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Research Article

Suppression of soil microbiota rather than neighbours facilitates absinthe *Artemisia absinthium* invasion in native grasslands

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Many mechanisms can lead to successful plant invasion, but their importance is often context dependent. One such mechanism is allelopathy: chemical inhibition of neighbouring plants. The importance of allelopathy may be mediated by soil microbiota and environmental conditions, and depend upon the species or functional group affected. To better understand how these factors alter allelopathy and competition, we conducted a combined field and greenhouse experiment focusing on the invasive species absinthe *Artemisia absinthium*. We experimentally introduced absinthe into native grassland via disturbances and collected soil from beneath these plants after three years. We then tested how invaded versus uninvaded field soil, within burned or unburned grassland, affected the performance of absinthe, two forbs (*Achillea millefolium* and *Medicago sativa*), and two grasses (*Bromus inermis* and *Elymus lanceolatus*) in a greenhouse competition experiment. We included activated carbon and soil sterilization treatments to test for allelopathic and microbial effects. Microbial inhibition, rather than allelopathy, drove competitive interactions. In uninvaded, unburned soil all species were inhibited and absinthe had no competitive effect. However, when absinthe was released from microbial inhibition by soil sterilization or prescribed fire, it suppressed other species. Microbial inhibition was also reduced for all species in invaded soil, suggesting suppression of pathogens by absinthe. Responses also varied between functional groups, with grasses being more vulnerable to microbial inhibition. Our findings highlight the complexity of invasion effects on soils and the potential for feedbacks on invasion outcomes. They also suggest that disturbance may facilitate invasion via effects on both plants and soil microbes.

Keywords: allelopathy, disturbance, functional groups, grassland invasion, microbial feedbacks

Introduction

Invasive plant species disrupt ecosystems by altering plant community structure, thereby reducing overall biodiversity and ecosystem functions (Vasquez et al. 2010, Livingstone et al. 2020). The success and impact of invaders is often ascribed to highly

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competitive traits such as rapid growth (van Kleunen et al. 2010), yet more specialized mechanisms may exist, such as allelopathy. Allelopathy can be defined as negative plant–plant interactions via the direct and indirect effects of plant chemical production (Fitter 2003). These allelochemicals are usually secondary metabolites, produced in leaf and root tissues, which are not essential for basic metabolic processes but have specialized functions (Bais et al. 2003, Callaway and Ridenour 2004, Mosunova et al. 2021). If these allelochemicals are not present in the native community, the lack of co-evolved defenses can increase invasive species establishment (i.e. the novel weapons hypothesis; Callaway and Ridenour 2004). Allelopathic effects are often difficult to detect yet may have long-term effects on ecosystem health, even following control of the invasive species (Grove et al. 2012, Del Fabbro and Prati 2015). For this reason, understanding the role of allelopathy in invasion is essential for management.

Allelopathic effects may depend on the species or functional group affected. Related species may be unaffected or even facilitated if they produce similar allelochemicals (Zhang et al. 2021). For example, many *Artemisia* species produce similar secondary metabolites (Jakupovic et al. 1991, Liu and Mabry 2004, Szopa et al. 2020, Li et al. 2021), yet the response to these allelochemicals can be species specific (Hoffman and Hazlett 1977). Conversely, allelopathic effects are often stronger against different functional groups, especially if there are strong competitive interactions (Ortega and Pearson 2005, Meiners et al. 2012). For example, graminoids are typically the dominant competitors in grasslands (Silletti et al. 2004, McCain et al. 2010) and thus allelopathic forbs may develop allelochemicals specific to graminoids, increasing their potential ecosystem impacts (Scharfy et al. 2011, Meiners et al. 2012). Consequently, allelopathic inhibition may increase with phylogenetic distance and competitive interactions.

To understand how the plant community might respond to an allelopathic invader, it may be necessary to compare co-occurring functional groups. Graminoids and forbs, the predominant grassland functional groups, are generally expected to diverge in their allelopathic responses (Scharfy et al. 2011, Grange et al. 2023). These groups can be further differentiated by origin (i.e. native versus non-native species) as well as resource acquisition strategies (i.e. growth rate, nitrogen fixation). For example, Scharfy et al. (2011) found that invasive forb species exhibited stronger allelopathic inhibitory effects than native forbs on a co-occurring native graminoid species. However, another study found that native *Artemisia* seedlings were able to establish in native *Elymus* stands, but not in non-native *Bromus* stands, the authors demonstrated that this outcome was due to differences in resource competition (Booth et al. 2003). Consequently, allelopathy studies should test how differing resource acquisition strategies impact invasion outcomes, based on the mode of action of the allelochemical. For example, in a pot experiment testing how *Festuca* leachates affected two native grasses, allelochemicals inhibited the fast-growing, competitive grass by interfering with nutrient uptake, while having no effect on the slow-growing, conservative grass (Viard-Crétat et al. 2012). Likewise, nitrogen-fixing species may be inhibited if allelochemicals interfere with rhizobia symbioses (Wardle et al. 1994, Portales-Reyes et al. 2015), yet may be facilitated if allelochemicals stimulate nodulation (Morvillo et al. 2011). Further, considering resource competition is necessary in allelopathy studies, as allelopathic effects in direct competition experiments may differ greatly from bioassay germination trials (Morvillo et al. 2011).

Soil microbiota are also important in determining allelopathy outcomes. Soil microorganisms can enhance allelopathic effects by increasing mobility or activity of allelochemicals (Bains et al. 2009, Cipollini et al. 2012) or negate allelopathic effects by rapidly degrading plant exudates, especially if the microbial community has adapted to those metabolites due to long-term exposure (Li et al. 2017, Revillini et al. 2023). Conversely, allelochemicals can indirectly affect plant growth by harming beneficial soil microorganisms (Cipollini et al. 2012). For example, artemisinin, produced by *Artemisia* species, can inhibit rhizobia and other beneficial microorganisms, if it is novel to the microbial community (Herrmann et al. 2013, Martínez et al. 2014). These impacts on the microbial community can then affect subsequent plant growth (plant–soil feedbacks; van der Putten et al. 2013), such as the ability of native species to reestablish following invasion.

Allelopathic interactions may also be altered by environmental conditions. Where resources such as nutrients or water are abundant, this may increase the ability to produce certain secondary metabolites (Men et al. 2018, Gao et al. 2020). Conversely, the production of secondary metabolites can be stimulated in response to stress (Tuomi et al. 1984, Yadav et al. 2021). In grasslands, resource availability and competition are often altered by disturbance, such as fire (Wan et al. 2001, Alba et al. 2015), which may thus alter allelochemical production. Reduced competition following disturbance may also increase the ability to produce allelochemicals by freeing up resources (Rivoal et al. 2011). Rapid establishment by invasive species in disturbed areas may allow invaders to pre-empt resource access and increase allelopathic suppression of any later establishing native species, yet it remains unclear how well disturbance and allelopathy are linked.

Absinthe *Artemisia absinthium* is an invasive, perennial forb found in both native and seeded grasslands of the Canadian prairies (Selleck 1964, Maw et al. 1985). Absinthe is unpalatable to livestock and most wildlife due to its bitter taste and the same compounds are thought to make the plant allelopathic (Selleck 1964, Hoffman and Hazlett 1977, Maw et al. 1985). For example, linalool extracted from absinthe has been shown to interfere with root hair development (Jiang et al. 2021) and artemisinin can cause cell lysis (Ni et al. 2021). Early absinthe allelopathy field experiments noted improved neighbour growth with increasing distance from absinthe plants and inhibitory effects when leaves were incorporated into the soil (Bode 1940, Funke 1943). In laboratory bioassays, however, aqueous extracts of absinthe leaves have shown inhibitory, neutral and stimulatory effects on

native and domesticated species (Hoffman and Hazlett 1977, Turker et al. 2008, Kapoor et al. 2019, Szparaga et al. 2021, Erhatić et al. 2023), indicating strong interspecific variability in response to these compounds. These studies, however, lacked the necessary controls required to separate allelopathy from other competition mechanisms (Willis 1985, Inderjit and Callaway 2003, Weidenhamer 2008) and did not consider how resource competition could explain inhibitory effects under realistic conditions for allelopathy to be active (Inderjit and Del Moral 1997, Inderjit and Weston 2000). Moreover, absinthe extracts can also inhibit pathogenic bacteria and fungi, nematodes, and the overall microbial community (Fiamegos et al. 2011, Ali et al. 2015, Pino-Otín et al. 2019), but it is unclear how these effects on the soil biome affect the role of allelopathy in absinthe invasion.

To explore variation in allelopathy and its role in invasion, we used a combined field and greenhouse study focusing on absinthe. We conducted a three-year invasion study in a native grassland where we experimentally introduced absinthe plants following disturbances (herbicide and prescribed fire). The first year of this experiment is described by Wasan et al. (2023). Following this, we collected field soil from these mature experimental plants and paired uninvaded plots, within burned and unburned grassland, for a greenhouse allelopathy experiment. We studied how these soils affected the performance of a related native forb (yarrow; *Achillea millefolium*), a native grass (northern wheatgrass; *Elymus lanceolatus*), and an invasive grass (smooth brome; *Bromus inermis*), both alone and with an absinthe competitor. Given that absinthe is also invasive in tame forage systems, we also included a non-native legume (alfalfa; *Medicago sativa*). To investigate conspecific effects of absinthe-invaded soil (such as autotoxicity), we also grew absinthe alone. We included three soil treatments: untreated control, activated carbon (AC) to sorb allelochemicals, and soil sterilization to estimate microbial effects.

We hypothesized that:

1. Responses to absinthe-invaded soil would vary between species: the related forb would be unaffected, the legume would be moderately inhibited, and the two grass species would be strongly inhibited.
2. Absinthe would grow better in untreated absinthe-invaded soil than in uninvaded soil or AC-treated or sterilized invaded soil, allowing it to be a better competitor in those conditions.
3. In soils from burned areas, increased nutrients would strengthen inhibitory effects from the absinthe-invaded soil and would thus also improve absinthe competitive ability.

Material and methods

Absinthe invasion field experiment

As a source of absinthe allelochemicals for a greenhouse pot experiment, we collected soil from an absinthe invasion experiment that we established in 2021 at a native grassland near Saskatoon, Canada in the Northern Great Plains (52°10'N, 106°31'W; Wasan et al. 2023). In April 2021, we conducted a low-severity prescribed fire (1.5 ha area). Following the burn, we established ten blocks, with five blocks placed within the burned area and five outside the burned area (within 25 m of the fire perimeter). Blocks were placed randomly to create independence. Blocks were 5 × 4 m and subdivided into four 2.5 × 2.0 m plots (40 plots total). Then in a factorial design, we applied herbicide (glyphosate; Roundup Super Concentrate, 356 g l^{-1}, 1 ml m^{-2}) and fertilizer (14-13-13 N-P-K slow-release fertilizer; Plant Prod Nutricote Type 100, 71 g m^{-2}) treatments in May. Following these treatments, in June 2021, we transplanted two 7-week-old absinthe seedlings into each plot, spaced 1 m apart.

Greenhouse allelopathy experiment

To test how absinthe invasion affects the growth of different grassland species, we established a greenhouse experiment (Fig. 1) at the University of Saskatchewan (Saskatoon, Canada) using soils from the field invasion study described in the previous section.

Field soil sources

We randomly selected three blocks from each of the burned and unburned areas to serve as soil sources for the greenhouse experiment. From 8–11 August 2023, we collected root-zone soil from under the two surviving absinthe plants in each block. We sterilized all equipment with 70% ethanol before collecting soil from a different soil source. We pooled soils between the control and fertilized plots within the herbicide-treated half (where absinthe did establish) to obtain sufficient soil, approximately 18 l per block. We collected an equal amount of soil from the uninvaded, non-herbicide-treated vegetation within 3 m of the absinthe plants, again pooling from both fertilized and unfertilized plots. In total there were 12 soil sources (burned versus unburned × 3 blocks × 2 invasion groups). To preserve the sample and prevent contamination, the soil was stored in a sterilized bucket and sealed in a plastic bag with ice packs in the field, then refrigerated at 4°C the same day. Subsamples of the pooled soil were ground and sent to the Natural Resources Analytical Laboratory at the University of Alberta for chemical analysis.

Greenhouse soil treatments

In this experiment, we had three soil manipulation treatments: control (full field soil), field soil with activated carbon, and sterilized field soil. To separate resource competition from allelopathic effects, we used activated carbon (AC), as it has high specific surface area, porosity and polarity, and can thus adsorb organic molecules, but has low affinity for soil nutrients (Lau et al. 2008). Thus, improved growth of neighbour plants with AC addition may indicate release from allelopathic effects and not from resource competition. Since soil microorganisms can mediate invasion and allelopathic interactions (Cipollini et al. 2012, Revillini et al. 2023, Zhang et al. 2023), we also included a sterilization treatment

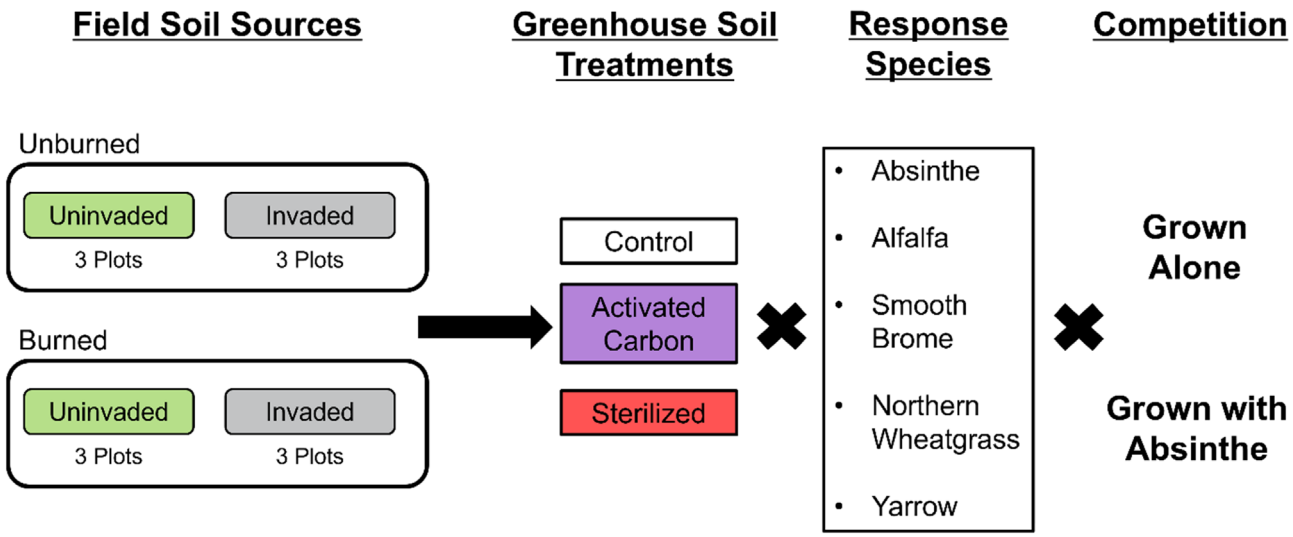


Figure 1. Experimental design for greenhouse allelopathy experiment. For northern wheatgrass, smooth brome and yarrow: 12 soil sources (2 invasion treatments × 2 fire treatments × 3 block replicates) × 3 species × 2 competition treatments × 3 soil treatments = 216 pots. For absinthe: 12 soil sources × 3 soil treatments = 36 pots. For alfalfa: 12 soil sources × 2 competition treatments × 2 soil treatments = 48 pots. Total number of pots was 300 in this experiment.

to separate microbial and chemical effects. Sterilization likely will not alter allelopathic effects, as it has been shown that sterilization does not degrade phenols or lactones or affect their toxicity, including during extractions from *Artemisia* species (Mares 1987, Kang and Lee 2013, Jambrec et al. 2015, Sanchiz et al. 2019).

Within two days of field soil collection, we potted the greenhouse experiment (8–12 August). We applied the soil manipulation treatments as follows. To remove rocks and debris, we passed the soils through a 4.75 mm sieve, but reincorporated any root material as absinthe produces allelochemical exudates from its roots (Llorens-Molina and Vacas 2015, Szopa et al. 2020). For the activated carbon treatment (activated carbon –20+40 mesh, Thermo Scientific), we mixed in 2% v/v for each batch (Del Fabbro and Prati 2015, Yuan et al. 2021). For the sterilization treatment, we sterilized the soil for 90 min at 112°C and 11.6 psi using a pressure-cooking device (Duo 80 V2 Instant Pot, Instant Brands), which has been shown to be effective for soil sterilization (Swenson et al. 2018).

Response species and competition treatments

We selected five responses species for this experiment, including absinthe itself. As a closely related native species, we selected yarrow *Achillea millefolium*, as it is common at the study site, and yarrow and absinthe are both members of the Anthemideae tribe within the Asteraceae family, thus yarrow should in theory be more tolerant of absinthe allelochemicals. For grasses, we used both a native (northern wheatgrass; *Elymus lanceolatus*) and non-native species (smooth brome; *Bromus inermis*) as both are common at the site and across Saskatchewan grasslands. Further, in previous research we found a positive association between smooth brome and absinthe establishment (Wasan et al. 2023), suggesting that plant origin may alter grass responses to absinthe allelochemicals. Finally, we selected the non-native forage species alfalfa *Medicago sativa* as it is economically important (Annicchiarico et al. 2015) and absinthe is a serious invader of seeded alfalfa pasture (Selleck and Coupland 1961, Maw et al. 1985). We tested all species against the twelve soil sources and three soil manipulation treatments, except for alfalfa, which was only included in the control and activated carbon treatments due to logistical constraints. We also had two competition treatments where response species (except absinthe) were grown in competition with absinthe and alone.

Experiment maintenance and data collection

We seeded the experiment immediately following soil treatments, which we maintained for 60 days. In total, there were 300 pots in this experiment. Into 750 ml conical pots, we added five seeds for alfalfa, northern wheatgrass and smooth brome or, for absinthe and yarrow, approximately 0.1 g due to small seed size and low germination. We watered the pots to saturation three times per week for eight weeks. On 21 August 2023 (10 days post seeding) we thinned alfalfa, northern wheatgrass and smooth brome plants to 1 plant per pot. Due to slower germination, we thinned absinthe and yarrow to 1 plant per pot on 30 August 2023 (19 days). From 10–13 October 2023, we harvested aboveground biomass (60 days). Plant biomass was dried at 55°C for 48 h and weighed.

Data analysis

We conducted all data analyses as linear mixed models in R ver. 4.3.2 using the 'lme4' package (Bates et al. 2015). To determine how absinthe invasion alters its own growth and its potential mediation by disturbance, we ran one model

focused only on absinthe shoot biomass without competition. This model included field fire disturbance, prior absinthe invasion, and the greenhouse soil treatment as factorial fixed effects, with field block (soil source) as a random effect. We did not include the competition treatment data in this initial model to keep it as simple as possible. We did, however, run a second absinthe model that included the absinthe shoot biomass data from the competition treatments. This model was structured as the previous one but included interactions with the competition treatment, which we coded as having four levels (alone, northern wheatgrass, smooth brome and yarrow). We did not include absinthe growth with alfalfa in this model as not all soil treatments were included when seeding alfalfa. To examine absinthe effects on the biomass of other species, we used two models – alfalfa on its own and the other three species (northern wheatgrass, smooth brome and yarrow) combined due to differences in experimental structure among species. The alfalfa model was structured similar to the absinthe competition model except both the competition and soil treatment variables only had two levels (without and with absinthe, and control and AC). For the three species model, the model was structured as the alfalfa model except species was included as a factorial fixed effect and the soil treatment factor again had three levels (control, AC and sterilization). Finally, to test for differences in nutrient content between the soil sources, we ran a mixed model on total nitrogen content (log-transformed) with prior invasion and fire disturbance as fixed effects and block as a random effect. For all models, we tested for normal distributions of model residuals using the Shapiro–Wilks test and plotting a histogram of model residuals in base R. We then conducted an F-test for each model using the 'lmerTest' package (Kuznetsova et al. 2017). Due to the small sample size and the complexity of the experiment, we interpreted p-values < 0.1 as significant. When interaction terms were significant, we used the 'emmeans' package to conduct pairwise, post hoc tests using the Tukey method (Lenth and Piaskowski 2023). We structured contrasts by comparing among smaller scale manipulations within larger scale manipulations (i.e. invasion within fire) and among combinations of greenhouse treatments within species or field treatments. Figures for all models were generated using the 'afex' package (Singmann et al. 2021). Boxplots of the distribution of the raw data are available in the Supporting information.

Results

Absinthe invasion and prescribed fire affected subsequent plant growth, but responses varied by species. When analyzing absinthe on its own, absinthe growth was dependent on interactions between invasion and fire, and invasion and the soil treatment ($p = 0.048$ and $p = 0.060$, respectively; see the Supporting information for full results). Absinthe grew best in invaded or burned soil, but poorly in uninvaded, unburned soil (Fig. 2A; post hoc $p = 0.010$ (uninvaded versus invaded within unburned); Supporting information). This may be due to increases in nutrient availability, as soil nitrogen was greater in burned soils and in invaded soils, however this did not occur in combination of invaded and burned soils ($p = 0.067$; Supporting information). Soil sterilization also increased absinthe growth by 92%, but only in uninvaded soil (Fig. 2A; post hoc $p = 0.088$; Supporting information), indicating that native microbes may limit initial absinthe invasion but not once absinthe has established. When including the competition treatments, the interaction between invasion and fire history was maintained ($p = 0.035$, Fig. 2B; post hoc $p = 0.008$ (uninvaded versus invaded within unburned); Supporting information); however, the soil sterilization effects changed. Soil sterilization still increased absinthe growth by 49% ($p = 0.011$, Fig. 2C; post hoc $p = 0.040$; Supporting information), but this effect was independent of all other treatments (Supporting information). Competition also had a significant effect that was independent of the other treatments ($p < 0.001$): competition always reduced absinthe growth (Fig. 2D; post hoc $p < 0.001$ against each species; Supporting information), but this effect was greatest for smooth brome (80%) and smallest for yarrow (43%; post hoc $p = 0.006$ (smooth brome versus yarrow); Supporting information).

Alfalfa responses were highly complex, as indicated by the four-way interaction between invasion, fire, activated carbon, and competition ($p = 0.007$; Supporting information). In undisturbed native prairie soil (unburned, uninvaded), alfalfa growth was low regardless of soil treatment and competition (Fig. 3). Prescribed fire increased alfalfa growth by 157% in uninvaded soil, but not in invaded soil, whereas invaded soil also increased alfalfa growth by 303%, but only in unburned soil ($p < 0.001$, Fig. 3, post hoc $p < 0.001$; Supporting information), consistent with the observed changes in soil nitrogen (Supporting information). Alfalfa growth in invaded unburned soil was further mediated by competition and AC: growth increased with either AC or an absinthe competitor (post hoc $p = 0.010$ and $p = 0.019$; Supporting information), but not when applied in combination.

For the combined analyses of smooth brome, northern wheatgrass, and yarrow responses, most treatment effects were consistent among species. All species performed better in invaded soil than uninvaded soil; however, the inhibition in uninvaded soil was mitigated by either soil sterilization (267% increase) or prescribed fire (137% increase from unburned control), but not the combination of the two (Fig. 4A; invaded × fire × soil treatment; $p = 0.012$; Supporting information). The effect of the absinthe competitor was also dependent on prescribed fire and soil treatment ($p = 0.052$). Within the unburned treatment, competition reduced the benefit plants saw from soil sterilization (42% increase from control when grown alone (post hoc $p = 0.002$; Supporting information), but not significant under competition), but otherwise had no effect (Fig. 4B). Conversely, in the burned treatment, response species growth was reduced by competition (35% between controls), but not following sterilization (post hoc $p = 0.062$ (control versus sterilized within competition); Supporting information). Despite

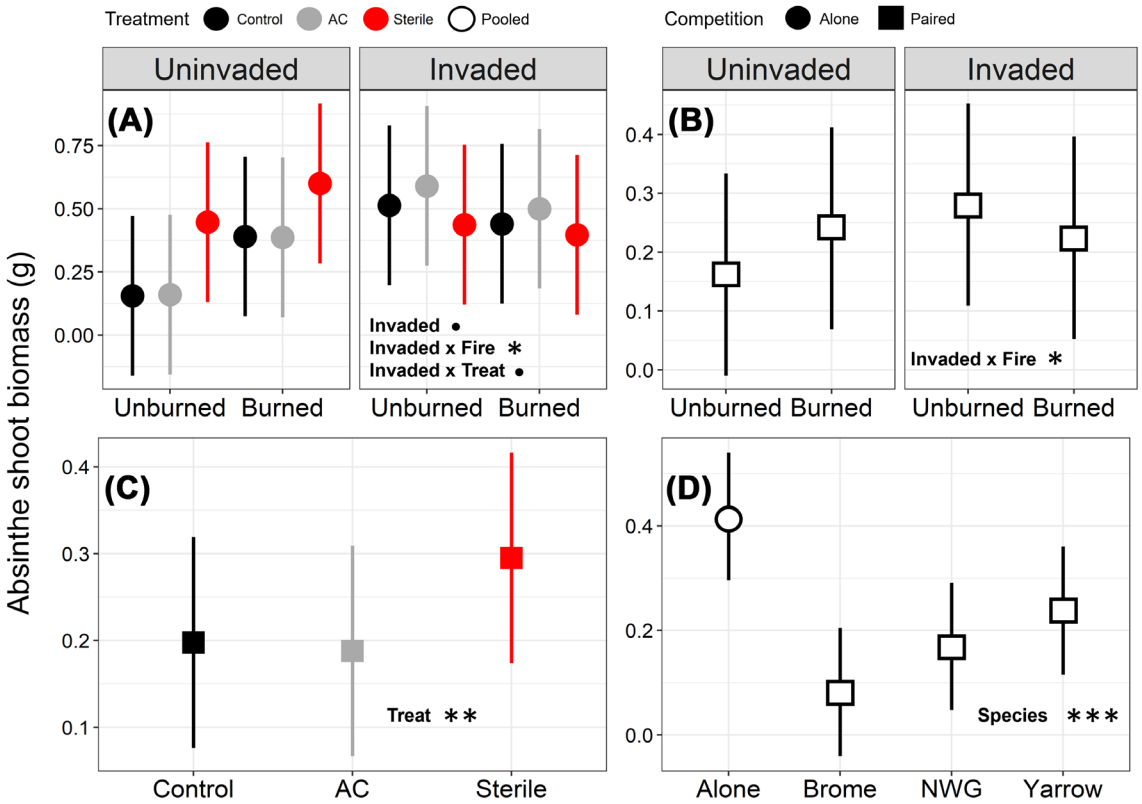


Figure 2. Absinthe shoot biomass responses to prior absinthe invasion, prescribed fire, and greenhouse soil sterilization and activated carbon treatments when grown alone (A). Absinthe shoot biomass responses to invasion and prescribed fire (B; pooled across soil treatments), greenhouse soil treatments (C), and target species (D; pooled across soil treatments) when grown under competition. Points and whiskers represent model estimated means and 95% confidence intervals. Significance levels are shown on the figure as follows: • $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

relatively consistent environmental effects on plant responses to soil treatments, the mean response to the soil treatments differed among response species ($p < 0.001$). Both grasses (smooth brome and northern wheatgrass) benefitted from soil sterilization (73 and 44% increase respectively; post hoc $p < 0.001$ and $p = 0.024$, respectively; Supporting information), but yarrow did not (Fig. 4C).

Discussion

Across a variety of plant species, absinthe invasion and the legacy effects of fire disturbance consistently affected subsequent plant growth. Contrary to our hypothesis, however, plant performance was worst in uninvaded, unburned soil for both the invader and the resident species. This negative effect of intact soils was mitigated by soil sterilization, highlighting the potential role of soil pathogens in limiting plant growth and suggesting that absinthe and, to a lesser extent, fire may suppress such pathogens. The presence of a live absinthe competitor affected plant species differently, with smooth brome (invasive grass) best able to compete with absinthe and yarrow (confamilial native forb) least able to compete. On average however, live absinthe did little to suppress neighbour growth except in sterilized unburned soils or in live burned soils, suggesting that competitive effects, and thus invasive impacts, are strongly context dependent.

We found limited evidence that inhibition of our response species by absinthe-conditioned soil or by an absinthe competitor occurred via allelopathy. If allelopathy had occurred, we would expect that AC application would have mitigated the inhibition by adsorbing allelochemicals. However, AC generally did not alter responses across species, except for alfalfa and then only in invaded and unburned soils. It is possible that absinthe allelochemicals do not persist at significant concentrations in the long-term. Degradation of allelochemicals, such as phenols, can occur within weeks of production (Weidenhamer and Romeo 2004, Nosko and Embury 2018), and may not have persisted in the field soils for the duration of the experiment. In the field, litter deposition and root exudates may still enable allelopathic inhibition of other plants, whereas in the greenhouse, the absinthe seedling may have been too small to exert significant allelopathic effects. Consequently, if allelopathy is a major driver of absinthe invasion, the effects are unlikely to persist and hinder any restoration efforts.

Although allelopathy had limited direct effects on plants, absinthe may have suppressed aspects of the soil microbiome. In uninvaded soil, sterilization increased absinthe growth, whereas in invaded soil, absinthe growth was significantly

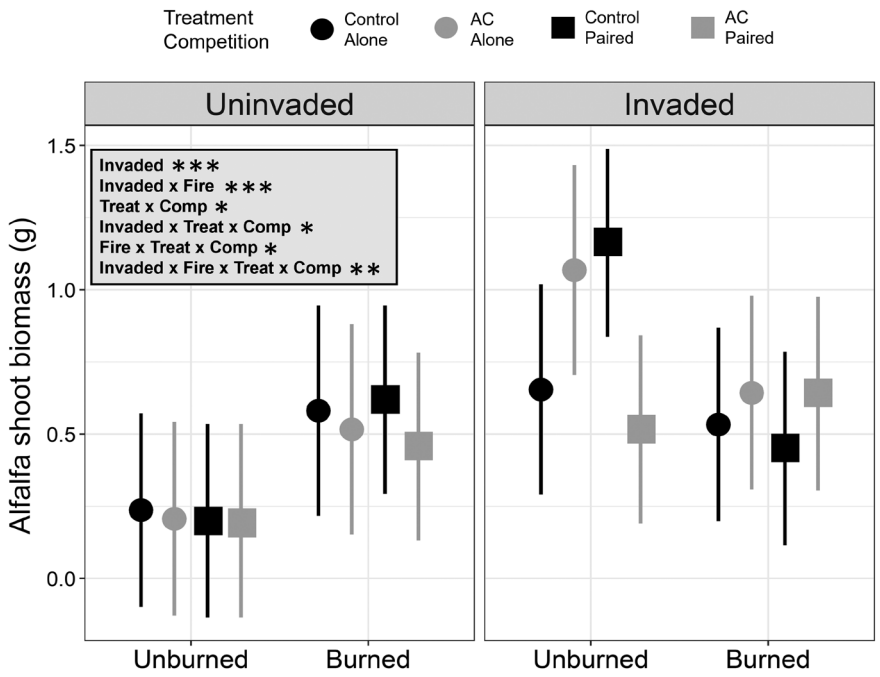


Figure 3. Alfalfa shoot biomass responses to prescribed fire, greenhouse activated carbon treatment, prior absinthe invasion, and competition with absinthe. Points and whiskers represent model estimated means and 95% confidence intervals. Significance levels are shown on the figure as follows: • $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

greater and unaffected by sterilization. This suggests absinthe was microbially inhibited in uninvaded soil, but released from this inhibition in invaded soil. Absinthe allelochemicals have been shown to have antimicrobial effects and to inhibit pathogenic bacteria (Fiamegos et al. 2011, Pino-Otín et al. 2019), and inoculants sourced from a congener *Artemisia annua* were shown to inhibit pathogenic fungi and promote plant growth (Wang et al. 2023). This suggests that native soil microbiota may limit initial absinthe invasion. However, if stronger mechanisms allow absinthe to establish, such as disturbance (Maw et al. 1985, Wasan et al. 2023), then absinthe may overcome this limitation and suppress pathogens.

We observed growth inhibition effects in uninvaded soils across species, which were reduced by both soil sterilization and absinthe invasion. While soil sterilization increased growth in uninvaded soil, performance also increased in invaded, absinthe-conditioned soils, yet here sterilization had no effect. It is thus possible that absinthe-induced positive feedbacks on other species were due to the suppression of pathogens. However, it is also possible that the observed negative feedbacks were the result of experimental conditions, such as soil sterilization increasing nutrient availability (Troelstra et al. 2001) or the short duration of the experiment creating a bias towards negative microbial effects (Kulmatiski et al. 2008, Brinkman et al. 2010). Other invasive species also suppress soil pathogens, which has been posited as a potential mechanism behind their invasion (Zhang et al. 2011). For absinthe, however, other species also benefitted from microbiome suppression and we found no interactions between competition and either soil sterilization or invasion history when considering absinthe growth in competition. Plant competition is typically a stronger factor than plant–soil feedbacks (Kulmatiski et al. 2011). Thus, while such suppression may be important for absinthe establishment, it is unlikely to give absinthe a competitive advantage over the dominant grasses within these ecosystems.

Although conspecific facilitation was expected for absinthe, the facilitation of other species was surprising, but reinforces the importance of pathogens in grassland ecosystems where negative plant–soil feedback dominates (Reinhart 2012). The negative feedbacks were particularly strong for the grass species (smooth brome and northern wheatgrass). Plant–soil feedbacks may inhibit the growth of graminoids in particular due to the accumulation of pathogens adapted to the dominant species (Kulmatiski et al. 2008, Li et al. 2020, Kohout et al. 2024), whereas the forb species (yarrow), while common, is much less abundant. Alternatively, yarrow may have escaped the negative feedback because it already invests heavily in suppression of pathogens (Cipollini et al. 2012, Ampt et al. 2022). This supports our hypothesis that there are strong species–specific differences in responses to absinthe-invaded soil, although not the responses we hypothesized. Further, it suggests that species within the same functional group may exhibit similar responses to absinthe-invaded soil.

Responses to competition with absinthe also varied among environments and response species and may have implications for future biotic resistance in these ecosystems. While absinthe did have competitive effects on the response species, it was mediated by soil sterilization, rather than allelopathy, contrary to our hypothesis. When absinthe was presumedly microbially inhibited (in unburned, uninvaded soil) it had no competitive effect on any species. When

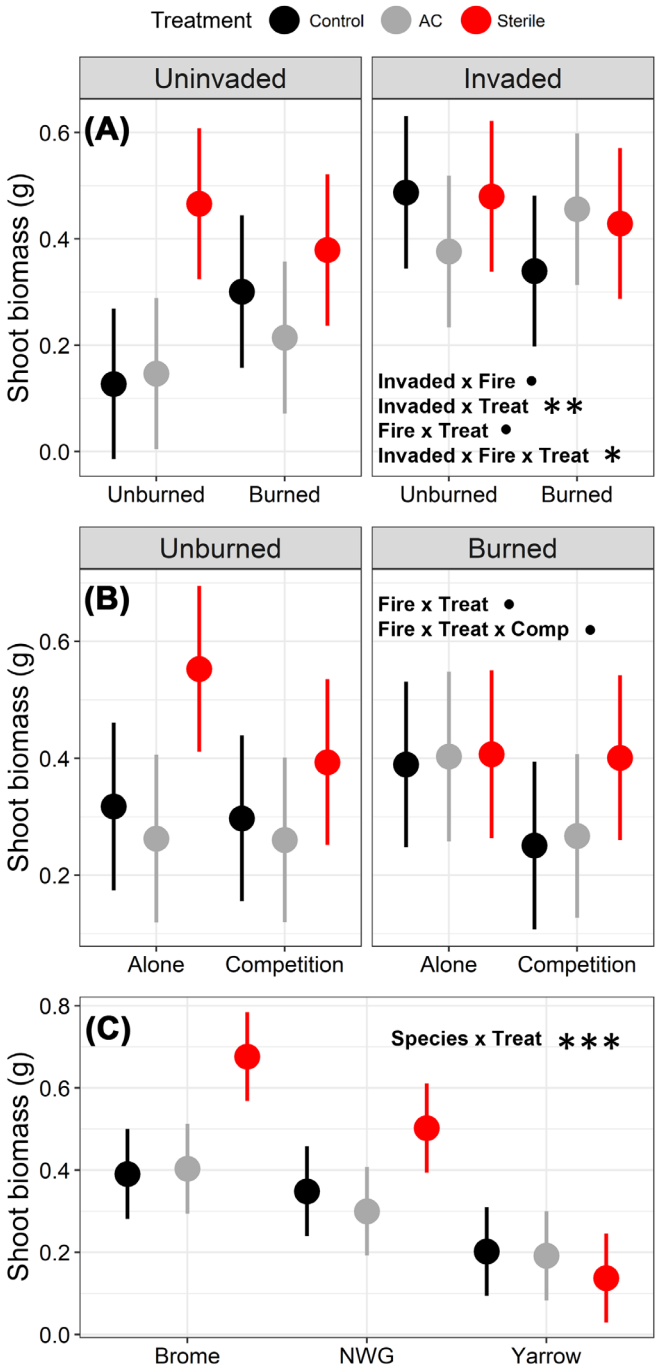


Figure 4. Smooth brome (Brome), northern wheatgrass (NWG) and yarrow shoot biomass responses to prior absinthe invasion, prescribed fire, greenhouse soil treatments, and competition with absinthe. Effects across these three species are shown in (A)–(B), species specific effects are shown in (C). Only significant interactions are shown: invasion × fire × treatment (A), fire × competition × treatment (B), and species × treatment (C). Points and whiskers represent model estimated means and 95% confidence intervals. Significance levels are shown on the figure as follows: ● $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

microbial inhibition was reduced (i.e. following sterilization, prescribed fire), absinthe suppressed response species growth. Prescribed fire may have also indirectly altered the microbial community by increasing forb abundance or nutrient availability (Reinhart et al. 2016, Adkins et al. 2020). This suggests that any disturbance that disrupts the soil microbiome may facilitate absinthe invasion by enhancing its competitive effect, although absinthe itself may not benefit as much as other invaders. Importantly, absinthe had the greatest effect against yarrow and least effect on smooth brome, with northern wheatgrass being intermediate. Further, absinthe facilitated alfalfa growth when competing, presumedly through allelochemical suppression of pathogens, although we did not test for microbial interactions. Combined, this suggests that absinthe is more likely to suppress native plant species, than other invasives, which could lead to invasional meltdown or secondary invasion (Lekberg et al. 2017, Stotz et al. 2020, Chen and van Kleunen 2022) and may explain positive associations between absinthe and other invasives (Wasan et al. 2023).

As an alternative to direct suppression of pathogens, it is also possible that the success of certain invasive species may be explained by the absence of natural enemies or pathogens in the novel range (enemy release hypothesis; Mitchell and Power 2003, Agrawal et al. 2005). For example, when native and introduced *Artemisia* and *Elymus* species were compared in a field trial, native species were more inhibited by pathogens than introduced species (Agrawal et al. 2005). However, in our study, we did not find that absinthe benefited from microbial enemy release as compared to native species. In control soils (unburned, uninvaded), absinthe grew poorly and exhibited no competitive effect on other species, yet responded positively following sterilization. Conversely, sterilization had no effect on the performance of the confamilial species, yarrow. Our results suggest that even if absinthe is released from its natural pathogens, it is still susceptible to pathogens in its novel range (Colautti et al. 2004), however it is likely able to mitigate those pathogens through allelopathic suppression.

We had hypothesized that prescribed fire would enhance the effects of absinthe on other species, mediated both through the soils and competition. The effects of prescribed fire, however, were complex. Fire improved plant growth in uninvaded soil across the response species, but only when the soils were not sterilized. Fire can increase soil nitrogen through the burning of aboveground biomass (Augustine et al. 2014) and we did find that soil nitrogen was greater in uninvaded, burned plots two years post-fire. This increase in nutrient content may have allowed plants to compensate for pathogens, but may have been insufficient to otherwise promote plant growth (Mordecai 2011, Mur et al. 2017, Van de Waal et al. 2023). Alternatively, fire could have altered the microbial community to reduce pathogen loads, as has been found elsewhere (Kardol et al. 2023, Hopkins and Bennet 2024). When competing with absinthe, however, fire had

no effect on plant growth, potentially because competition reduced any benefit from increased nutrients, including the ability of the response species to resist pathogens (Mur et al. 2017, Van de Waal et al. 2023).

Conclusions

Our study indicates the importance of a comprehensive approach in allelopathy studies. By combining a three-year field invasion experiment with a greenhouse study, we tested not only for allelopathic interactions, but also how environmental conditions and microbial effects might alter subsequent plant growth and competition with the invader. Inhibitory microbial feedbacks occurred across species in undisturbed native grassland soil, yet were alleviated following prescribed fire or invasion. We found no evidence for allelopathic inhibition, contrary to findings of previous laboratory bioassays and field studies. As such, future allelopathy studies should also test for alternative explanations for changes in plant performance and competitive interactions, such as microbial effects, environmental factors such as nutrient availability, and age of the invader and response species. We demonstrate that multiple mechanisms of competition and inhibition may be co-occurring with faciliatory effects of the invasive species. In terms of absinthe management, our findings suggest that absinthe is unlikely to successfully invade via allelopathy or have long-term allelopathic effects. Absinthe competes poorly in undisturbed grassland due to microbial inhibition, however it establishes well following disturbance due to release from microbial inhibition, increased nutrients, reduced competition, and other factors (Maw et al. 1985, Wasan et al. 2023). However, given that the negative effects of absinthe are either minimized or reversed for other non-native species, absinthe invasion may be a catalyst for further invasion with greater ecological impacts.

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Author contributions

John Paul Wasan: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (equal); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jonathan A. Bennett**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Visualization (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8pk0p2p3k (Wasan and Bennett 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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