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Microwave soil heating reduces seedling emergence of a wide range of species including invasives

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Abstract

*A microwave-based process to control invasive species (seeds and adult stages) in the field prior to plant community restoration is currently under development. We investigated the effect of four microwave treatment pairings of Power × Duration (2kW4min, 4kW2min, 2kW8min, and 4kW4min) on seedling emergence of (1) an abandoned field seed bank used as a model for various plant species and (2) seeds of three species invasive in Europe: *Datura stramonium* (Jimson weed), *Reynoutria × bohemica* (Bohemian knotweed), and *Solidago gigantea* (Giant goldenrod). In addition, we assessed whether nontreated seeds of these three invasive species could germinate on microwave-treated soils. As microwave soil heating usually leads to nonhomogeneous temperatures within a sample, we also assessed whether the position of seeds in the soil during microwave treatment (center vs. edges) impacted seedling emergence. Results show that the most intensive microwave treatments (2kW8min and 4kW4min), enabling the soil to reach 85 °C, are highly effective in inhibiting seedling emergence of invasive species and the seed bank. The 2kW8min treatment, combining lowest power and longest exposure, is the most effective, reducing seed bank seedling emergence by 98% compared to control. The results also reveal a species-specific response to heat, and lower microwave effectiveness on seeds located at the soil surface, which may explain the incomplete effectiveness of intensive treatments. Our results also suggest that prior microwave soil treatment does not prevent a considerable proportion of newly arrived invasive species seeds from germinating, suggesting that this method should be followed by restoration of native plant cover.*

Keywords: eradication, germination, restoration prerequisite, seed bank reduction

Implications for Practice

- Under specific power and duration conditions, microwave soil heating drastically reduces seedling emergence of several abandoned field species, suggesting its potential to control the seed bank of various invasive species.
- Species-specific resistance to microwave heating is revealed, pointing to the need to adapt treatment power and/or duration to the target species.
- Nontreated invasive species seeds are able to emerge on microwave-treated soil, suggesting that microwave heating does not prevent newly arrived invasive species seeds from germinating. Treatment will thus need to be followed by restoration of native plant cover, to avoid reinvasion.
- The use of soil microwave heating would be less suitable to control invasive species having high seed dispersal abilities because of their rapid recolonization potential from neighboring areas

Introduction

Several control methods are commonly used to reduce the dominance of invasive plant species, such as physical plant removal, herbicides use, or introduction of biological agents. However, large-scale interventions often complex and expensive (Rejmânek & Pitcairn 2002) and are rarely successful (Kettenring & Adams 2011). Eradications of invasions covering more than 1,000 ha are generally not feasible because of the high cost of the initial treatment coupled with the multiple repetitions (Rejmânek & Pitcairn 2002). Eradication is only feasible if undertaken soon after the introduction of the invasive species (Rejmânek & Pitcairn 2002) and germination over time of invasive plants from a long-lasting seed bank remains a main factor explaining the failure of many restoration programs (Berger 1993; Richardson & Kluge 2008). Indeed, invasion strategies are often based on a combination of vegetative (i.e. rhizomes) and sexual (i.e. seeds) reproductive capacities (Gioria et al. 2012), leading to the establishment of a highly persistent seed bank (Holm et al. 1977). Thus, ensuring the elimination of propagules and the loss of seed viability is crucial to the successful eradication of many invasive species and to the effective restoration of native communities (Myers et al. 1998; Regan et al. 2006).

Biological control using natural enemies is an effective method for reducing seed production and accumulation in the soil, through damage to or destruction of buds, flowers, and young pods (Morris et al. 1999; Zimmermann et al. 2004; Adair 2005). In the absence of natural enemies, alternative methods enabling the reduction of the soil seed bank of nondesirable species have been considered, mainly in agrosystems (Kremer 1993; Mirsky et al. 2010). Hand-pulling before establishment of the seeds has been shown to be effective in depleting the seed bank of small patches of invasives along roadsides or hiking

trails (Concilio 2013) or in isolated nature reserve (Ruffino et al. 2015), but requires annual treatments for at least 3 years and becomes impractical over large areas (Concilio 2013). Soil solarization, which consists in heating the soil by mulching it with plastic sheeting to inhibit seed viability (Cohen et al. 2008), has certain limitations, such as length of treatment (i.e. several months), sunlight dependency, and variable effectiveness (Cohen & Rubin 2007). Fire is another relatively cost-effective option for reducing seeds in leaf litter and upper seed banks in various ecosystems (Holmes 1989; Richardson & Kluge 2008). Carefully designed prescribed burning combined with adequate restoration measures (e.g. grazing, seed sowing) have shown promising results for invasion control and other conservation goals (Valkô et al. 2014). Applying fire as a control method is, in some cases, less easily feasible in biomes such as dune systems or riparian zones (Richardson & Kluge 2008). Furthermore, using fire is controversial because intense uncontrolled fires can sterilize soil for several years (Campbell et al. 1999).

Microwave treatments have been proposed as an alternative eradication method for invasive and pest species in soil, such as insects, nematodes, soil pathogens, fungi, and weed seeds (Nelson 1996). Microwave radiation induces the dielectric heating of moist materials, making it possible to reach the soil temperatures required for seed viability loss (i.e. 60–90°C; Barker & Craker 1991; Thompson et al. 1997; Sahin 2014). The use of such thermal methods is attracting interest mainly due to increased awareness of the environmental risks associated with chemical-based herbicides (i.e. growing list of herbicide-resistant weed biotypes; Heap 1997) and the need for a rapid, effective procedure free of undesirable residues (Brodie et al. 2011; Sahin 2014). However, some studies question the effectiveness of soil microwave treatments, in particular due to the rapid attenuation of microwave radiation in moist soils (Nelson 1996; Sartorato et al. 2006; Ascard et al. 2007). Control of weed seed germination is seen as the most promising soil application of microwave technology (Nelson 1996).

The study reported herein was realized in the framework of a project aiming to develop a microwave-based method for use directly in the field. It is thus part of a set of studies undertaken to help determine the technical characteristics of a continuous conveying tunnel with microwave equipment, designed for the treatment of infested soil collected in situ. The field process involves extracting infested soil, passing it through a microwave oven on a conveyor belt, and putting it back in place. This process is designed to treat large areas infested with a wide range of invasive plant species (vegetative and reproductive parts, including seeds). Several studies have tested the effect of microwave radiation on germination. However, most of them were conducted more than 20 years ago with microwave ovens whose characteristics (e.g. frequency and power, volume treated) may well have compromised the effectiveness of the treatments (e.g. Diprose et al. 1984; Nelson 1996). Furthermore, the

studies subjected only a few species to the impact of microwave treatments on germination (Bebawi et al. 2007; Brodie et al. 2009; Sahin 2014), rather than testing a diversity of species.

Among our set of studies, the first one was conducted to define the most effective microwave treatment pairing of Power \times Duration to inhibit seedling emergence of three invasive species in Europe (*Datura stramonium*, *Reynoutria \times bohemica*, and *Solidago gigantea*) depending on soil moisture (10, 13, 20%) and seed burial depth (2, 12 cm) (De Wilde et al. 2017). Treatments requiring relatively high power and duration were the most effective (e.g. the 2kW8min and 4kW4min treatments), and their effectiveness decreased with increasing soil moisture. Emergence of seeds located at the 12 cm depth was occasionally more strongly affected. This experiment, focusing only on three species, was carried out in conditions far from the future field process (i.e. seeds not directly mixed with soil, seedling emergence in Petri dishes placed in a growth chamber).

As seed survival and germination responses to heat vary greatly between species or genotypes within species (Melander & Jørgensen 2005; Wahid et al. 2007; Brodie et al. 2011), we aimed to evaluate the response of a higher diversity of species. Thus, we first assessed the capacity of four different microwave treatments previously tested by De Wilde et al. (2017) to destroy a seed bank of an abandoned organic cultivation field, chosen not for its invasion status (non-invaded) but because it contained a great diversity of species (Table S1, Supporting Information). Additionally, we introduced into the soil samples a specific number of seeds from three species invasive in Europe (*D. stramonium*, *R. \times bohemica*, and *S. gigantea*), also used in a previous study (De Wilde et al. 2017). This seed introduction was intended (1) to test the effect of microwaves directly on three important invasive plant species and (2) to evaluate the percentage of seedlings able to emerge after each treatment, when directly mixed with soil. The three species, noxious in some European countries (Weber 2003; Weber & Jakobs 2004; Van Kleunen et al. 2007), were chosen not only because they reproduce by seeds (Saayman 2000; Weber & Jakobs 2004; Gillies et al. 2016) but also mostly because their seeds differ in shape and size. Indeed, these characteristics are known as major determinants of seed sensitivity to microwave heating (Bebawi et al. 2007; Brodie et al. 2011).

Microwave treatments expose soils to high temperatures, with a predictable effect on soil-living organisms (especially microorganisms) and soil properties. This could disturb plant germination (Certini 2005; Brodie et al. 2015) and the recovery of fundamental ecosystem functionalities after treatment (Herrick et al. 2006). Through soil disturbance, soil microwave treatment could therefore prevent or limit invasive species reinvasion. To determine whether the response to microwave treatment in terms of seedling emergence is (1) only due to a direct effect of heat on seeds or (2) the result of this

direct effect on seeds combined with soil heating disturbances to soil properties and biota, we further assessed the capacity of seeds of *D. stramonium*, *R. × bohemica*, and *S. gigantea* to germinate on soil previously subjected to microwave treatments.

Brodie (2011) showed that microwave treatment commonly leads to the nonhomogeneous heating of exposed materials: temperatures at the edges of the exposed object are several degrees lower than in the center (output power 750W, after 150 seconds of heating). De Wilde et al. (2017) found seeds located at 12 cm depth more affected by microwave treatment than those at 2 cm depth. However, the question remains of whether seeds located at the surface (0–0.5 cm from the edges) of treated samples might be subjected to lower, nonlethal temperatures. The projected design for field use includes a conveyor belt carrying the extracted soil through a microwave oven. A relatively thin layer of soil containing seeds would thus be subjected to microwave radiations potentially resulting in heterogeneous temperatures (and potentially lower temperature close to the surface) that could seriously threaten complete eradication of invasive species in situ. We therefore also investigated whether the position (center vs. edge) of seeds in the soil sample during microwave treatment modified seedling emergence responses to microwave treatments.

Methods

Biological Materials

The experiments were performed on a seed bank contained in soil extracted in situ and also on seeds of three important plant species invasive in Europe (*Datura stramonium*, *Reynoutria × bohemica*, and *Solidago gigantea*), which are abundant seed-producers (Weaver & Warwick 1984; Weber & Jakobs 2004; Gillies et al. 2016). Information about *D. stramonium*, *R. × bohemica*, and *S. gigantea* ecology and invasion history is available in Appendix S1.

Soil Sampling

Topsoil, characterized as a silty loam (60% silt, 15% clay), was collected from uncultivated species-rich grassland that had developed on an abandoned organic hemp field (cultivation stopped in 2013) located near two rivers, La Cèze and La Tave (Laudun-L'Ardoise, France). The 25 fresh soil samples (135 cm \pm 15 length x 50 cm \pm 10 width x 10 cm depth) were mixed to ensure the homogeneity of soil and seed bank. Blended soil cleared of stones and organic residues was distributed in 1-kg batches just prior to microwave treatments. This soil was used for all the experiments.

Seed Sampling of the Three Invasive Species

Seeds of *D. stramonium* were gathered in October 2014 from stands growing along the Rhône River, Drôme (France). Achenes of *R. × bohemica* and *S. gigantea* were collected in March 2015 for the first experiment and in March 2016 for the second experiment along the Isère River, Savoie (France). The achenes and seeds were collected randomly from 10 ramets of the same population and then pooled. Then achenes and seeds were stored under dry conditions at room temperature until used for experiments. We assume that these storage conditions do not affect the achene and seed viability and germination capacity of these species (Benvenuti & Macchia 1997; Engler et al. 2011; Bochenek et al. 2016). The term “seed” will be used for both seeds and achenes.

Microwave System

An AMW200 batch microwave system (SAIREM SAS, Neyron, France) was used in this study (De Wilde et al. 2017). The 304L microwave stainless steel chamber can contain a block of 600 x 400 x 250 mm maximum size and 30 kg maximum weight. The microwave system has a polyethylene sliding table with a usable surface of 840 x 620 mm and a pneumatically driven sliding door, both making block loading/unloading easier. The microwave system operates at 915 MHz, which allows greater penetration and treatment of thicker materials (up to 25 cm) than the frequently used 2,450 MHz microwave frequency (approximately a 3-fold increase). Coupling microwave heating from above and below and rotating the turntable enhance heating homogeneity. The output power of 10 kW maximum is produced by 2 x 5 kW generators (magnetron), adjustable from 1 to 10 kW. The system is water-cooled.

Experimental Design

Effect of Microwave Treatments on Seedling Emergence From Soil Seed Bank and Sown Invasive Species. We applied four microwave treatments using the following Power x Duration pairings: 2kW4min, 2kW8min, 4kW2min, and 4kW4min. Microwave treatments were performed on the premises of SAIREM (Neyron, France), each treatment being applied on 1-kg soil replicates placed in 16 cm high x 7.5 cm diameter plastic cylinders. For each treatment, we used eight replicates of soil containing (1) only the natural seed bank, (2) 10 seeds of each tested invasive species sown before treatment, or (3) 10 seeds of each tested invasive species sown after treatment. Controls without treatment were soil containing (1) only the natural seed bank and (2) 10 seeds of each added invasive species. Soil temperature was measured immediately after microwave treatment in each replicate, using mercury thermometers. Before treatment, soil temperature was 18°C, and soil moisture content was 7.6%±0.5 (mean±SD). After treatment, samples were dried for 8 days at 30°C.

Seedling emergence was monitored in an outdoor, pollen-free greenhouse, reducing the risk of granivory and contamination by seeds from the outside (Institute Tour du Valat, Arles, France). After microwave treatment and drying, each sample was spread in a 1–1.5 cm thick layer over 19 cm diameter perforated plastic saucers already containing, from bottom to top: (1) a 21 cm diameter Diatex filter (500–60µm mesh size to prevent loss of coarse sand), (2) 1.5 cm of sterilized and desalted sand, and (3) a 23 cm diameter Diatex filter (50–75 µm mesh size to avoid the loss of silt and seeds). The plastic saucers were randomly placed in containers where a 1 cm water layer was constantly adjusted so as to maintain soil moisture at a level conducive to germination and prevent submersion. To detect possible contamination, three control saucers containing only sterilized and desalted sand were added to the experimental design. Seedling emergences were recorded weekly for 8 weeks from 28 September to 6 November 2015. Identified individuals were regularly removed to reduce competition.

Effect on Seedling Emergence of Seed Position in Soil During Microwave Treatment. This experiment was performed using seeds of *R. × bohemica* and *S. gigantea*. Three seed positions in the soil during microwave treatments were tested: (1) at the soil surface (0–0.5 cm depth, in the center), (2) 7 cm below the surface at the periphery (0–0.5 cm from the edge of the cylinder), and (3) 7 cm below the surface in the center. These three positions will be hereafter called (1) “at the surface,” (2) “at periphery,” and (3) “in the center,” respectively. We applied three microwave treatments using the following Power x Duration pairings: 2kW4min, 2kW8min, and 4kW4min. Before treatment, soil temperature was 17°C and soil moisture content was 10.7%±0.5 (mean±SD). One replicate consisted of three paper baking bags containing 10 seeds of each of the two selected invasive species (*R. × bohemica* and *S. gigantea*), one bag placed at each of the three test positions, in a 15 cm high x 8 cm diameter plastic cylinder containing the same soil as in the previous experiment. We chose this cylinder height because the thickness of the soil layer used in the final design will be close. There were eight replicates per treatment. As a control treatment, eight paper bags were not subjected to microwave radiation. After microwave treatment, soil temperature was immediately measured in each replicate, using mercury thermometers inserted in the center and at the periphery of the cylinder.

After exposure to treatments, the seeds from both bags (20 seeds) were stuck to double-sided plastic films, themselves stuck to tissues (Diatex filters permeable to 0.2–20µm particles), and placed on a Petri dish (6 cm diameter) on cotton soaked in distilled water. The Petri dishes were placed in a growth chamber (Hotcold-GL: 12 K lux) with a photoperiod of 14h day/10 h night and temperature controlled at 25°C day/ 15°C night. Seedling emergence was monitored every 3 days until no seedling emergence was observed (from 5 April 2016 to 5 May 2016). Seedlings were removed as they

germinated, to avoid their pre-empting of resources and thereby potentially preventing the germination of other individuals.

Statistical Analysis

Effect of Microwave Treatments on Seedling Emergence of Soil Seed Bank and Sown Invasive Species. We analyzed variation in numbers of seedling emergences for each species category (total seed bank, monocotyledons, dicotyledons, Asteraceae, Fabaceae, Poaceae) depending on the explanatory variable “microwave treatment” (control: absence of microwave treatment and four Power x Duration microwave treatment pairings: 2kW4min, 4kW2min, 2kW8min, and 4kW4min) using generalized linear models (GLMs) with negative binomial error distribution to account for over-dispersion (Crawley 2007). Tests were performed in R with function “glm.nb” in the package “MASS” (R Core Team 2015).

We analyzed variation in percentages of seedling emergences of each species (*D. stramonium*, *R. × bohemica*, and *S. gigantea*) depending on the explanatory variable “microwave treatment” using GLMs with binomial error distribution (Crawley 2007). Tests were performed with function “glm” in R (R Core Team 2015).

When the effect of microwave treatment was significant, we conducted pairwise comparisons with Tukey’s pairwise comparison tests using function “glht” in the package “multcomp” in R (R Core Team 2015). For all tests, *p*-values lower than 0.05 were considered as statistically significant.

Effect on Seedling Emergence of Seed Position in Soil During Microwave Treatment. We analyzed variation in percentages of seedling emergence for each species (*R. × bohemica* and *S. gigantea*) and each Power x Duration microwave treatment pairing (2kW4min, 2kW8min, and 4kW4min) depending on the explanatory variable “seed position” (“center,” “periphery,” and “surface”) using GLMs with binomial error distribution (Crawley 2007). Tests were performed with function “glm” in R (R Core Team 2015). The *p*-values lower than 0.05 were considered as statistically significant.

Results

Effect of Microwave Treatments on Seedling Emergence of Soil Seed Bank and Sown Invasive Species

Soil Temperature. After treatment, we recorded mean soil temperatures close to 85°C for the 2kW8min and 4kW4min treatments, and temperatures around 65°C for the 2kW4min and 4kW2min treatments. Temperatures exceeding 100°C were not recorded whatever the treatment.

Total Seed Bank. Over the course of the experiment, 797 individuals were recorded (all treatments combined), distributed among 28 genera, including 31 identified species (Table S1). Four families of monocotyledons accounted for 11 genera, 12 species, and 489 individuals. Ten families of dicotyledons accounted for 17 genera, 21 species, and 308 individuals. The plant community was dominated by Poaceae, with 60.3% of the total number of individuals. Two Poaceae species, *Rostraria cristata* and *Lolium rigidum*, accounted for 20.7 and 36.3% of the total number of individuals, respectively. Dominant dicotyledon families were Asteraceae and Fabaceae, with 14.6 and 10.4% of the total number of individuals, respectively.

Soil exposure to microwave treatment significantly impacted the number of seedling emergences of the total seed bank (degrees of freedom [df] = 35, Wald $\chi^2 = 37.5$, $p < 0.001$). The four microwave treatments significantly reduced the number of seedling emergences compared with the control ($p < 0.001$; Fig. 1A). The number of seedling emergences was significantly higher in the 2kW4min and 4kW2min treatments than those in the 2kW8min and 4kW4min treatments ($p < 0.01$; Fig. 1A). The other comparisons did not reveal any significant difference.

Dicotyledons. Soil exposure to microwave treatment significantly impacted the number of seedling emergences of the dicotyledons ($df = 35$, Wald $\chi^2 = 38.6$, $p < 0.001$). The four microwave treatments significantly reduced the number of seedling emergences compared with the control ($p < 0.05$; Fig. 1B). The number of seedling emergences was significantly higher in the 2kW4min treatment than those in the 2kW8min treatment ($p < 0.01$; Fig. 1B). The number of seedling emergences was also significantly higher in the 4kW2min treatment than those in the 2kW8min and 4kW4min treatments ($p < 0.05$; Fig. 1B). The other comparisons did not reveal any significant difference.

Monocotyledons. Soil exposure to microwave treatment significantly impacted the number of seedling emergences of the monocotyledons ($df = 35$, Wald $\chi^2 = 33.9$, $p < 0.001$). The 2kW4min, 4kW2min, and 4kW4min treatments significantly reduced the number of seedling emergences compared with the control ($p < 0.001$; Fig. 1C). No seedling was found in the 2kW8min treatment; thus, statistical tests were not performed for this treatment. The number of seedling emergences was significantly higher in the 2kW4min and 4kW2min treatments than in the 4kW4min treatment ($p < 0.01$; Fig. 1C). The other comparisons did not reveal any significant difference.

Asteraceae. Soil exposure to microwave treatment significantly impacted the number of seedling emergences of the Asteraceae ($df = 35$, Wald $\chi^2 = 34.4$, $p < 0.001$). The 2kW4min, 4kW2min, and 4kW4min treatments significantly reduced the number of seedling emergences compared with the control ($p < 0.05$; Fig. 1D). No seedling was found in the 2kW8min treatment; thus, statistical tests were

not performed for this treatment. The number of seedling emergences was significantly higher in the 4kW2min treatment than in the 4kW4min treatment ($p < 0.05$; Fig. 1D). The other comparisons did not reveal any significant difference.

Fabaceae. Soil exposure to microwave treatment did not significantly impact the number of seedling emergences of the Fabaceae ($df = 35$, Wald $\chi^2 = 35.1$, $p = 0.747$; Fig. 1E).

Poaceae. Soil exposure to microwave treatment significantly impacted the number of seedling emergences of the Poaceae ($df = 35$, Wald $\chi^2 = 30.9$, $p < 0.001$). The 2kW4min and 4kW2min treatments significantly reduced the number of seedling emergences compared with the control ($p < 0.001$; Fig. 1F). No seedling was found in the 2kW8min and 4kW4min treatments; thus, statistical tests were not performed for these treatments. The other comparisons did not reveal any significant difference.

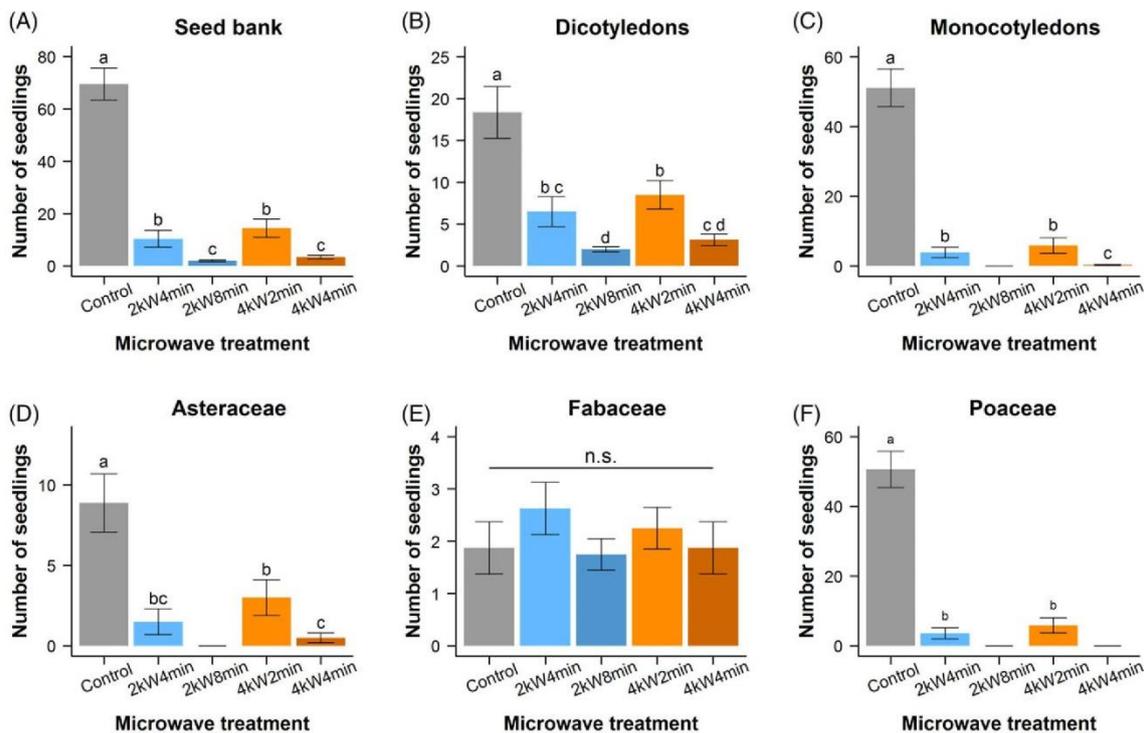


Figure 1. Effect of microwave soil heating on the number of seedling emergences of seed bank plants by category (A) the whole seed bank, (B) dicotyledons, (C) monocotyledons, (D) Asteraceae, (E) Fabaceae, and (F) Poaceae that emerged without soil microwave treatment (control) and after different soil microwave treatments (2kW4min, 2kW8min, 4kW2min, and 4kW4min Power x Duration). Values are expressed as mean \pm SE of the eight replicates. Letters refer to the results of post hoc Tukey's test. Treatments with no letter in common are significantly different ($p < 0.05$). n.s. means "nonsignificant," when the general effect of microwave treatment is not statistically significant ($p < 0.05$).

Invasive Species Sown Before Microwave Treatment. Soil exposure to microwave treatment significantly impacted the percentage of seedling emergences of *Datura stramonium* and *Reynoutria × bohemica* ($df = 35$, Wald $\chi^2 = 31.3$ and 32.6 respectively, $p < 0.001$). As no seedling of *Solidago gigantea* was found after microwave treatment, no statistical test was performed for this species. Both the 2kW4min and 4kW2min treatments significantly reduced the seedling emergence percentage of *D. stramonium* and *R. × bohemica* compared with the control ($p < 0.001$; Fig. 2A). For *D. stramonium*, the 4kW4min treatment significantly reduced the seedling emergence percentage compared with the control ($p < 0.001$; Fig. 2A), while for *R. × bohemica*, no seedling was found. For both species, no seedling was found after the 2kW8min treatment; thus, statistical tests were not performed for this treatment. The other comparisons did not reveal any significant difference.

Invasive Species Sown After Microwave Treatment. While prior exposure of soil to microwave treatment did not significantly impact the seedling emergence percentage of *R. × bohemica* ($df = 35$, Wald $\chi^2 = 65.5$, $p = 0.487$, respectively; Fig. 2B), the 2kW4min and 4kW4min treatments significantly reduced the seedling emergence percentage of *D. stramonium* and *S. gigantea* compared with the control ($df = 35$, Wald $\chi^2 = 91.1$ and 78.8 , respectively, $p < 0.001$; Fig. 2B). The percentage of seedling emergence of *D. stramonium* after the 2kW4min treatment was significantly lower than after the 4kW2min treatment ($p < 0.01$, Fig. 2B). The percentage of seedling emergence of *S. gigantea* was significantly lower after the 2kW4min treatment than after the 2kW8min and 4kW2min treatments ($p < 0.05$, Fig. 2B). The other comparisons did not reveal any significant difference.

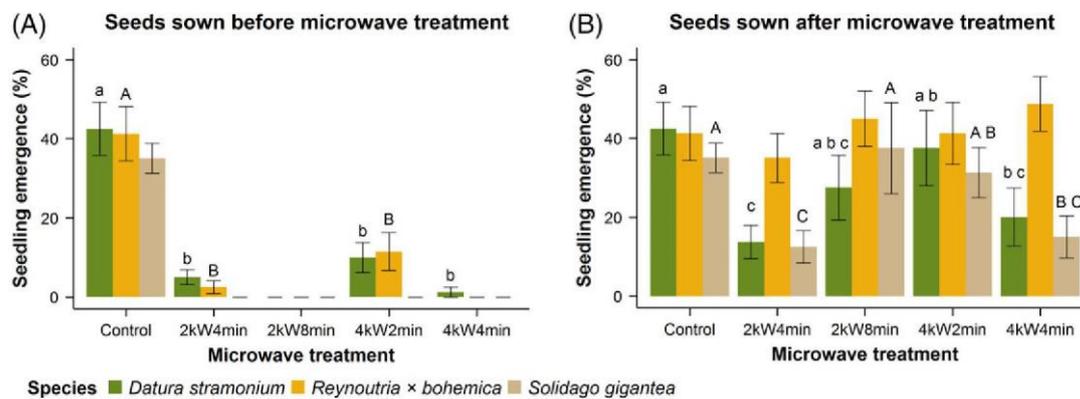


Figure 2. Effect of microwave soil heating on the percentages of seedling emergence of *Datura stramonium*, *Reynoutria × bohemica*, and *Solidago gigantea* sown (A) before and (B) after soil microwave treatment (2kW4min, 2kW8min, 4kW2min, and 4kW4min Power x Duration) or without soil microwave treatment (control). Values are expressed as mean \pm SE of the eight replicates. Letters refer to the results of post hoc Tukey's test. Uppercase and lowercase letters refer to different species. Treatments with no letter in common are significantly different ($p < 0.05$).

Effect of Seed Position in Soil During Microwave Treatment on Seedling Emergence

Soil Temperature. We recorded higher mean temperatures in the center than at the periphery after exposure to all the microwave treatments (eight replicates). In the 2kW4min treatment, soil temperature was around 55°C in average with a difference of 8°C between the center and the periphery. Soil reached mean temperatures close to 85°C in both the 2kW8min and 4kW4min treatments, with a difference of 6°C in average between the center and the periphery. Temperatures exceeding 100°C were not recorded whatever the treatment.

***Reynoutria × bohémica*.** With the 2kW8min and 4kW4min treatments, seedlings were only recorded for seeds placed at the surface during microwave treatment (Fig. 3A). Thus, statistical tests were not performed for these treatments. The 2kW4min treatment showed no significant difference between the three seed positions ($df = 21$, Wald $\chi^2 = 0.1$, $p = 0.046$ but post hoc tests nonsignificant; Fig. 3A).

***Solidago gigantea*.** With the 4kW4min treatment, seedlings were only recorded for seeds placed at the surface during microwave treatment (Fig. 3B). Thus, statistical tests were not performed for this treatment. Seed position in the soil during microwave treatment significantly impacted the seedling emergence percentage for the 2kW4min treatment ($df = 21$, Wald $\chi^2 = 42.4$, $p < 0.001$) and for the 2kW8min treatment ($df = 12$, Wald $\chi^2 = 85.2$, $p < 0.001$). With the 2kW4min treatment, the seedling emergence percentage was significantly higher at the periphery and at the surface than in the center ($p < 0.01$; Fig. 3B). For the 2kW8min treatment, the seedling emergence percentage was significantly higher at the surface than at the periphery and in the center ($p < 0.001$; Fig. 3B). The other comparisons did not reveal any significant difference.

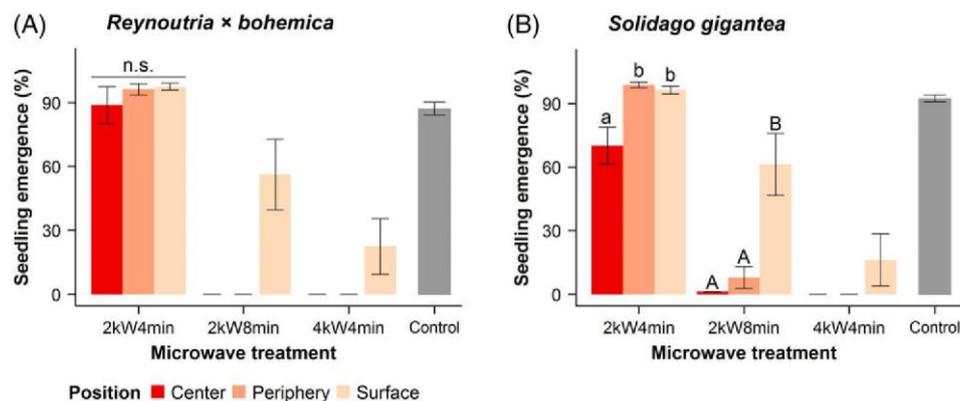


Figure 3. Effect of position of seeds in the soil on seedling emergence percentages of (A) *Reynoutria × bohémica* and (B) *Solidago gigantea* without microwave treatment (control) and after microwave treatment (2kW4min,

2kW8min, and 4kW4min Power \times Duration). “Center” indicates seeds placed 7 cm below the surface in the center of the cylinder, “periphery” indicates seeds placed 7 cm below the surface at the periphery of the cylinder, and “surface” indicates seeds placed close to the soil surface at the center of the cylinder. Values are expressed as mean \pm SE of the eight replicates. Letters refer to the results of post hoc Tukey’s test. Uppercase and lowercase letters refer to different microwave treatments. Seed positions with no letter in common are significantly different ($p < 0.05$). n.s. means “nonsignificant,” when the general effect of seed position is not statistically significant ($p < 0.05$).

Discussion

Seed susceptibility to microwave treatment is mainly attributed to the direct effect of heat transfer from the surrounding soil (Nelson 1996) and is entirely temperature-dependent (Barker & Craker 1991). Studies have shown that soil microwave treatment can kill seeds of several species in the soil (Davis et al. 1971; Barker & Craker 1991; Brodie et al. 2009; De Wilde et al. 2017). In our experiment, the drastic reduction of seedling emergences from a seed bank exposed to certain treatments confirms the effectiveness of soil microwave treatment in inhibiting the seedling emergence of a wide diversity of species (here, at least 31 species). We found the 2kW8min treatment, the lowest power, and the longest exposure, to be the most effective: enabling soil temperature to reach 85°C, it reduced total seedling emergence by 98% compared to the control. Possible reasons for the extreme effectiveness of this treatment are that (1) a lethal temperature is maintained for a longer time than with the shorter treatment (i.e. 4kW4min), and (2) temperature homogeneity within the sample is greater due to longer thermal diffusion from the zones where the microwave energy is being absorbed to the rest of the material.

As the effectiveness of microwave treatments in reducing seedling emergence is dependent on soil conditions such as soil moisture and texture (Brodie et al. 2011; De Wilde et al. 2017), treatment power and/or duration would probably need to be adapted to each site’s specific soil characteristics. Naturally, economic viability calls for the shortest and least energy-consuming treatment. While the 2kW4min and 4kW2min treatments were not very effective in our experiment, not permitting the soil to reach mean temperatures above 65°C, they may work better under other soil conditions (Brodie et al. 2011) and should be explored as an option. None of the four treatments tested completely inhibited seedling emergence: we recorded a few seedling emergences even with the two most intensive treatments (i.e. 4kW4min and 2kW8min). A species-specific response to soil microwave heating seems a strong hypothesis to explain this result. Studies have already shown that seed survival and seedling emergence responses to soil heating vary greatly between species or between genotypes

within species (Melander & Jørgensen 2005; Wahid et al. 2007; Brodie et al. 2011). *S. gigantea* appeared to be very sensitive to soil microwave heating compared to *D. stramonium* and *R. × bohemica*. This high sensitivity may be related to its small seed size (large size and mass are correlated with high tolerance to heat; Davis et al. 1971; Diprose et al. 1984; Gashaw & Michelsen 2001). It must, however, be noticed that, for each invasive species, response to soil microwave heating was tested on seeds originating from a single population: the response could thus be population-specific (Wahid et al. 2007) and not reflect the average response of the species. To generalize our results, experiments examining the response of several populations should be implemented.

Regarding the dominant plant families in the seed bank, Asteraceae and Poaceae exhibited very different seedling emergence responses compared to Fabaceae. While Asteraceae and Poaceae showed a drastic decrease in the number of seedling emergences after microwave treatment compared with the control (e.g. absence of seedling emergence in the 2kW8min treatment), Fabaceae showed no significant response to soil microwave heating. Most Fabaceae species produce hard seeds (Baskin & Baskin 1998), characterized by a thick seed coat impermeable to water and/or gases and which imposes physical dormancy (Herranz et al. 1998). Hard seeds are highly resistant to extreme temperatures (Bradbeer 2013) and can be softened by short exposure to high temperatures (i.e. 60–100°C for 5 minutes; Lodge et al. 1990; Baskin & Baskin 1998; Herranz et al. 1998). The absence of significant response of Fabaceae to soil microwave heating suggests that the treatments do not overcome seed dormancy, nor inhibit seedling emergence. Some Fabaceae seeds, resistant to high temperatures, may remain dormant in soil. To assess the proportion of dormant seeds, complementary experiments should test the sensitivity of a controlled number of Fabaceae seeds to microwave treatment, followed by a viability test. Adaptation of the treatment (e.g. longer treatment, higher power) may be required to eradicate Fabaceae seed banks, as well as seeds of other species having a high resistance to heat (e.g. adapted to fire; Overbeck et al. 2006). It should also be noticed that the number of Asteraceae and Fabaceae seedlings recorded during the experiment is small: additional experiments using a larger number of seeds should be conducted to reinforce our conclusions. Further experiments to determine how seed traits can influence the effectiveness of microwave treatment (i.e. size and/or mass, coat characteristics, type of dormancy, composition, etc.) are needed to explain differences in seedling emergence.

In addition to a species-specific response to heat, the few seedlings observed after the most intensive treatments (i.e. 4kW4min and 2kW8min) could also be the result of nonuniform microwave heating of soil samples. Brodie (2011) found the hottest place in the heating pattern of a soil cylinder a few centimeters below the surface along the center line, and temperatures at the edges of the exposed object several degrees lower than in the center (output power 750 W, after 150 seconds of heating). In our

experiment, we found seedling emergence percentages of seeds placed at the surface (0–0.5 cm depth) higher than seedling emergence percentages of seeds placed 7 cm below the surface at the periphery and in the center. As seeds' susceptibility to soil microwave treatment is due more to heat transfer from the soil than to direct interactions of seeds with microwave radiation (Nelson 1996), the reduced treatment effectiveness on seeds placed at the surface could be due to the reduction in contact between seed surface and soil. Thus, the incomplete effectiveness of even the most intensive treatments could also be explained by seed position: some seeds could have survived at the surface. As the projected design involves passing a given thickness of extracted soil through the microwave oven, such ineffectiveness at the surface would compromise the overall effectiveness of the method in the field. Solutions (i.e. technical improvements to the machine or increasing overall soil temperature during treatment) need to be found to ensure satisfactory impact on seeds located at the surface. In this experiment, the lower effectiveness of the 2kW8min treatment compared with the 4kW4min treatment can be explained by temperature variations between replicates, most likely caused by an experimental problem. We found seedlings of *S. gigantea* in the center and at the periphery in the three replicates where center temperatures were lower than 85°C, highlighting the importance of reaching a lethal temperature to inhibit seedling emergence. Between the first and the second experiments, we noticed differences in the invasive seedling emergence percentages after exposure to the 2kW4min treatment, independently of seed position in soil (close to 10 vs. 90%, respectively). The use of different germination methods could explain this variability. In the first experiment, soil samples containing seeds germinated in an outdoor greenhouse, whereas in the second one, seeds were placed in a growth chamber with optimal germination conditions.

Raising soil temperature by microwave treatment also potentially affects soil-living organisms and soil abiotic properties (Barker et al. 1972; Vela & Wu 1979; Brodie et al. 2015). Such disturbances can indirectly impact seedling emergence (Dawson et al. 1965). Soil microwave treatment could therefore decrease invasive species seedling emergence through a direct effect of heat on seeds, and in a second step, through modifications of soil properties and functioning. In the study of De Wilde et al. (2017), heating effects on soil properties and biota could not be assessed because seedling emergence was not performed on treated soil. In the present study, the significant decrease in *D. stramonium* and *S. gigantea* percentages of seedling emergence after soil exposure to the 2kW4min and 4kW4min treatments is surprising, as the longest and highly effective treatment, 2kW8min, had no impact compared with the control. Given the high variability in the percentages of seedling emergence, an experimental artifact seems the most likely explanation. The seedling emergence percentage of *R. × bohemica* sown after treatment was not impacted. These results show that a substantial proportion of invasive species seedlings is able to emerge, when sown on previously treated soil. This suggests that

microwave heating does not prevent newly arrived invasive species seeds from germinating. Consequently, this method could be less effective in the long term to control invasive species having high dispersal abilities, such as *S. gigantea*. Microwave heating induces a rapid dehydration of plant tissues, causing plant death within a few seconds of treatment (Brodie et al. 2011). Rhizomes would therefore be easily destroyed by microwave treatments used to control seedling emergence. However, it will be necessary to test the effectiveness of the method for each targeted clonal invasive species. In cases where rhizomes are buried too deep in soil to be extracted, this method would be less suitable.

Because this method would lead to bare soil cleared of viable seeds favorable to plant recolonization, restoration measures such as rapid revegetation would be required, to recover ecosystem functions, and prevent recolonization by invasive species. It is therefore essential now to assess seedling emergence response of native species sown on previously treated soil. In addition, it would be vital to investigate the effect of soil microwave heating on ecosystem components playing essential functional roles, such as some soil abiotic parameters (e.g. pH, nutrient availability, organic matter content) and soil-living organisms (e.g. microorganisms, nematodes, insects; Neary et al. 1999; Van Der Heijden 2002; Herrick et al. 2006; Meysman et al. 2006) before applying the method in the field. The absence of selectivity of this thermal method should also be borne in mind: only after careful consideration of the impact on the whole seed bank (native and invasive species) should it be implemented. In cases where plants with high ecological values are present, efforts to ensure their survival (e.g. seed or plant individual collection) must be undertaken. By removing the upper soil layer, this method may also not be feasible on rocky and heavy (clay reach) soils, because it may cause a severe disturbance to soil structure.

In conclusion, the findings of this study lend support to developing the in situ process. Consistent with other studies, our results show that Power \times Duration pairings enabling soil to reach 85°C are effective in reducing seedling emergence of a wide variety of species. Our study also raises two major issues to be considered when selecting the power and duration of the treatment: the species-specific response to soil microwave heating and the treatment's limited effectiveness on seeds located at the soil surface. Determining more specifically which seed traits influence the effectiveness of microwave treatment is the next step in refining the applicability of the method. Our results indicate that prior exposure of soil to microwave treatment does not prevent seedling emergence of a considerable proportion of invasive species sown after treatment, suggesting that invasive species would be able to reinvade previously treated soils. This control method should therefore be coupled with restoration measures (e.g. rapid revegetation) to occupy niches that will not be available to invasive species colonization. This result also suggests that this method could be less suitable to control invasive species having high dispersal abilities because of their rapid recolonization potential. The suitability of the

method to control invasive plants reproducing by rhizomes must also be assessed. Finally, it will be essential to test the effectiveness of this process in different soil types, especially in rocky and heterogeneous ones.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Characteristics of the invasive species tested.

Table S1. Seed bank composition classified by group (dicotyledon or monocotyledon), family, and species.

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