In our greenhouse experiment, aboveground biomass of *D. graveolens* was strongly suppressed by competition with two different European annual grasses. The rapid growth of annual grasses intensifies competition aboveground for light and belowground for nutrients and water (Coleman & Levine 2007), and their removal could facilitate *D. graveolens* spread into rangelands.

Other invasive species that spread along roadsides also show limited competitive ability. In its invaded range in Europe, *Ambrosia artemisiifolia* recruitment increased when competitors were removed and soils were disturbed (Fumanal et al. 2008). Similarly, establishment of *Phragmites australis* is constrained by competition, with germination and seedling establishment occurring most successfully in bare roadside soils (Brisson et al. 2010). *Conyza canadensis* also tends to dominate disturbed soils, and is suppressed in sites with dense perennial cover (Weaver 2001). Together, these examples illustrate that many roadside invaders succeed not through strong competitive ability, but by exploiting disturbance and the absence of established vegetation.

Primary drivers of competition in D. graveolens

The primary mechanism limiting *D. graveolens* in field experiments appeared to be belowground competition, although aboveground competition also played a lesser role. In year one, removing aboveground biomass or thatch had no effect, while removing above + belowground competition resulted in both higher survival and higher biomass. In year two, removing belowground competition increased survival by 61 %, while removing only aboveground competition increased survival by only 32 %. Our trenching and weed cloth treatments showed increased survival with reduced belowground competition, while adding water or nutrients had no measurable effect, leaving open the question of the mechanism behind root competition. Finally, shading likely also negatively affected survival, consistent with findings by Brownsey et al. (2014) and Brinkmann (2020); however, disproportionate herbivory in shaded treatments may have contributed to this effect in our study. High mortality in year two, caused by unseasonal heat and intense drought, complicated efforts to fully disentangle competition mechanisms.

Soil played an important role in *D. graveolens* performance. In our greenhouse experiment, *D. graveolens* performed worse in engineered fill (a roadside soil proxy) compared to nutrient-rich field topsoil. The reduced growth in engineered fill was likely due to its significantly lower nutrient content, with approximately 11 times less nitrogen, 13 times less carbon, and 22 times less phosphorus than field topsoil. These fertility differences likely drove the observed growth patterns. Seed germination was slightly lower in engineered fill than in field topsoil, contrasting with the species' frequent association with disturbed roadside soils. Organic matter in field topsoil may have influenced soil moisture and microbial communities, subtly affecting germination outcomes. However, the effects of soil type on germination were quite modest overall.

Managing invasion away from roadsides

Although *D. graveolens* is commonly found along transportation corridors in both its native range and in California (Lustenhouwer & Parker 2022; Melen et al. 2024), its ability to thrive in nutrient-rich soils suggests the potential to spread beyond these disturbed areas. This pattern mirrors other invasive species spreading from roadsides into adjacent habitats (e.g., Gelbard & Belnap 2003; McDougall et al. 2018; Sărățeanu et al. 2010). Across multiple field experiments over two years, we consistently found evidence that *D. graveolens* is a poor competitor, primarily limited by belowground root competition. We also found that the effect of competition on *D. graveolens* in the greenhouse was much stronger in the nutrient-rich field soil than in the construction soil. Taken together, our results suggest that the distribution of *D. graveolens* is constrained to roadsides by competition. Gioria et al. (2023) highlight that invaded ecosystems often include frequent disturbance, and both natural and anthropogenic disturbance create space for colonization.

Our results have several implications for management. Spread is opportunistic for *D. graveolens*, exploiting disturbed or patchy areas, while competition from resident plant communities restricts its establishment. Where feasible, land managers should support dense vegetation cover near spread vectors (e.g., transportation corridors, footpaths, riparian zones, construction areas) to protect sensitive habitats. Roadside verges present a special challenge: vegetation is often deliberately kept sparse for safety and visibility, making it unrealistic to rely on plant competition in these areas. In such contexts, early detection and rapid response will be essential, with spot-checking disturbed roadside sites as a critical step to prevent new establishment from wind-dispersed seeds. In adjacent habitats, perennials and early-germinating annuals with dense canopies and root systems may provide strong early-season competition, limiting *D. graveolens* survival and plant size at reproduction. Thus, management practices that reduce competition in the spring may facilitate *D. graveolens* establishment, and disturbances from cattle, mowing, and agricultural equipment that create bare soil are likely to increase invasion risk. Overall, this work underscores a broader principle in restoration ecology, that fostering strong, competitive native plant communities remains our best defense against opportunistic invaders like *D. graveolens*, even as roadside verges continue to pose unique management constraints.

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Competing Interests

The authors declare none.

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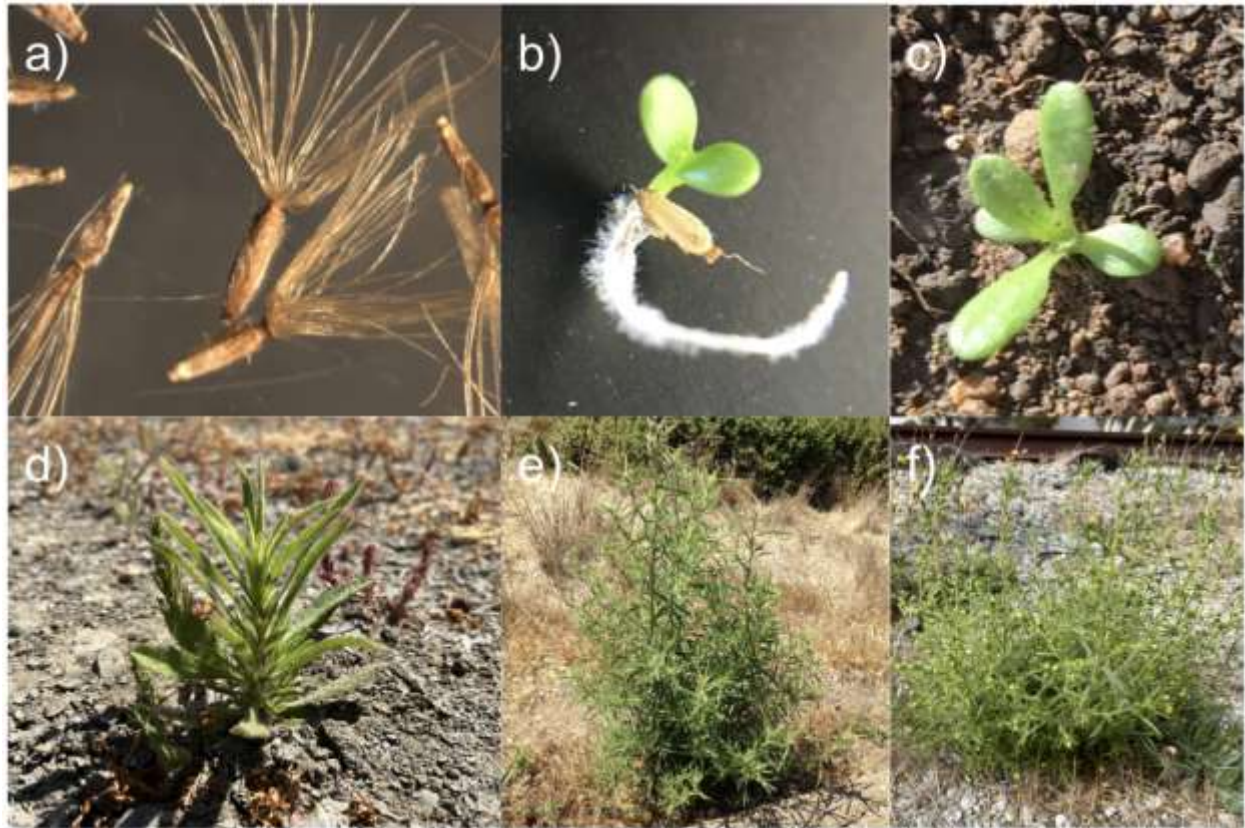


Figure 1. Growth stages of *D. graveolens* showing a) seeds, b) newly germinated seedling, c) seedling at the time of field transplanting, d) juvenile starting to bolt in the wild, e) non-reproductive adult growing in mowed grassland, and f) flowering adult.

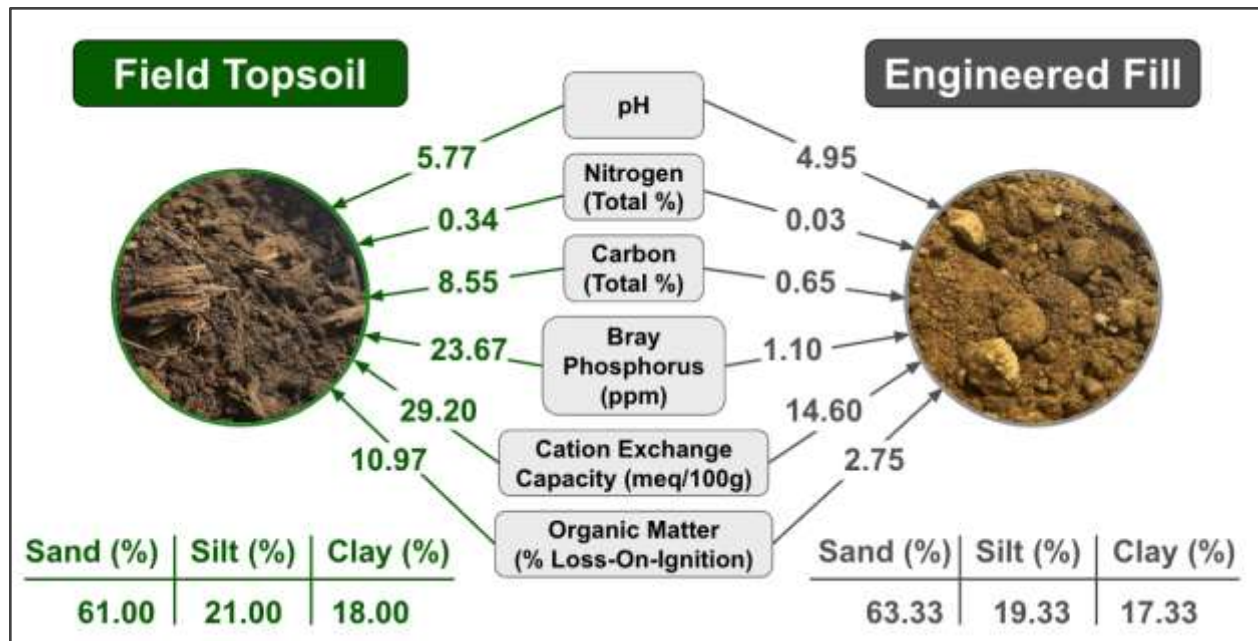


Figure 2. Soils used in germination and greenhouse experiments were collected from a central soil storage location at UC Santa Cruz. Field topsoil was collected from a woodland site on campus, and engineered fill was taken from a campus construction project. The soils were exposed to outdoor conditions, which allowed microbial communities to persist. We subsampled each soil type and homogenized the collected soil for our experiments. Samples were sent to UC Davis Analytical Laboratory, Davis, CA for analysis.

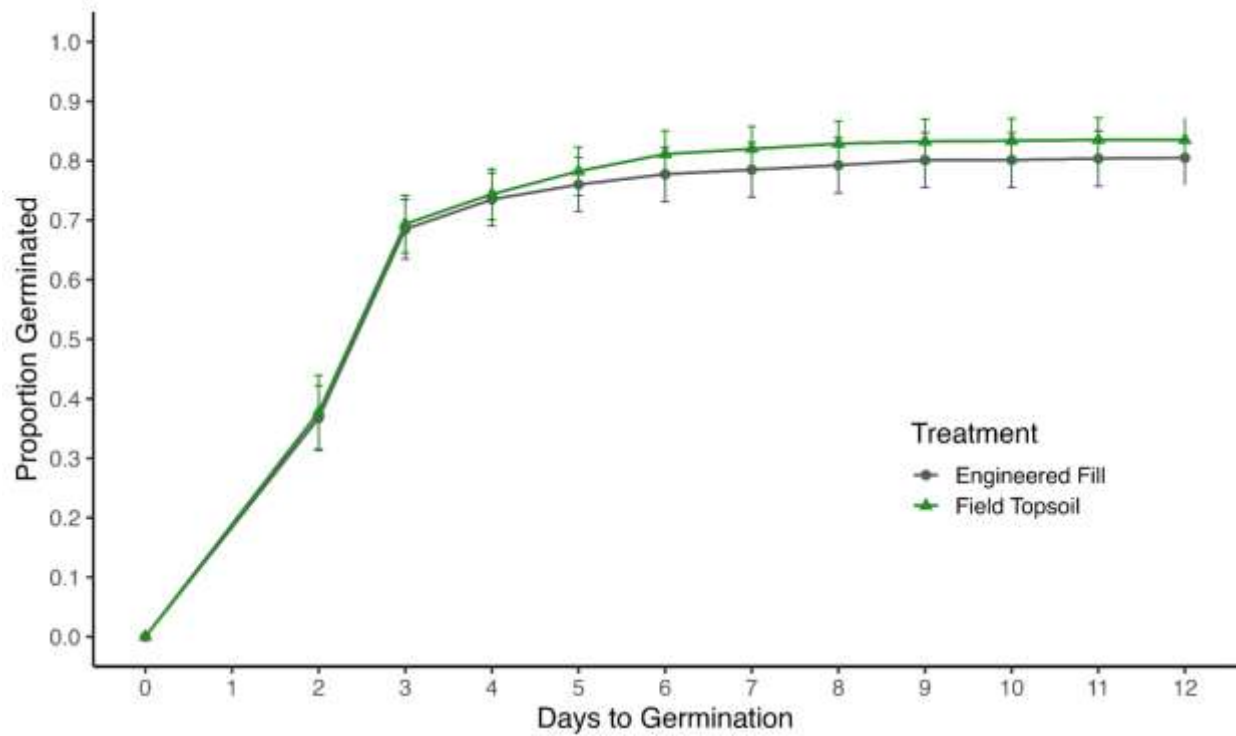


Figure 3: Cumulative proportion germinating per day of *D. graveolens* seeds germinated on engineered fill (gray circles) and field topsoil (green triangles). Values shown are means ± 1 SE, showing variance across 16 seed sources (sites).

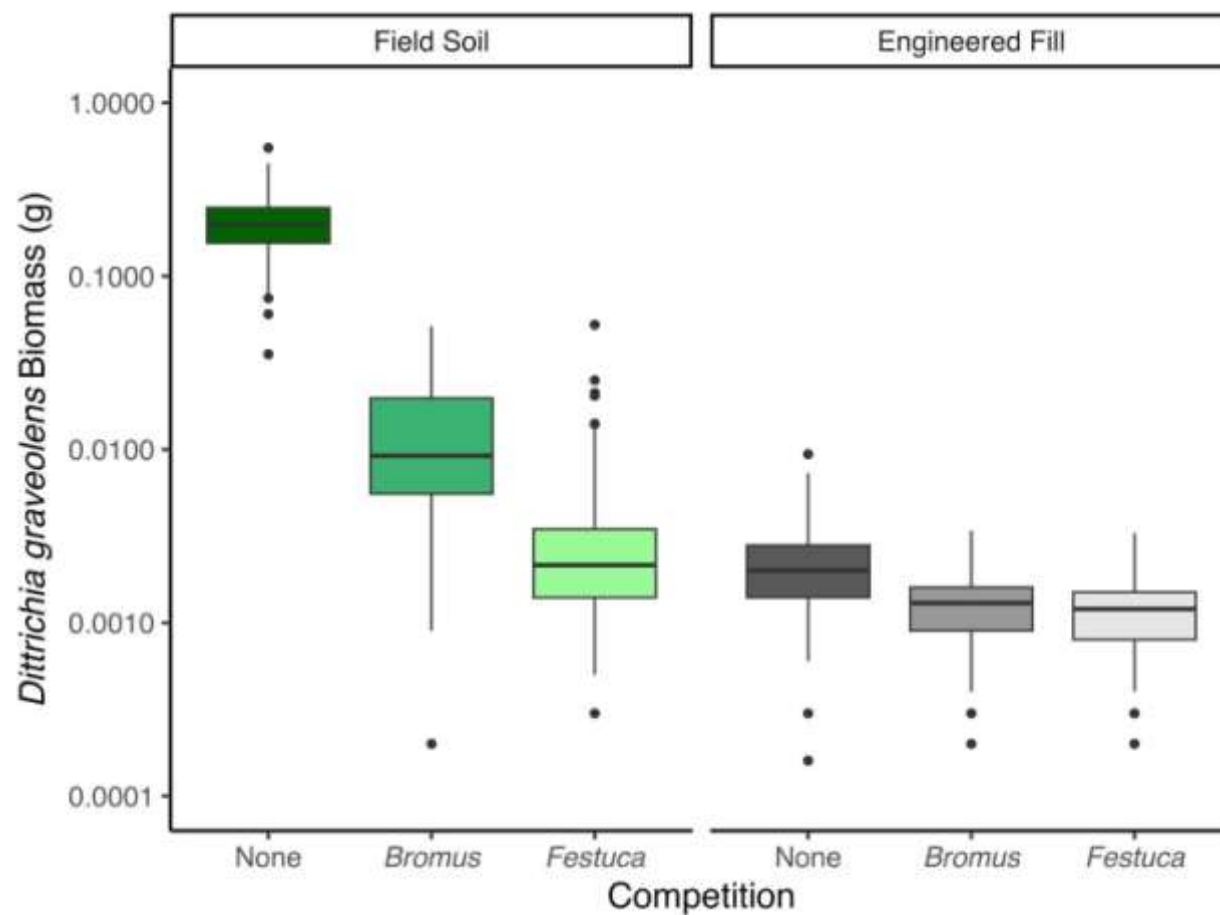


Figure 4. Biomass (g) of *D. graveolens* grown in a greenhouse experiment alone or with each of two grass competitors (*Bromus hordeaceus* and *Festuca perennis*), planted into (a) field topsoil (green), or (b) engineered fill (gray). Boxes correspond to the median, first and third quartiles, and whiskers extend to the furthest value within $1.5 \times$ the inter-quartile range. Note the log scale.

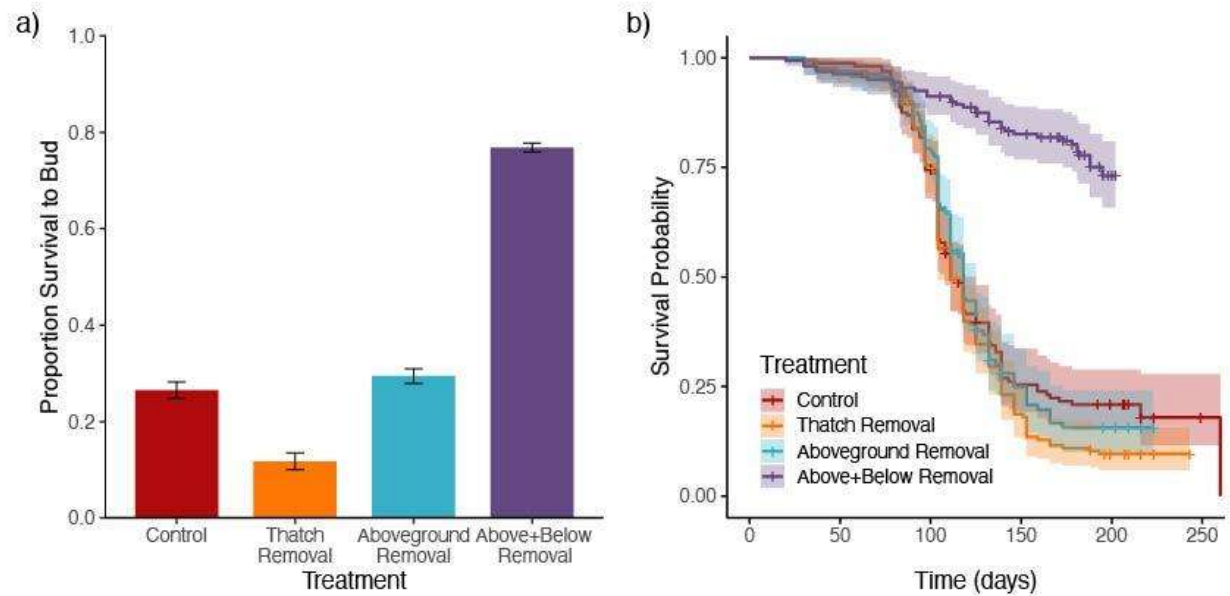


Figure 5. (a) Proportion of *D. graveolens* individuals that survived to reproduction by treatment in year 1 of the field experiment. Plants were transplanted as seedlings into control plots with undisturbed grassland, plots from which dry thatch was removed, plots where aboveground biomass was clipped, and plots where both above- and belowground biomass of all plant neighbors was removed. (b) Survival probability for *D. graveolens* over time; plants were censored from the analysis if they began to flower (and were harvested). Treatments indicated by color as in (a). Kaplan-Meier survival curves with 95% confidence intervals reflect fixed effects (Treatment) only.

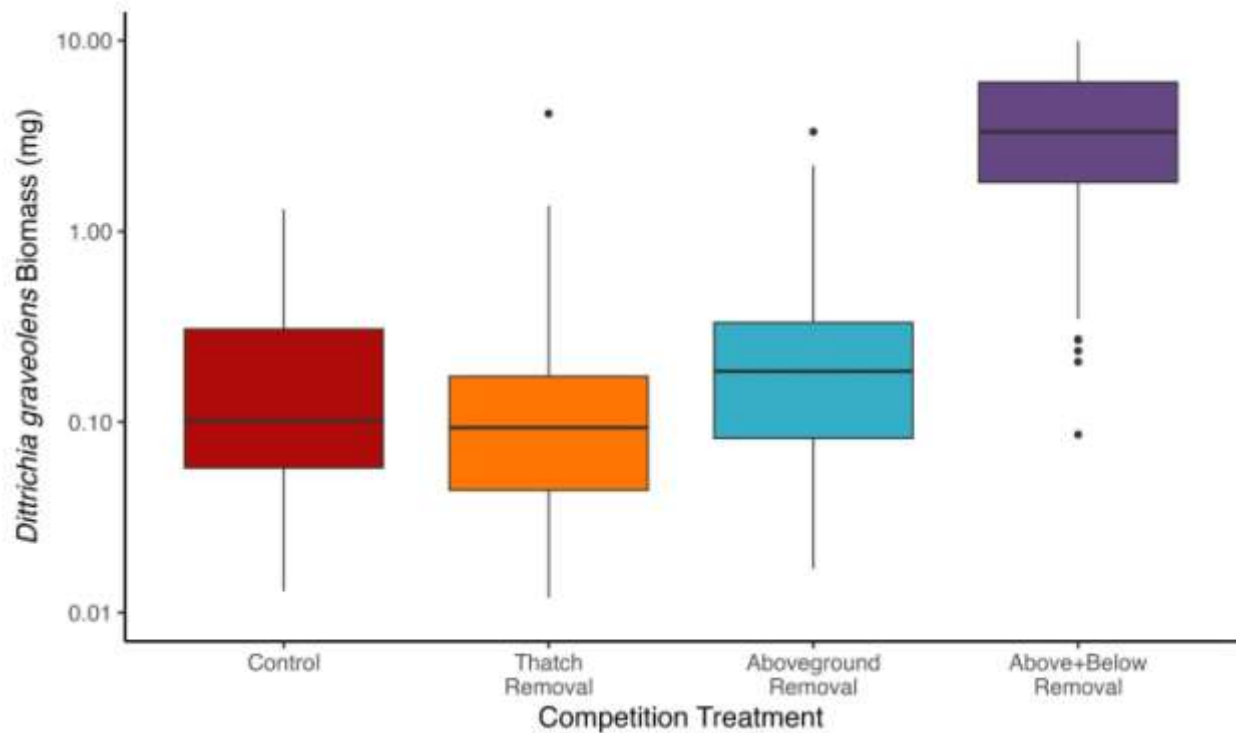


Figure 6. Differences in *D. graveolens* aboveground biomass for plants transplanted as seedlings into control plots with undisturbed grassland, plots from which dry thatch was removed, plots where aboveground biomass was clipped, and plots where both above- and belowground biomass of all plant neighbors was removed. Boxes correspond to the median, first and third quartiles, and whiskers extend to the furthest value within $1.5 \times$ the interquartile range.

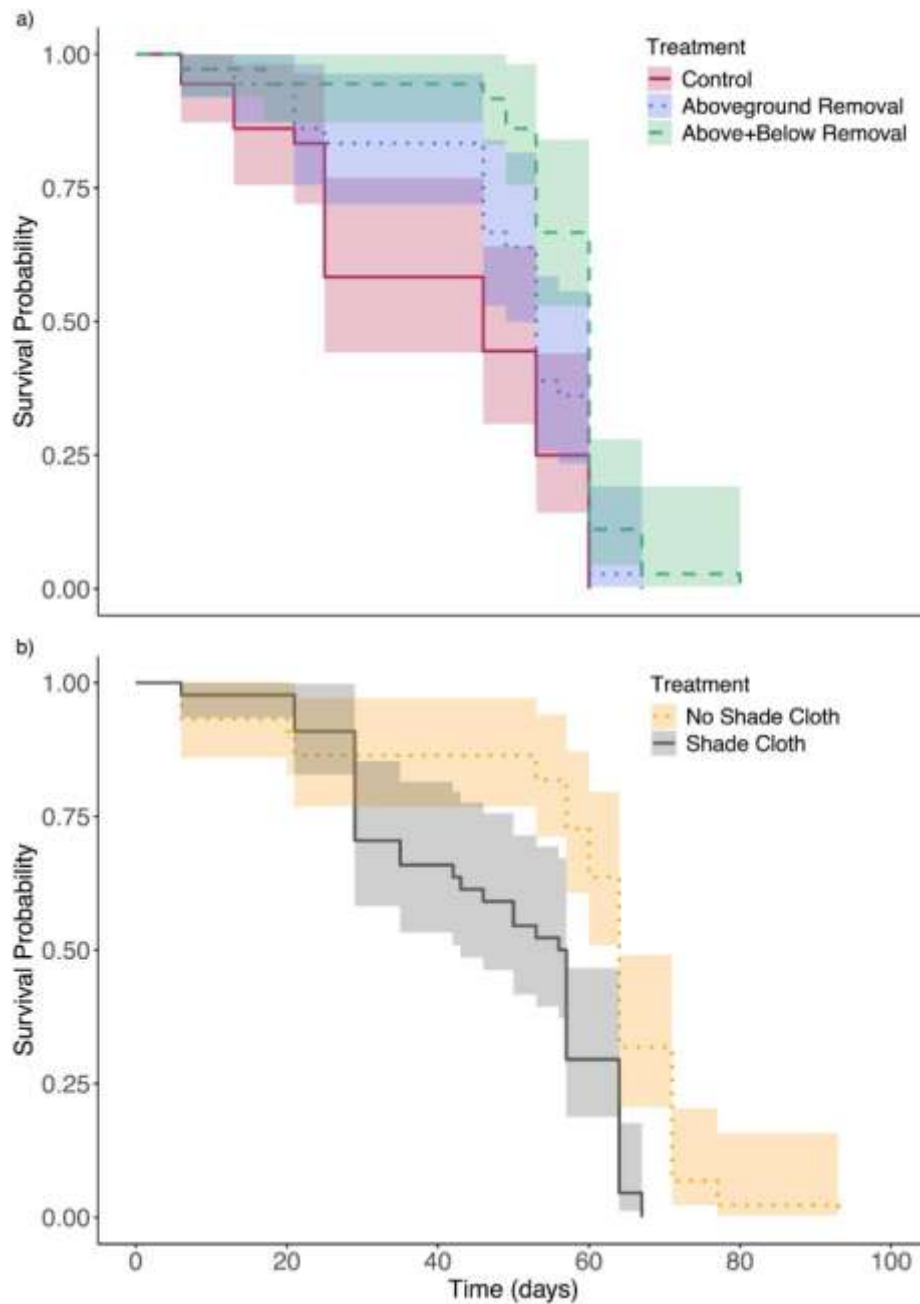


Figure 7. Survival of plants transplanted as seedlings into field plots in 2nd-year experiment. (a) Control plots with undisturbed grassland (solid lines, red), plots where aboveground biomass was clipped (dotted lines, blue), and plots where above- and belowground biomass of all plant neighbors was removed (dashed lines, green). (b) Plots with no shade cloth (dotted lines, yellow) and with shade cloth (solid lines, gray).

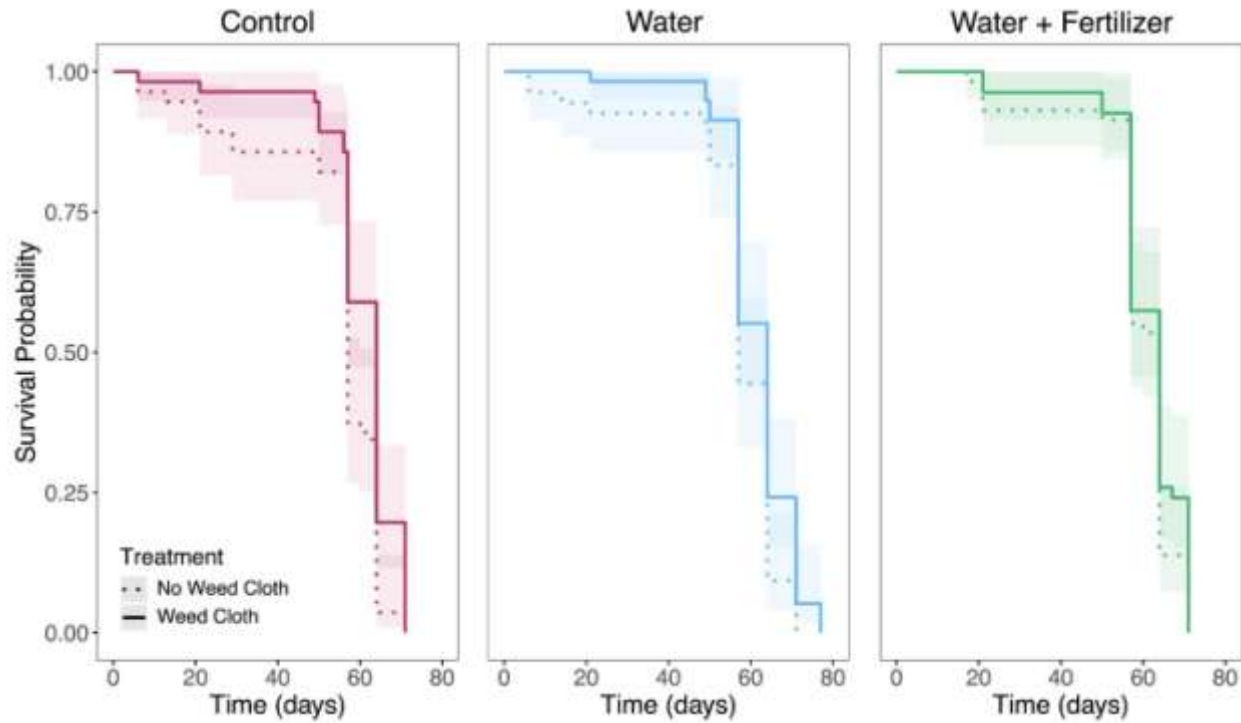


Figure 8. Survival in 2nd-year experiment exploring mechanisms of below-ground competition. Plants were either protected from competition with weed cloth (solid lines), or open to competition (dotted lines), and received one of three resource addition treatments (control, in red, water, in blue, or water + fertilizer, in green). Kaplan-Meier survival curves with 95% confidence intervals reflect fixed effects (Treatment) only.