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Biosolarization as an alternative method to inhibit parasitic *Phelipanche ramosa* germination

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Phelipanche ramosa, or branched broomrape, is a parasitic weed that attaches to the roots of host plants and can cause great agricultural losses, from reduced yield to crop termination without harvest. Conventional approaches to manage broomrape infestations include fumigation with toxic compounds, such as methyl bromide. Solarization has been used as well, but can leave a field out of service for entire seasons. Biosolarization is an alternative pest management strategy with a shorter timeframe that can reduce the need for fumigants and preplant herbicides by amending soil with organic matter, covering with a clear tarp, and irrigating. Weed seeds subjected to biosolarization experience a variety of stresses –including biocidal organic acids, high temperatures, and low oxygen– that can prevent future germination. This study evaluated the application of biosolarization with two different amendments, three amendment rates, and three temperatures for reduction of *P. ramosa* germinability. Simulated biosolarization was carried out in anaerobic bioreactors of wetted and amended soil with seeds incorporated. Tomato pomace and spent mushroom substrate were used as the organic matter amendments. Soil pH, electrical conductivity, and production of biocidal organic acids were evaluated before and after biosolarization, alongside germination capacity of *P. ramosa* seeds. Soil metrics of biosolarization treatments were compared to unamended, solarized soil and seed germination capacity was compared to that of untreated, control seeds. Broomrape germination is triggered by strigolactone, a plant hormone released into the rhizosphere. Therefore, a strigolactone analog was used to test the germinability of the treated seeds in absence of a host. To isolate the effects of biocidal organic acid exposure on broomrape germinability, seeds were also exposed to the acids produced during biosolarization, but without the added thermal and low oxygen stresses. The results suggest that biosolarization is an effective method to reduce *P. ramosa* germinability by >99% with amendment rates as low as 1.0% by dry weight and temperatures of 35 °C, which can inform future validation in field studies. Use of biosolarization may help protect the production of host plants on an infested field, while reducing the need for toxic compounds or lengthy treatments.

KEYWORDS

biosolarization, broomrape, pest management, soil, sustainable agriculture, weeds

1 Introduction

Weed management consistently challenges both conventional and organic farmers. Currently, conventional weed management relies heavily on application of herbicides and, in some crops, fumigation. In 2020, 12 million kilograms of herbicides and 17 million kilograms of fumigants were applied in California (DPR, 2022). In contrast, organic growers rely more on manual weed removal, tillage, crop rotations and cover cropping (DeDecker et al., 2014; Finney and Creamer, 2008; Gallandt, 2014). Consequently, organic farms experience greater weed stresses than conventional ones (Mwangi et al., 2024). Furthermore, surveys of organic farmers have reported weed control and weed-related production losses as the greatest obstacles to agricultural production and farm profitability (Snyder et al., 2022; Walz, 2004). For broomrape management specifically, there is currently ongoing research for chemical management (Fatino and Hanson, 2025), but not for organic growers. Biosolarization could address this need.

Phelipanche ramosa, or branched broomrape, is listed as a Category A noxious weed by the California Department of Food and Agriculture (CDFA) and can cause devastating losses for farmers because fields in which branched broomrape has been identified are subject to regulatory action (CDFA, 2021; Osipitan et al., 2021; Rivas, 2023). Broomrapes are obligate root parasites, meaning that they require a host to germinate and survive. Strigolactone, a hormone secreted from plant roots, is recognized and hydrolyzed in broomrape seeds, triggering germination and radicle growth until it encounters and attaches to the host root (Joel et al., 2013). The optimum germination temperature for *P. ramosa* is 20 °C (Gibot-Leclerc et al., 2004). The weed can reduce aboveground biomass, leaf chlorophyll content, and photosynthetic rate of the host plant, greatly inhibiting its growth and productivity (Mauromicale et al., 2008). In California, broomrape has been recently identified in Yolo, Solano and San Joaquin counties (Osipitan et al., 2021; Rivas, 2023).

The CDFA guidance for broomrape control is fumigation with methyl bromide (CDFA, 2009, 2022). Methyl bromide was classified as a Class 1 Ozone Depleting Substance (ODS) in the 1987 Montreal Protocol and was subjected to a 100% phaseout by 2005 and 2015 in developed and developing countries, respectively (EPA, 2025b; UNEP). Nonetheless, exceptions for methyl bromide application still exist for “critical uses” and “quarantine and preshipment uses,” which are authorized by the Environmental Protection Agency (EPA) and the Parties to the Montreal Protocol (EPA, 2025c). Other fumigants and herbicides, such as chloropicrin, 1,3-dichloropropene, and rimsulfuron have also been used to suppress broomrape (Abdel-Aaty et al., 2020; Fatino and Hanson, 2025; Lombardo et al., 2012). However, application of these products is regulated (DPR, 2024a, 2024b; EPA, 2025a, 2025c).

Fumigants and herbicides are costly, highly regulated, can have negative environmental and health consequences, and are not available to organic producers (Choi et al., 2021; EPA, 2008; Kaushik, 2021; Reed and Lim, 2014; von Ehrenstein et al., 2019). Alternative methods of weed control, such as biosolarization, may be safer for the person handling them and the ecosystem to which they are applied.

In an attempt to move away from the use of these chemicals, solarization has been studied as an alternative method for broomrape suppression. Solarization is similar to biosolarization but does not incorporate organic matter amendments into the soil, thereby relying mainly on passive solar heating as the pest inactivation mechanism (D’Addabbo et al., 2010). Treatments that have inactivated at least 90% of broomrape seeds solarize soil for 50 to 60 days to achieve these results (Lombardo et al., 2012; Mauromicale et al., 2005; Mauro et al., 2015; Sauerborn et al., 1989).

Biosolarization is an alternative pre-plant method of soil pest suppression that can be used to manage not only weeds, but also other pests such as phytoparasitic nematodes and fungal pathogens (Achmon et al., 2017; Pastrana et al., 2022; Shea et al., 2022). This is accomplished by amending soil with labile organic matter, irrigating, and mulching the soil with transparent film. Food industry byproduct streams, such as tomato pomace and rice bran, can be used as amendments for biosolarization (Achmon et al., 2016; Khadka et al., 2020). The addition of organic matter provides an energy source for microorganisms in the soil and on the amendments, while the irrigation displaces oxygen in the soil and promotes fermentation to create a micro-aerobic or anaerobic environment (Simmons et al., 2013, 2016). The transparent film helps maintain the anaerobicity of the covered soil, while simultaneously trapping heat from solar radiation to increase the temperature of the soil (Al-Karaghoul et al., 1990). Weed control defined as >95% seed inactivation has been accomplished after eight-day biosolarization periods (Achmon et al., 2017).

Fermentation of the organic matter amendment in the soil produces a variety of organic acids with biopesticidal potential (Fernandez-Bayo et al., 2020; Simmons et al., 2016). In addition to the thermal stress, accumulation of these acids can also be phytotoxic, so biosolarization has the potential to inactivate weed propagules without the use of synthetic chemicals while providing an avenue for valorization of a food industry waste stream (Achmon et al., 2017; Shea et al., 2021). Tomato pomace, primarily skins and seeds remaining after tomato juice separation from the fruit, is a main by-product of tomato processing, and has been used as an amendment for biosolarization (Achmon et al., 2017; Osipitan et al., 2022). Production of tomato pomace in the United States has been predicted to be between 143,000 and 476,000 metric tons annually (Vidyarthi and Simmons, 2020). Spent mushroom substrate (SMS) is the main by-product of mushroom production and has been used as an amendment for improved soil characteristics, including fertility and structure (Barua et al., 2024; Medina et al., 2012; Othman et al., 2020). SMS can be composed of a variety of materials, including cereal straw, coffee pulp, manure, rice bran, soybean hulls and hardwood sawdust, depending on what is available to the grower (Barua et al., 2024; Paredes et al., 2009; Salmones et al., 2005). Approximately 5 kilograms of substrate are needed for each kilogram of mushroom produced, and mushroom consumption continues to steadily increase (FAO, 2023; Jordan et al., 2008). Currently, tomato pomace and SMS have been used as feed supplements for livestock and for the extraction of bioactive compounds or enzymes for other food and industrial uses (Aldoori et al., 2015; Choo and Saik, 2021; Chou et al., 2013; Correia et al., 2017; Fazaeli et al., 2014; Hosseini-Vashan et al., 2016; Kwak et al.,

2015; Lim et al., 2013; Lu et al., 2019; Previtera et al., 2016; Simitzis and Deligeorgis, 2018; Zhu et al., 2012). However, most of these uses require additional processing steps. Biosolarization can provide a way to use these by-products directly.

Biosolarization of short duration, such as the eight-day periods used here, has not been studied as a way to control *P. ramosa* infestations. The objective of this study was to identify a biosolarization method to inhibit *P. ramosa* germination by $\geq 99\%$ that does not rely on conventional pesticides while delivering more rapid inactivation than solarization.

2 Materials and methods

2.1 Soil, amendments, and seeds

The soil used was a Yolo series loam soil. Soil was collected from the Armstrong Plant Pathology Research Field in Davis, CA (collection coordinates 38°31'07.9"N 121°46'07.8"W). Soil was sieved through a 4 mm sieve before use. Volatile solids content of the soil was 0.03 g/g dry weight, pH was 7.02 and EC was 421.14 $\mu\text{S}/\text{cm}$. Soil texture was previously reported as 32% sand and 25% clay (USDA NRCS). Spent mushroom substrate (SMS) was sourced from Goal Zen Mushroom in Dixon, CA and was composed of 50% soybean hulls and 50% oak sawdust by dry weight. Fresh tomato pomace was sourced in August 2023 during the tomato harvest season from a commercial tomato processing facility in the California Central Valley. Tomato pomace was solar dried and SMS was oven dried (40 °C for 3 days) to their storage moisture contents of 5.3% and 4.8%, respectively. The volatile solids content of both amendments was 0.97 g/g dry weight.

The *P. ramosa* seeds used here were collected from plants in a tomato field in Woodland, CA in August/September 2023. Seed capsules were collected at maturity and transported to the research site under appropriate California plant pest permit conditions. The capsules were then dried at room temperature, crushed, and sifted for seed retrieval. Seeds were then stored in the dark at 4 °C until use.

2.2 Simulated biosolarization

A lab-scale soil bioreactor system was used to simulate field biosolarization conditions. The bioreactors were 8-ounce wide-mouth glass jars with tin-plated steel lids (Kerr). Tomato pomace (TP) and SMS were amended into soil by dry weight percentage. Water was added to each bioreactor to reach field capacity of the amended soil and simulate irrigated field conditions (see section 2.2.1) (Achmon et al., 2016). Amended soil was incubated for 8 days in bioreactors at different temperatures to test potential efficacy of the treatment in different climates. All treatments had 5 replicates. Each treatment and replicate was assigned and labeled with a randomized code for the duration of the experiment.

The first experiment included a constant amendment rate of either TP or SMS (1.5% by dry weight) with three incubation temperature treatments above the optimum *P. ramosa* germination temperature (25, 35 and 45 °C) for a typical biosolarization duration

of 8 days (Achmon et al., 2017; Pastrana et al., 2022). An unamended control was also included for each temperature as a simulated solarization treatment. The second experiment had a constant incubation temperature (35 °C) for 8 days and three amendment rate treatments (0.5, 1.0, and 1.5%) of either TP or SMS, as well as an unamended control. These three rates correspond to field amendment rates from 9 to 27 tons per hectare.

For preparation of the bioreactors, they were filled halfway with the wetted and amended soil, a premade seed pouch was added, and then the rest of the amended soil was added to fill the bioreactor. For preparation of weed seed pouches, seeds were removed from 4 °C storage and added to a 100-micron mesh nylon bag (Dulytek). One pouch was made for each replicate by adding 0.7 cm³ of *P. ramosa* seeds to each bag.

2.2.1 Moisture content and field capacity

Moisture content (MC) and field capacity (FC) of the soil and amendments were determined to inform the calculation of the water needed in the bioreactors to simulate the condition of the soil after irrigation to initiate biosolarization (Haber et al., 2022). Water content was determined gravimetrically by drying the soil and amendments to constant weight in a drying oven at 105 °C and comparing against the initial fresh weight. Moisture content was calculated on a wet basis using Equation 1.

$$\text{MC} (\%) = \frac{\text{water content (g)}}{\text{initial fresh weight (g)}} \times 100 \quad (1)$$

Field capacity was estimated by saturating a known amount of dry soil or amendment with water and allowing it to drain freely for 24 hours. The weight of the soil after the water content stabilized and the weight of the oven-dried soil were used to calculate the field capacity of the material using Equation 2. Field capacity of the amended soil (FC_{AS}) was estimated using Equation 3.

$$\text{FC} (\%) = \frac{\text{fresh weight} - \text{dry weight (g)}}{\text{dry weight (g)}} \times 100 \quad (2)$$

$$\text{FC}_{\text{AS}} = \text{FC}_{\text{amendment}} \times \text{amendment rate} + \text{FC}_{\text{soil}} \times (1 - \text{amendment rate}) \quad (3)$$

2.2.2 pH, electrical conductivity and biocidal organic acid analysis

Soil from each bioreactor was sampled on Day 0 and Day 8 of biosolarization. Two 5-gram samples were taken from each bioreactor for pH, electrical conductivity (EC) and biocidal organic acid (BOA) analysis. For pH and EC determination, aqueous extracts of each sample were made by combining water and soil in a 1:1 ratio by mass, followed by vortexing (Fisher Scientific Analog Vortex Mixer) at 3,200 rpm for 30 seconds and centrifugation (Sorvall Legend XTR) at 4,800xg for 15 minutes. Soil pH and EC were measured for each sample in the supernatant.

For BOA analysis, the supernatant was filtered into 2-mL glass HPLC vials using a disposable syringe and a 0.22-micron polytetrafluoroethylene (PTFE) filter (Thermo Scientific). BOAs

were identified and quantified in the filtrate via HPLC (Agilent 1260 Infinity II) using a sulfonated styrene-divinylbenzene column (Agilent Hi-Plex H) and a multiple wavelength detector (Agilent 1260 Infinity II MWD). The mobile phase was 5mM sulfuric acid (Honeywell Research Chemicals) at a flow rate of 0.6 mL/min. For each sample, 20 μ L was injected into the column (column temperature was 60 °C) with a run time of 30 minutes per injection. Citric, malic, formic, acetic, lactic, propionic, butyric and isobutyric acids were detected at 210 nm and succinic acid was detected at 195 nm (Ball et al., 2011; Fernandez-Bayo et al., 2020). Seven-point standard curves were produced with dilutions of each acid mentioned above (Sigma Aldrich, Fisher Chemical, and MP Biomedicals) from 31.25 to 2,000 μ g/mL in water.

2.3 Biocidal organic acid formulation and incubation

An experiment was conducted to directly examine the effects of BOAs on *P. ramosa* seed germination inhibition. BOA treatments were made using HPLC-grade reagents at concentrations observed in the soil amended with 1.0% TP, 1.0% SMS, 1.5% TP, and 1.5% SMS, all incubated at 35 °C. These treatments were chosen because they reduced *P. ramosa* germinability by >99%, while also outperforming the unamended control of the same temperature (the added 45 °C stress led to >99% reduction even in unamended samples, see section 3). Organic acid stocks described in section 2.2.2 were diluted in water and combined to reach the target concentrations found via HPLC (Table 1). A solution of 2,000 μ g acetic acid/mL was tested as a positive control for germination inhibition and a treatment of water was included to identify any effects on *P. ramosa* seeds from exposure to the water in the solutions.

Before exposure to BOA solutions, seeds were sanitized as described in section 2.4. After rinsing with water to remove the sanitizer, seeds were transferred to a 60-mm petri plate lined with filter paper (Whatman No. 1) and 0.6 mL of the corresponding

BOA solution or water was added to each plate before sealing the plate with Parafilm (Amcor). All treatments had 5 replicates. Plates were incubated at 25 °C for 8 days, then removed from the incubator, opened, and allowed to dry for volatilization of the acids. Once dry, 0.6 mL of water was added to each plate. At this time, control plates were made with untreated control seeds and all plates were then subjected to the 21-day germination bioassay procedure (see section 2.4).

2.4 Germination bioassays

After simulated biosolarization, seed pouches were retrieved from bioreactors and prepared for germination assays (Hosseini et al., 2025). Retrieved seed pouches were rinsed with tap water to remove excess soil from the outer surface of the pouch. Seeds were then removed from the pouches, surface sanitized with 0.1% MG 4-Quat Sanitizer (Morgan Gallacher, Inc), and rinsed again with deionized water. Wet seeds were then added to a 60-mm petri plate lined with filter paper (Whatman No. 1). Control plates were made with untreated seeds from the seed stock that were surface sanitized and rinsed in the same way to determine the baseline germination capacity of the seed stock. Plates were incubated at 25 °C in the dark for preconditioning. After 11 days, plates were taken out of the incubator and 0.6 mL of 10^{-5} M solution of GR-24 strigolactone analog (PhytoTech Labs) was added to each plate to trigger germination in the absence of a host. Plates were then returned to the incubator at 25 °C in the dark for 10 more days.

Germination was quantified after the 21-day incubation by counting the number of germinated and ungerminated seeds to determine germination capacities using Equation 4. Seeds were considered germinated when a protruding radicle was visible. The germination capacity of untreated control seeds (germination capacity₀) was used to determine germination inhibition using Equation 5.

$$\text{Germination capacity (\%)} = \frac{\text{germinated seeds}}{\text{total seeds}} \times 100 \quad (4)$$

$$\text{Germination inhibition (\%)} =$$

$$= \left(1 - \frac{\text{germination capacity}}{\text{germination capacity}_0}\right) \times 100 \quad (5)$$

2.5 Statistical methods

For pH, EC, germination capacity, and BOA content, comparison of treatment means was conducted via one-way ANOVA. Where significant differences ($P \leq 0.05$) were found, Tukey's honest significant difference (HSD) *post-hoc* test was used to compare all treatments to each other and the controls. Main and interaction effects of biosolarization process variables were evaluated using multiway ANCOVA for pH, BOA content and germination capacity. Two-way ANOVA with repeated measures was used to determine the effects of treatment and multiple timepoints on soil pH. Statistical analyses were performed using JMP 18 software (SAS Institute Inc.).

TABLE 1 Composition of solutions used for the biocidal organic acid (BOA) exposure experiment.

Treatment	BOA	BOA concentration (μ g/mL)
Replication of 1.5% TP incubated at 35 °C	Acetic Butyric	586 310
Replication of 1.5% SMS incubated at 35 °C	Acetic Butyric	316 61
Replication of 1.0% TP incubated at 35 °C	Acetic Butyric Propionic	592 225 45
Replication of 1.0% SMS incubated at 35 °C	Acetic	253
2,000 μ g/mL	Acetic	2,000
Water	–	0

The first four treatments replicate BOA profiles in biosolarized soil amended with tomato pomace (TP) or spent mushroom substrate (SMS).

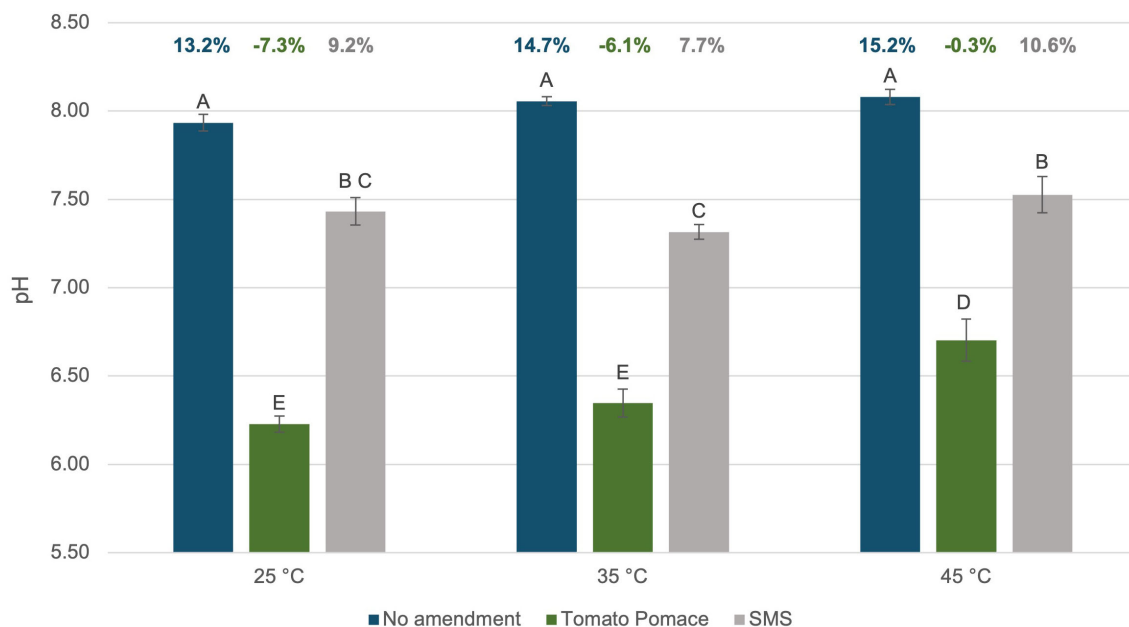


FIGURE 1

Soil pH after simulated biosolarization of soil amended with 1.5% tomato pomace, 1.5% spent mushroom substrate (SMS), or no amendment. Percentage values above each bar correspond to the change in pH from day 0 to day 8. Soil was incubated at 25, 35 and 45 °C. Values that do not share a letter are significantly different as determined by Tukey's HSD ($P \leq 0.05$). Error bars represent ± 1 standard deviation and $n=5$.

3 Results

3.1 Soil pH

Changes in pH during biosolarization varied with temperature, amendment type, and amendment rate. Amendment and incubation temperature showed significant main effects on soil pH at the end of biosolarization ($P < 0.0001$ for both) and the two variables had a significant interaction effect ($P < 0.0001$, [Supplementary Table 1](#)), as the effect of amendment type on final pH was more pronounced at lower temperatures.

Tomato pomace-amended soil consistently had significantly lower pH, ranging from 6.23 to 6.70, than SMS and unamended treatments after biosolarization at 25, 35 and 45 °C ($P < 0.05$, [Figure 1](#)). Unamended soil had significantly higher pH, from 7.93 to 8.08, than SMS and tomato pomace treatments at all temperatures ($P < 0.05$, [Figure 1](#)). SMS-amended soil and unamended soil pH increased during incubation at the three temperatures tested. After incubations at 25 and 35 °C, only soil amended with tomato pomace had a lower pH compared to the initial pH on day 0. By day 8 of the

45 °C biosolarization, none of the treatments had a lower pH than that of day 0.

Two-way ANOVA with repeated measures confirmed that treatment, timepoint and their interaction had significant effects on soil pH ([Table 2](#)), as the magnitude of the pH change over time depended on the biosolarization treatment ([Figure 1](#)).

At 35 °C, amendment type and amendment rate both had significant effects on final soil pH ($P < 0.0001$ for both) and a significant interaction effect ($P < 0.0001$, [Supplementary Table 2](#)). The difference between the pH of soils with different amendment types increased with increasing amendment rate. Within the six treatments of soil amended with tomato pomace or SMS at 0.5, 1.0 or 1.5%, all except SMS 0.5% had significantly lower pH than that of the unamended soil at the end of biosolarization ($P < 0.05$, [Figure 2](#)). Within each amendment, there was a significant trend of decreasing day-8 pH with increasing amendment rate. Two-way ANOVA confirmed that treatment, timepoint and their interaction had significant effects on soil pH ([Table 3](#)). The magnitude of the pH changes over time varied by biosolarization treatment ([Figure 2](#)).

As demonstrated in the experiment testing different temperatures ([Figure 1](#)), the pH of unamended soil increased after biosolarization. This was evident again when testing different amendment rates, as the pH of unamended incubated soil increased from 6.92 to 8.12.

When soil was amended with either TP or SMS at a rate of 0.5% by dry weight, pH increased after biosolarization at 35 °C. Soil with 0.5% tomato pomace produced a smaller increase in pH, as seen by the smaller percent change of 9%, compared to 17% for both the unamended and 0.5% SMS treatments ([Figure 2](#)). After biosolarization with 1.0% amendment, pH of soil increased for SMS-amended soil but remained the same for tomato pomace-amended soil. The pH of soil amended with 1.5% SMS increased

TABLE 2 Effect tests of treatment and timepoint on soil pH before and after simulated biosolarization at different temperatures determined via two-way ANOVA with repeated measures.

Source	Degrees of freedom	F Ratio	Prob > F
Treatment	8	534.7709	<0.0001*
Timepoint	1	1442.777	<0.0001*
Timepoint*Treatment	8	300.0377	<0.0001*

Asterisks indicate statistically significant values ($P \leq 0.05$).

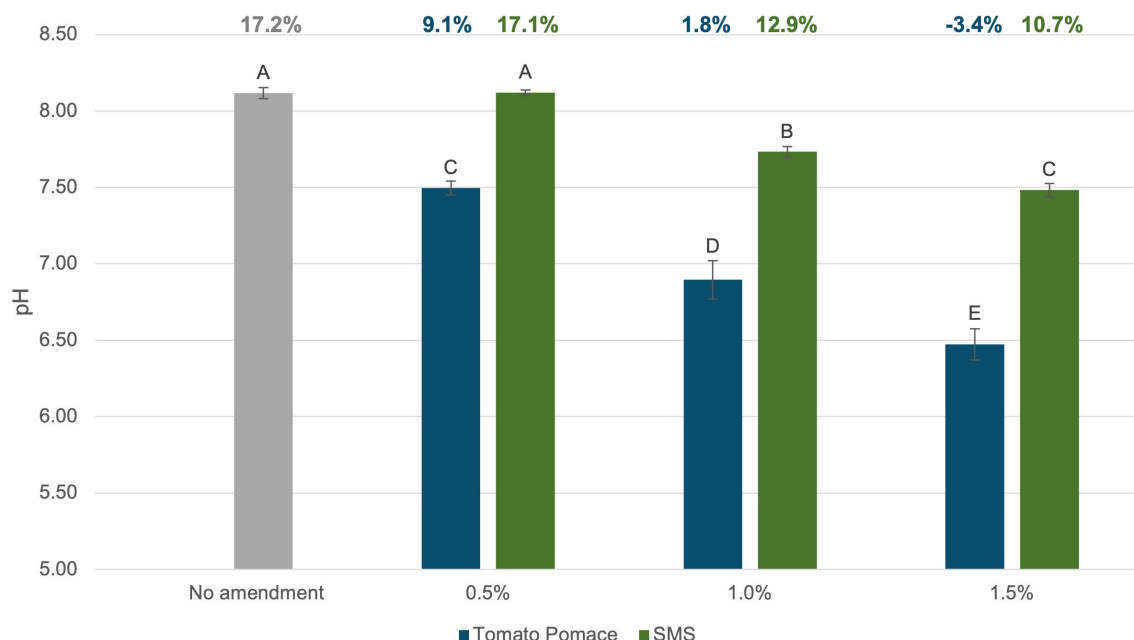


FIGURE 2

Soil pH after simulated biosolarization of soil amended with tomato pomace (TP), spent mushroom substrate (SMS), or no amendment. Percentage values above each bar correspond to the change in pH from day 0 to day 8. Amendments were incorporated at rates of 0.5, 1.0 and 1.5%. Values that do not share a letter are significantly different as determined by Tukey's HSD ($P \leq 0.05$). Error bars represent ± 1 standard deviation and $n=5$.

from 6.76 to 7.48. The pH of soil amended with 1.5% tomato pomace decreased after biosolarization from 6.70 to 6.47, making it the only treatment to have lower pH on day 8 than day 0.

3.2 Electrical conductivity

Electrical conductivity (EC) of tomato pomace-amended soil was significantly greater ($P \leq 0.05$) than unamended and SMS-amended soil at all temperatures and amendment rates. Of the different temperatures tested, 35 °C caused the greatest increase in EC for both amendments (Figure 3). Within each temperature, the different amendment types had significantly different EC ($P \leq 0.05$). Tomato pomace treatments EC ranged from 851 to 1196 $\mu\text{S}/\text{cm}$, followed by SMS with 491 to 671 $\mu\text{S}/\text{cm}$, and unamended with 184 to 306 $\mu\text{S}/\text{cm}$.

When varying the amendment rates, EC increased with increasing amendment rate for both amendments (Figure 4). For each rate, tomato pomace had significantly greater EC than SMS ($P \leq 0.05$). Tomato pomace treatments EC ranged from 694 to 1021 $\mu\text{S}/\text{cm}$, followed by SMS with 268 to 586 $\mu\text{S}/\text{cm}$, and unamended with 204 $\mu\text{S}/\text{cm}$.

TABLE 3 Effect tests of treatment and timepoint on soil pH before and after simulated biosolarization with varying amendment rates determined via two-way ANOVA with repeated measures.

Source	Degrees of freedom	F Ratio	Prob > F
Treatment	6	437.6362	<0.0001*
Timepoint	1	2099.178	<0.0001*
Timepoint*Treatment	6	203.8912	<0.0001*

Asterisks indicate statistically significant values ($P \leq 0.05$).

3.3 Biocidal organic acid production

Amendment and incubation temperature both showed significant main effects on soil biocidal organic acid (BOA) concentration ($P < 0.0001$ for both) and the two variables had a significant interaction effect ($P = 0.0002$, Supplementary Table 3), as the differences in BOA content among treatments decreased with increasing temperature. All treatments produced a significant increase in BOAs during biosolarization except for the unamended soil, which did not have BOAs before or after biosolarization.

Tomato pomace treatments consistently had the greatest concentration of BOAs across all temperatures and amendment rates (Figures 5, 6). In soils amended with 1.5% tomato pomace, BOA production was highest at 25 and 35 °C, with 937 and 950 $\mu\text{g}/\text{g}$ dry soil, respectively, followed by 697 $\mu\text{g}/\text{g}$ dry soil for the 45 °C incubation (Figure 5). The BOA content from the 45 °C tomato pomace treatment was significantly lower from the other two temperatures. Total BOA concentrations in the SMS-amended soil were lower compared to tomato pomace for the three temperatures tested, with 305, 376 and 284 $\mu\text{g}/\text{g}$ dry soil for 25, 35 and 45 °C, respectively. BOAs were not detected in unamended soil after incubation at any temperature.

The main acid present in all treatments was acetic acid, ranging from 62.5% of total BOAs found in tomato pomace 45 °C to 100.0% of the total BOAs present in SMS 25 °C and SMS 45 °C. Butyric acid was also present in all treatments except those that only had acetic acid. Tomato pomace-amended soil incubated at 45 °C was the only treatment with detectable amounts of additional acids: formic and lactic.

When varying the rate of incorporation for tomato pomace and SMS, amendment type and rate both showed significant main effects on soil BOA content ($P < 0.0001$ for both) but the two

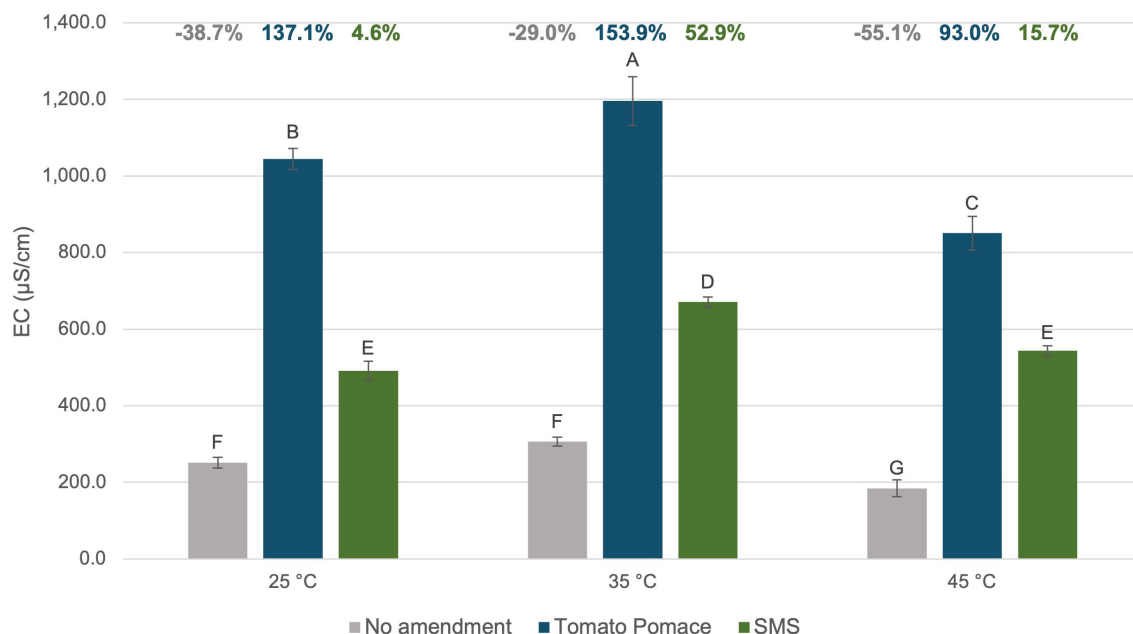


FIGURE 3

Electrical conductivity (EC) of soil following biosolarization of soil amended with 1.5% tomato pomace, 1.5% spent mushroom substrate (SMS), or no amendment. Soil was incubated at 25, 35 and 45 °C. Percentage values above each bar correspond to the change in EC from day 0 to day 8. Values that do not share a letter are significantly different as determined by Tukey's HSD ($P \leq 0.05$). Error bars represent ± 1 standard deviation and $n=5$.

variables did not have a significant interaction effect ($P = 0.4739$, [Supplementary Table 4](#)), suggesting that the effect of amendment rate did not depend on the type of amendment.

The higher amendment rates (1.0 and 1.5%) of each amendment led to significantly greater BOA production than the 0.5% rate. At the end of the 35 °C biosolarization, 1.0 and 1.5%

tomato pomace had mean BOA concentrations of 862 and 954 µg/g dry soil, respectively, while the 0.5% tomato pomace treatment had 481 µg/g dry soil ([Figure 6](#)). The 1.0 and 1.5% SMS treatments had 253 and 371 µg/g dry soil, respectively, while there was no BOA production in the 0.5% SMS treatment. Again, there was no BOA production in the unamended soil.

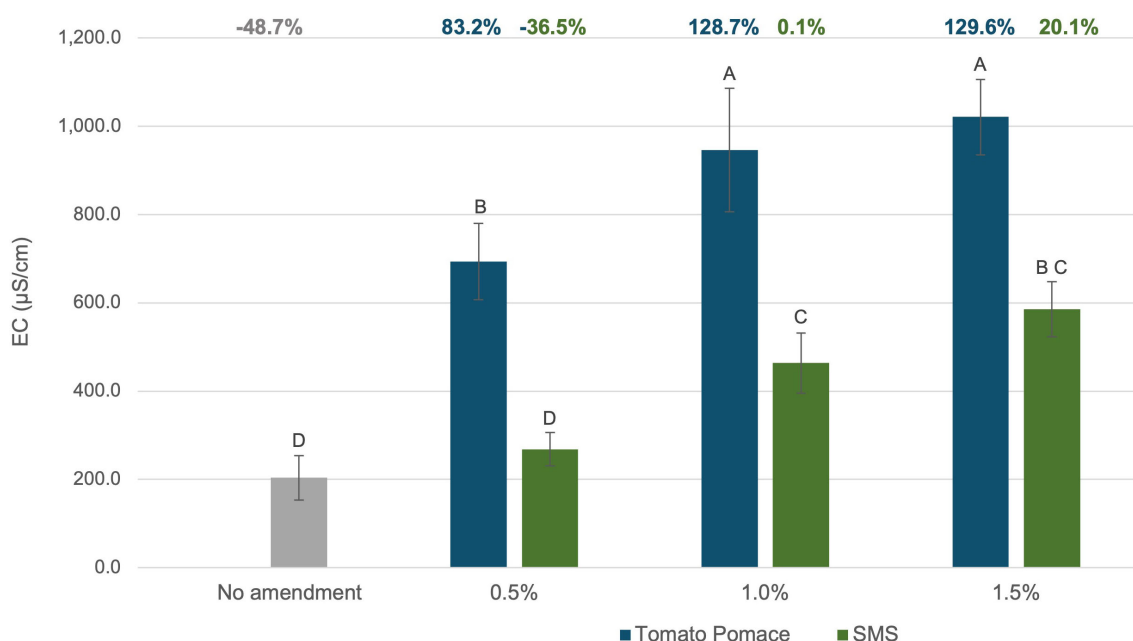


FIGURE 4

Electrical conductivity (EC) of soil after 8 days of simulated biosolarization of soil amended with tomato pomace, spent mushroom substrate (SMS), or no amendment. Amendments were incorporated at rates of 0.5, 1.0 and 1.5% by dry weight. Percentage values above each bar correspond to the change in EC from day 0 to day 8. Values that do not share a letter are significantly different as determined by Tukey's HSD ($P \leq 0.05$). Error bars represent ± 1 standard deviation and $n=5$.

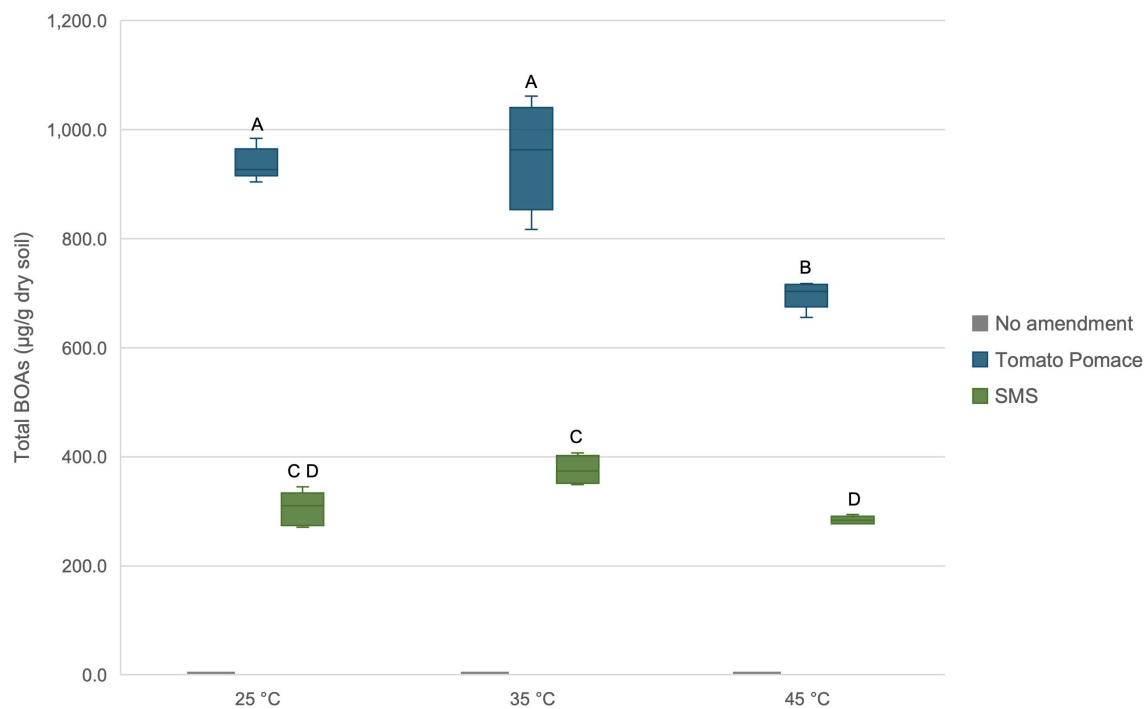


FIGURE 5

Biocidal organic acid (BOA) content after biosolarization of soil amended with 1.5% tomato pomace, 1.5% spent mushroom substrate (SMS), or no amendment. Soil was incubated at 25, 35 and 45 °C. Values that do not share a letter are significantly different ($P \leq 0.05$). ANOVA and Tukey's HSD were performed on treatments with non-zero values. Error bars represent ± 1 standard deviation and $n=5$.

Acetic acid was again the main acid present in all treatments, ranging from 67% of total BOAs in the tomato pomace 1.5% treatment to 100% in SMS 1.0% and 1.5%. The remainder of the acids were butyric and propionic in the tomato pomace-amended soils.

3.4 *Phelipanche ramosa* germination

Seed germination capacity was determined after the 8-day simulated solarization or biosolarization. Amendment and incubation temperature showed significant main effects on *P. ramosa* germination ($P < 0.0001$ for both) and the two variables had a significant interaction effect ($P = 0.0009$, [Supplementary Table 5](#)), as the effect of amendment type on germination capacity was more pronounced with lower temperatures ([Figure 7](#)). There were significant differences among treatments at 25 and 35 °C, but none at 45 °C ($P \leq 0.05$). All three temperatures tested significantly reduced *P. ramosa* germinability compared to the untreated controls, regardless of amendment, including the unamended soil. The untreated control seeds had a mean germination capacity of 88.1%.

The 25 °C incubation of unamended and amended soil led to germination capacities between 3.3 and 26.8%, with the tomato pomace and unamended treatments corresponding to the lowest and highest rates, respectively ([Figure 7](#)). The seeds in the SMS-amended soil incubated at 25 °C had a germination capacity of 20.8%. This corresponds to germination inhibition of 70.2, 76.9, and 96.3% for unamended, 1.5% SMS and 1.5% tomato pomace, respectively.

After the 35 °C simulated biosolarization, both amendments led to lower germination capacity, while that of the unamended treatment remained similar to the 25 °C incubation. Seeds in the unamended soil, 1.5% SMS and 1.5% tomato pomace had germination capacities of 18.8, 0.2, and 0.7%, respectively.

The 45 °C biosolarization decreased germination capacity even further, compared to 25 and 35 °C, to 0.4, 0.0 and 0.1% for unamended, 1.5% SMS and 1.5% tomato pomace, respectively. This corresponds to germination inhibition of >99% for all 45 °C treatments and both amended 35 °C treatments.

The three amendment rates of both amendments tested resulted in significantly lower broomrape germination when compared to the control seeds or the unamended treatment ([Figure 8](#)). Within each amendment, broomrape germination decreased with increasing amendment rates, but no significant differences were found among the amended treatments. Germination capacity of the seeds from amended treatments ranged between 0.0 and 2.1% ([Figure 8](#)), which correspond to germination inhibition of 97.6 to 100.0% with SMS 0.5% and SMS 1.5% producing the lowest and highest inactivation, respectively. Tomato pomace 1.0%, tomato pomace 1.5%, SMS 1.0% and SMS 1.5% all inhibited *P. ramosa* germination by $\geq 99\%$. The unamended treatment had broomrape seed germination of 9.4%, while the untreated controls had 86.0% seed germination. Statistical analysis (ANCOVA) of results from only the amended treatments showed that amendment rate had a significant main effect on germination capacity ($P = 0.0006$), while amendment type did not ([Supplementary Table 6](#)).

The BOA exposure experiment isolated the effect of exposure to the acids produced during biosolarization on *P. ramosa* seeds. Individual BOA profiles did not have a significant effect on

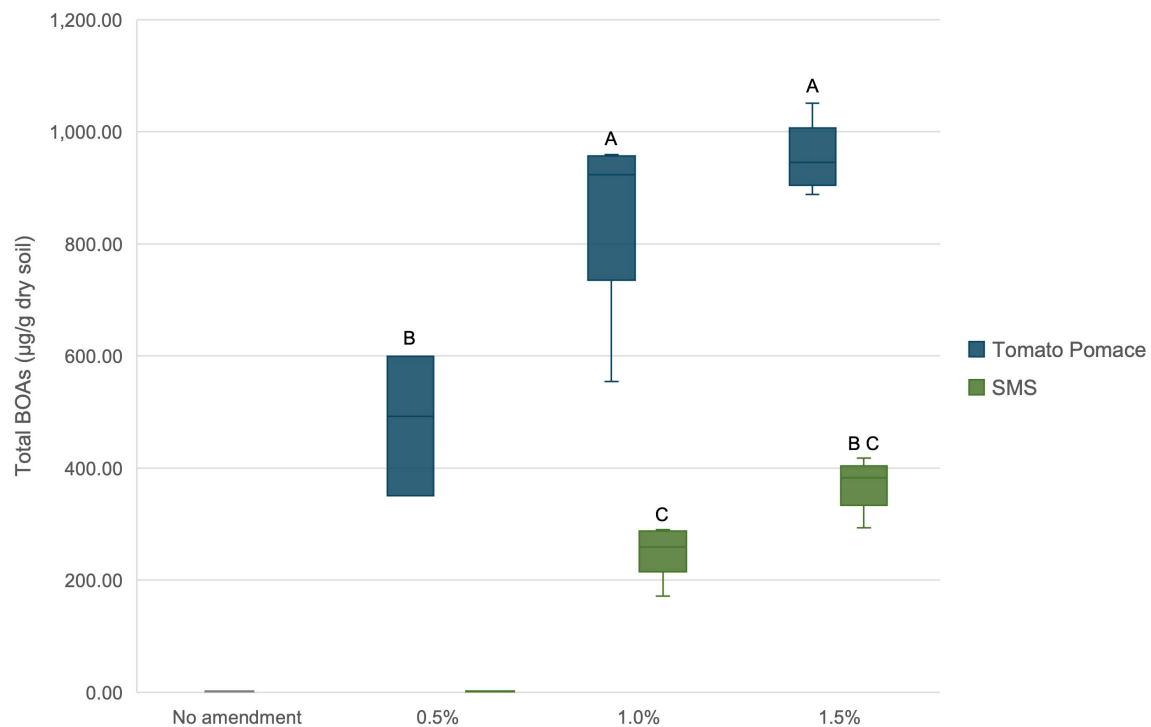


FIGURE 6

Total biocidal organic acid (BOA) content after simulated biosolarization at 35°C of soil amended with tomato pomace, spent mushroom substrate (SMS), or no amendment. Amendments were incorporated at rates of 0.5, 1.0 and 1.5% by dry weight. Values that do not share a letter are significantly different ($P \leq 0.05$). ANOVA and Tukey's HSD were performed on treatments with non-zero values. Error bars represent ± 1 standard deviation and $n=5$.

germination capacity compared to the treatment of only water. However, treatments were grouped to compare the effect of biosolarization BOA profiles to the water treatment and the negative control, which showed that biosolarization acid

production significantly decreased broomrape seed germination capacity ($P < 0.0001$ for the difference observed between biosolarization and the control and $P = 0.0066$ for the difference between biosolarization and seeds exposed to pure water, Figure 9).

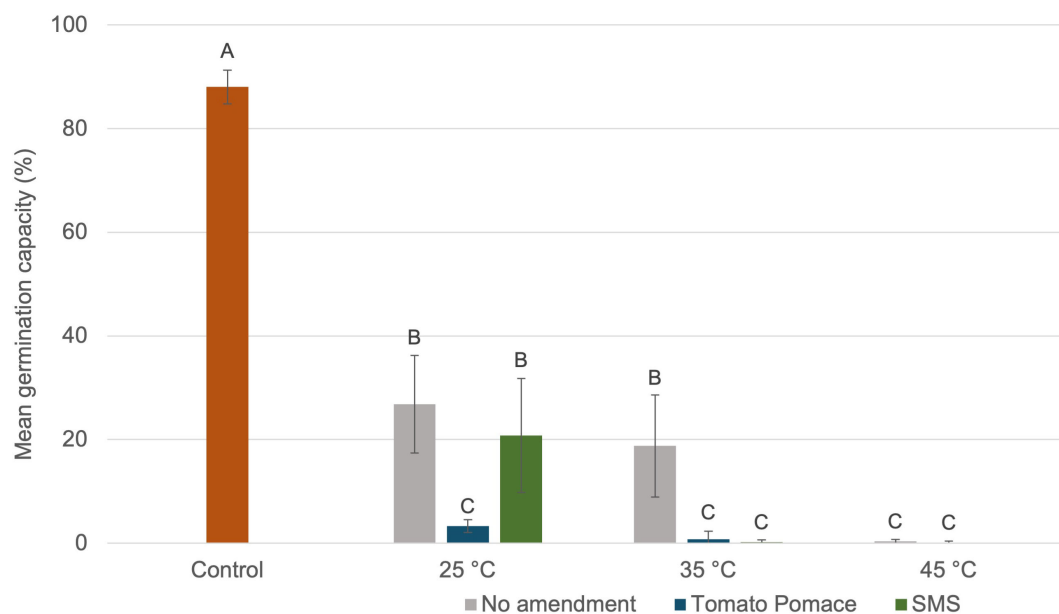


FIGURE 7

Mean germination capacity of branched broomrape seeds following simulated biosolarization of soil at 25, 35, and 45 °C. Soil was amended with 1.5% tomato pomace, 1.5% spent mushroom substrate (SMS), or no amendment. Soil was amended by percent dry weight. The control consisted of untreated seeds. Values that do not share a letter are significantly different ($P \leq 0.05$). ANOVA and Tukey's HSD were performed on treatments with non-zero values. Error bars represent ± 1 standard deviation and $n=5$.

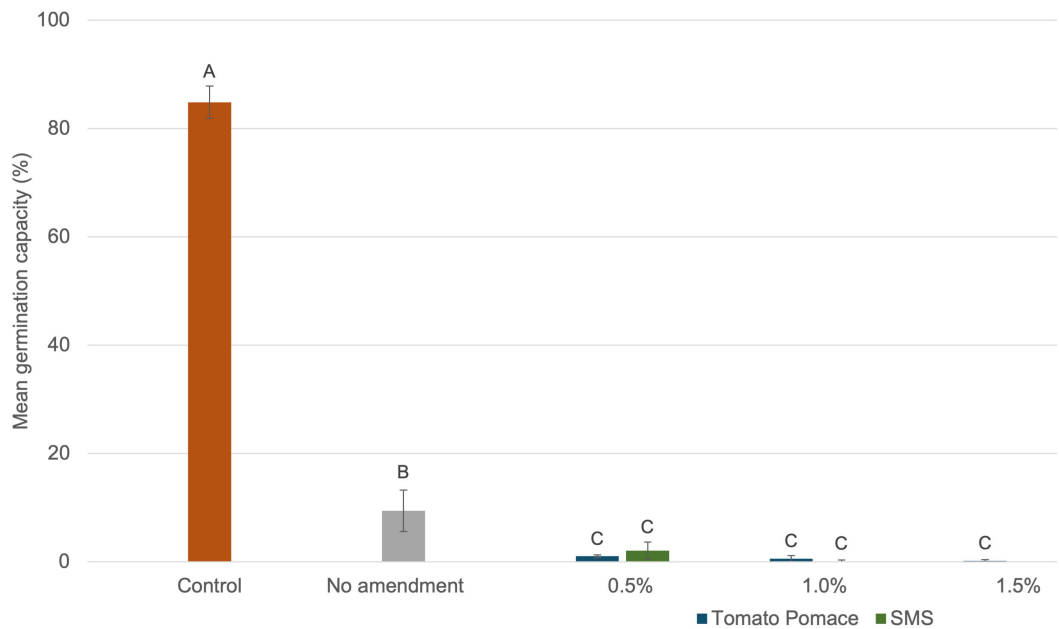


FIGURE 8
Mean germination capacity of branched broomrape seeds following simulated biosolarization at 35°C with two amendments at three amendment rates. The amendments used were tomato pomace and spent mushroom substrate (SMS) at rates of 0.5, 1.0 and 1.5%, or no amendment. Soil was amended by percent dry weight. The control consisted of untreated seeds. Values that do not share a letter within each figure are significantly different ($P \leq 0.05$). ANOVA and Tukey's HSD were performed on treatments with non-zero values. Error bars represent ± 1 standard deviation and $n=5$.

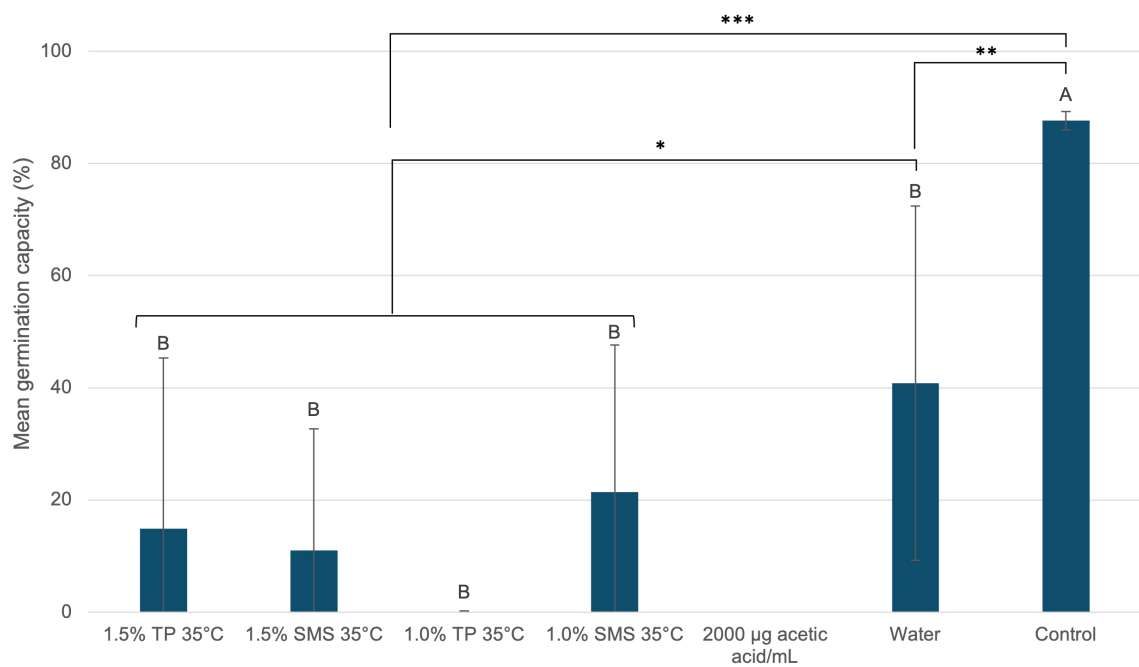


FIGURE 9
Mean germination capacity of *Phelipanche ramosa* seeds following exposure to biocidal organic acids in concentrations found in biosolarized soil amended with spent mushroom substrate (SMS) or tomato pomace (TP). The control consisted of untreated seeds. Individual treatments that do not share a letter are significantly different ($P \leq 0.05$). ANOVA and Tukey's HSD were performed on treatments with non-zero values. Biosolarization treatments were grouped together for further analysis. Asterisks indicate significant differences (***) represents $P < 0.0001$, ** represents $P = 0.0066$, and * represents $P = 0.0329$). Error bars represent ± 1 standard deviation and $n=5$.

The average broomrape germination for control seeds was 87.6%, while that of the seeds exposed to water for 8 days was 40.8%. Exposure to the solution of 2,000 µg acetic acid/mL led to 0.0% germination in all replicates. The average germination capacity of all biosolarization treatments was 11.3%.

4 Discussion

Prevention of branched broomrape parasitism is critical in infested agricultural fields. This study investigated the effects of simulated biosolarization on germination of *P. ramosa* seeds. Soil pH, electrical conductivity and BOA concentrations were analyzed alongside germinability of seeds subjected to simulated biosolarization with tomato pomace or SMS at different amendment rates and incubation temperatures.

The experiment with different temperatures demonstrated that 35 °C is sufficient for ≥ 99% broomrape seed germination inhibition, suggesting that biosolarization for the purpose of *P. ramosa* suppression may be successfully carried out during an extended period of the year or in varying climates. In broomrape affected regions in California, such as the San Joaquin and Sacramento Valleys, this suggests infested fields may be treated between May and October, instead of strictly in the summer months. This contradicts previous findings of anaerobic soil disinfestation (ASD) where weed suppression was only evident after high temperature (> 35 °C) treatments across pot and field experiments (Shrestha et al., 2016). However, while the study examined a variety of weeds, it did not include any broomrape species.

The highest temperature examined here, 45 °C, was effective at reducing germinability even in the absence of an organic matter amendment (Figure 7). This suggests that a short solarization may also be examined as an effective broomrape control strategy during the summers in hotter climates, since soil temperature under plastic mulch can be 9–10 °C higher than uncovered soil (Lombardo et al., 2012; Mauromicale et al., 2005).

Soil solarization has previously been tested as a method to control Orobanchaceae infestations, but results by solarization alone can vary greatly. Without the addition of an amendment, similar inhibition (99%) was found after a 60-day greenhouse solarization treatment, and total inactivation was achieved after 2 consecutive years of 60-day solarization treatments (Mauro et al., 2015). Another 60-day summer solarization inactivated 95% of *P. ramosa* seeds (Mauromicale et al., 2005). A study comparing different lengths of field solarization found that a 10-day treatment increased broomrape shoot emergence on an infested field of faba bean and lentil, while 20 and 50-day treatments decreased emergence on average by 55.4 and 91.1%, respectively (Sauerborn et al., 1989). This contradicts the findings of this study, in which 8-day laboratory simulated solarizations decreased broomrape seed germination significantly. Nonetheless, the 8-day simulated biosolarization treatments in this study suggest that organic amendments could contribute to a more time-efficient *P. ramosa* seed inactivation strategy. The consistent reduction in germinability observed after 8-day treatments suggests that

addition of an organic amendment for biosolarization is beneficial for reliable *P. ramosa* control (Figures 7, 8).

One field study found that solarization needed supplementation of either an herbicide or phosphoric acid for best results. The herbicide (Gesaprim) was applied once after solarization at a rate of 5g/L water. Solarization alone for 30 days led to broomrape infection incidence in tomatoes between 10.9 and 11.2% of that of the control, while solarization combined with the herbicide brought infection incidence down to 4.1 to 4.4% of the controls (Abdel-Aaty et al., 2020). The current study suggests that biosolarization could provide a more time-efficient solution that avoids the use of chemical inputs. It is important to note, however, that although the biosolarization process can be shorter than solarization, a period of remediation after biosolarization is needed for BOAs to volatilize or degrade before planting the crop of interest (Pastrana et al., 2022). Previous work has shown that 1 to 4 weeks can be appropriate depending on the amendment used, amendment rate and, consequently, the BOA concentrations produced (Haber et al., 2022; Shea et al., 2021). For tomato pomace and SMS, 2 weeks of remediation are sufficient before planting, keeping total treatment time below the previously used methods mentioned above (Achmon et al., 2018; Haber et al., 2022; Conte et al., 2025). The addition of organic matter for biosolarization maintains the efficacy of a longer treatment, with the added benefit of a shorter timeline, more consistent results, and valorization of a waste stream.

Previous research in biosolarization has also shown efficacy in suppressing *P. ramosa* germinability, supporting the present findings. A greenhouse biosolarization trial was conducted using a commercially formulated humus product as the organic amendment, resulting in total inactivation of the seedbank after one 60-day treatment during summer months (Mauro et al., 2015). Another field trial compared biosolarization with a commercial product of cattle and chicken manure with roasted leather as the amendment to conventional fumigation with chloropicrin in combination with 1,3-dichloropropene (Lombardo et al., 2012). This resulted in zero *P. ramosa* emergence in biosolarized tomato plots, while the fumigated treatments had 2 to 3% broomrape shoot emergence compared to the control. Additionally, the biosolarized treatments produced significantly more total fresh fruit yield of tomato. However, these treatments extended to 52 and 54 days, contrasting with the present study which found significant reductions in *P. ramosa* germinability in 8 days. While field-scale studies are necessary to confirm this result, biosolarization may control *P. ramosa* while creating less disruption within crop schedules through a reduced treatment period. Additionally, the SMS and TP amendments used in the present study may be obtained directly from the source where the waste is produced with no need for further processing, potentially decreasing the cost associated with the treatment.

The pH results demonstrate that both simulated biosolarization and solarization can significantly impact soil acidity. The effect of tomato pomace on soil pH after simulated biosolarization depended on both amendment rate and temperature, while SMS consistently increased soil pH regardless of amendment rate or incubation temperature (Figures 1, 2). However, the observed increases in pH of the SMS-amended treatments were consistently smaller

compared to the non-amended controls, likely due to the production of BOAs in the amended soil. Increases in SMS amendment rate resulted in decreasing soil pH (Figure 2) and increasing BOA concentrations (Figure 6). The lack of BOAs in soil amended with 0.5% SMS at 35 °C suggests that 0.5% is not a sufficient SMS amendment rate for BOA production.

The greater production of BOAs in the tomato pomace-amended soil is reflected in the pH data, as soils amended with 1.5% tomato pomace were the only samples with a pH decrease during biosolarization. However, not all 1.5% tomato pomace treatments led to a decrease in pH, as observed in the 45 °C incubation (Figure 1). Because pH changes were not consistently associated with broomrape germinability results, temporary changes in pH due to biosolarization do not appear to be a consistent predictor of performance.

There was also a decrease in BOA production at 45 °C, compared to 25 and 35 °C, pointing to a decrease in fermentation potential. While these treatments also led to >99% reduction in *P. ramosa* germinability (Figure 7), there were no significant differences between amended and unamended soils, indicating that the temperature was the main mechanism of germination suppression in this case.

The 25 and 35 °C incubations produced more varied results. Although there was no significant difference between the BOAs of the 25 and 35 °C incubation temperatures of SMS-amended soil, the 35 °C incubation led to significantly lower germination capacity (Figure 7), which speaks to the synergistic effect of biosolarization variables at lower temperatures since similar levels of BOAs did not have the same effect. However, with higher BOA levels, such as those observed in both the 25 and 35 °C tomato pomace simulated biosolarizations, this temperature effect becomes less pronounced as the broomrape germination capacity was not significantly different between these treatments. This suggests that at 25 °C, more BOAs than those observed in SMS-amended soil would be needed for greater reductions in broomrape germinability, while at 45 °C, BOA content is less critical for germinability reduction. At 35 °C, BOA content may be more predictive of potential broomrape germinability, since seeds from soils with BOA production had germination capacity below 1.0%, while those from soil with no detectable BOAs had higher germination capacity (Figure 7). This suggests that BOA has a greater effect on broomrape germinability than pH. Further research is needed to understand the nuances of the interaction between BOA production and temperature in terms of their effects on broomrape seed germinability.

The decrease in BOA production observed after the 45 °C incubation may be due to the temperature being too high for microbial activity of strictly mesophilic microorganisms, but on the lower end of the temperature preferences of strictly thermophilic microbes (Gonzalez et al., 2023; Pietikäinen et al., 2005). Further studies may also focus on identifying changes in the microbial communities of amended soil incubated at different temperatures in order to provide more context to the differences in BOA production.

Soil EC indicates the ability of the soil to conduct electrical current and is determined by the concentration of ions in soil. The

highest measured EC was 1,196 $\mu\text{S}/\text{cm}$ in 1.5% tomato pomace incubated at 35 °C (Figure 3), which is well below the 4,000 $\mu\text{S}/\text{cm}$ threshold above which soil is considered saline and also below the 2,000 $\mu\text{S}/\text{cm}$ level at which salinity-sensitive plants can be adversely affected (Weil and Brady, 2017). EC can elucidate differences in relative fermentation among treatments since it can rise with the production of fermentation byproducts and has been used as a proxy for fermentation progress (Aceves-Lara et al., 2012; Loo-Miranda et al., 2020). This can be seen in EC values reported here, which followed the same trends as BOA content (Figures 3-6), further supporting the idea that fermentation potential in the soil increases with increasing amendment rate, but decreases at higher temperatures.

EC can also be used as an indicator for relative differences in soluble nutrient levels between samples (Mirzakhani et al., 2022; Smith and Doran, 1997). In both the temperature and amendment rate variation experiments, all amended treatments had significantly higher EC than unamended soil, except for the 0.5% SMS soil, with tomato pomace-amended soil having the highest EC within each experiment (Figures 3, 4).

The BOA exposure experiment helps to elucidate the direct impact of organic acid production during biosolarization on seed germinability. The lack of differences in germination capacity between individual biosolarization treatments and the seeds exposed to water points to the germinability reduction being due to a synergistic effect between a variety of conditions achieved during biosolarization such as organic acid presence, anaerobicity and microbial activity. However, the significant difference between grouped biosolarization treatments and water confirms that there is an inhibitory effect by the BOAs that is greater than just exposure to water (Figure 9). It also confirms that the effect of biosolarization on *P. ramosa* germinability may not be associated with a specific treatment. This is reflected in the biosolarization bioreactor experiments as well, in which there were no significant differences in germination among varying amendments or amendment rates (Figure 8).

The 0% germination capacity of the 2,000 μg acetic acid/mL control show that acid concentrations that can be achieved during biosolarization are able to prevent germination of the seeds regardless of temperature or saturation. Though this concentration was not observed in the biosolarization treatments of this study, its effectiveness in reducing germinability demonstrates that at high enough concentrations, BOAs on their own can prevent *P. ramosa* germination. Biosolarization has produced organic acids exceeding this level in multiple instances, including with treatments of 2.5% tomato pomace (reached approximately 2,500 $\mu\text{g}/\text{mL}$) and 1.3% almond hulls (3,100 $\mu\text{g}/\text{mL}$) (Achmon et al., 2017; Fernandez-Bayo et al., 2020).

The results discussed here are encouraging for the introduction of a new, alternative method to control broomrape infestations. Application of the treatments from this study on a broomrape-infested field would provide an opportunity for field validation of the laboratory results. While this study presents valuable data for *P. ramosa* germination suppression, the key limitation is that laboratory conditions are not fully reproducible on a field, where there may be more variable results. Field studies are subject to

greater variability in environmental conditions, such as temperature and moisture uniformity. However, simulated biosolarization using incubated bioreactors has been validated as a method that translates to field trials (Simmons et al., 2013). A previously infested site would be needed for this study since broomrape seeds cannot legally be introduced to a field in California. Future research should confirm the efficacy of biosolarization for broomrape control at field-scale and include crop and soil metrics such as marketable yield and mineralized plant nutrients in the soil to understand the impact of using biosolarization as a pest management method on subsequent crop growth and soil health.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Conte, Carolina (2025), “Data for Biosolarization to inhibit *P. ramosa* germination”, Mendeley Data, V1, doi: 10.17632/spx5y93867.1.

Author contributions

CC: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. SM: Conceptualization, Writing – review & editing. BH: Conceptualization, Funding acquisition, Resources, Writing – review & editing. CS: Writing – review & editing, Funding acquisition, Resources, Supervision, Validation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2026.1717415/full#supplementary-material>

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