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The effect of temperature and exposure time on redroot pigweed (*Amaranthus retroflexus*) and yellow foxtail (*Setaria pumila*) seed mortality in the natural soil seedbank

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Research Article

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Abstract

Heat disinfection of soil can be used to reduce the content of the soil seedbank. However, species differ in the lethal temperature needed for seed destruction and mortality. Laboratory research was conducted on the seeds of two weed species, redroot pigweed (*Amaranthus retroflexus* L.) and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult]. The soil samples were collected at the experimental station Šašinovečki Lug, Zagreb, Croatia (45.850289°N, 16.180465°E), and exposed to linearly increasing constant temperatures of 40, 50, 60, 80, 100, and 120 C and exposure times of 30, 60, and 90 min in a laboratory oven. Weed seeds were then extracted from the soil using the sieve separation method and survival was measured by germinating seeds on filter paper. Germination counts were converted into percentages of mortality compared with untreated seeds. The results show that both temperature and exposure time significantly affected seed mortality of both weed species. *Amaranthus retroflexus* shows a greater susceptibility to high temperatures than *S. pumila.* A fitted three-parameter sigmoid model was used to define the relationship between temperature and exposure time needed for 50% (LT_{50}) and 90% (LT_{90}) seed mortality. The estimated LT_{50} values for *A. retroflexus* are 58.89 to 46.08 C over the 30- to 90-min exposure times; the estimated LT_{90} values were 113.36 to 65.72 C for the same durations. The estimated LT_{50} values for *S. pumila* over the 30- to 90-min exposure times ranged from 91.33 to 75.15 C; the estimated LT_{90} ranged from 98.79 to 90.32 C over the same durations. The research results contribute to the knowledge about the thermal sensitivity of seeds. Estimating efficacy of soil-heating treatments is essential when comparing the environmental, economic, and social costs of alternatives to conventional weed control methods.

Introduction

Thermal treatment of soil has been used in agriculture for decades to control pests, but has recently become more attractive for weed control because of legislative changes in the European Union aimed at reducing the use of herbicides. Methods such as flaming (Knezevic et al. 2014), hot water (De Cauwer et al. 2015), steam (Melander and Jørgensen 2005), solarization (Cohen et al. 2019), and soil microwave heating (De Wilde et al. 2017) have been re-examined as possibilities for aboveground weed control (Kristoffersen et al. 2008). Additionally, heat treatments are used to remove undesirable soil organisms (pests, pathogens, and weed seeds). The purpose of soil disinfection for weed control can vary. For example, heat treatments (hot air, steam) are often used as part of experimental protocols in weed research to obtain weed-free soil (Dimaano et al. 2022; Smith and Burns 2022) or for disinfection when soil is transported and moved to other locations due to the construction of buildings, railways, and roads (Bitarafan et al. 2022).

In agricultural areas, removing weed seeds from the soil reduces future recruitment, an essential goal of sustainable weed control programs. Studies have shown that only 4% to 15% of the seeds that enter the weed seedbank germinate in a given year (Mahé et al. 2021), creating persistent seedbanks with the potential to harm crops for decades. There are practices available that are able to significantly remove weed seeds from the weed seedbank. The exception is heat treatment of soil, but this is impractical in many cases because of the cost and lack of technology to apply the heat properly. A knowledge of the economic or environmental cost of heat treatment is essential when attempting to gauge potential use of

alternative technologies such as soil heating. These costs can only be predicted with a good understanding of the effects of heat on soil-borne seeds.

The success of thermal methods of weed control depends on the weed species present in the soil and the temperature and the duration of exposure to the temperature. Weed species can have different tolerances to high temperatures, which are mainly determined by seed characteristics and seed moisture (Egley 1990; Thompson et al. 1997). Dahlquist et al. (2007) reported that the seeds of six weed species reached thermal death when exposed to temperatures above 50 C. However, susceptibility to high temperatures varied among the weed species studied. Thompson et al. (1997) found that the lethal temperature for wild oat (*Avena fatua* L.) seeds was 105 C, while redroot pigweed (*Amaranthus retroflexus* L.) seeds reached thermal death at 85 C. Hoyle and McElroy (2012) found that the temperature needed for 50% seed mortality after 20 s of exposure varied from 83 C for large crabgrass [*Digitaria sanguinalis* (L.) Scop.] to 97 C for Virginia buttonweed (*Diodia virginiana* L.).

While there are benefits of heat control, including not only weed control but also the reduction of pathogens and pests in the soil, long-term exposure to heat can have negative effects on beneficial organisms (Fenoglio et al. 2006; Roux-Michollet et al. 2008) and soil properties (Agbeshie et al. 2022). Although very effective for weed control, high-temperature methods such as flaming can reach 1,121 C (Hoyle et al. 2012) and may pose a serious threat to beneficial insects and microorganisms. Therefore, it is crucial to estimate the threshold temperature for thermal death of certain weed species in order to mitigate negative effects on soil biology.

This study investigated the effect of temperature and exposure time on two weed species, *A. retroflexus* and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult], problematic annual summer weeds on agricultural land worldwide. In Croatia, *A. retroflexus* is the third most common annual dicotyledonous weed species, while *S. pumila* is the second most common annual monocotyledonous species (Šarić et al. 2011) in arable fields. The long-term presence of these species in crops globally is also made evident by the development of resistance to repeatedly applied herbicides. Currently, 51 cases of herbicide resistance in *A. retroflexus* and five cases of resistance in *S. pumila* are known worldwide (Heap 2023). The species are characterized as prolific seed producers with a production of 230,000 to 500,000 seeds of *A. retroflexus* and 3,600 to 12,000 seeds of *S. pumila* per plant (Peters and Yokum 1961; Stevens 1957). The dormancy of these two species is described as non–deep physiological dormancy (Baskin and Baskin 2004). A small proportion of the buried seeds of *A. retroflexus* remain viable for more than 30 yr (Crocker 1916), but Egley and Chandler (1983) found that only 1% of the seeds are still viable after 5.5 yr. In addition, the depth to which seed is sown can also influence the viability of the seeds. For example, seed buried 107-cm deep in Duvel's burial experiment had a germination percentage of 48% after 10 yr (Goss 1924; Toole 1946). *Setaria pumila* seeds lose their viability after 3 yr of burial in the soil (Masin et al. 2006).

The aim of the experiment was to determine mortality of *A. retroflexus* and *S. pumila* in the natural soil seedbank when exposed to linearly increasing constant temperatures (40, 50, 60, 80, 100, and 120 C) and exposure times (30, 60, and 90 min). In addition, the lethal temperature was estimated for 50% (LT_{50}) and 90% (LT_{90}) of the seed mortality of *A. retroflexus* and *S. pumila* at each exposure time (30, 60, and 90 min).

Materials and Methods

Soil Sampling and Preparation

Soil sampling was carried out on November 2, 2022, at the Experimental Station of the University of Zagreb, Faculty of Agriculture, Šašinovečki Lug (45.850289°N, 16.180465°E) on a 2-ha arable field. The soil was silt loam (11.6% sand, 66.9% silt, and 21.5% clay) with 2.7% humus, 1.3% organic carbon content, and a pH (H_2O) of 8.2. The site was previously cultivated with soybean [*Glycine max* (L.) Merr.] that was harvested on October 13, 2022. The soil samples were collected in a W-shaped pattern across the field (Forcella et al. 1992). A total of 190 topsoil samples were collected to a depth of 5 cm (Csontos 2007) using a 5-cm-diameter soil probe (Sample Liner, Eijkelkamp Soil & Water B.V., Royal Eijkalkamp, Giesbeek, The Netherlands), which corresponds to a total soil sample volume of 19,000 cm^3 (28.5 kg). The soil samples were taken at a depth of 5 cm to collect the newly dispersed seeds in the soil seedbank together with aged seed in the soil seedbank (Clements et al. 1996; Gardarin et al. 2010). The soil samples were then mixed into a homogeneous sample and stored in a plastic container (54.8 by 38.4 by 28.3 cm) in the dark at 5 C until the start of the experiment on March 2, 2023 (González and Ghermandi 2012).

Soil Disinfection

Soil samples were exposed to temperatures of 40, 50, 60, 80, 100, and 120 C and for durations of 30, 60, and 90 min in a laboratory oven (UF 260, Memmert, Germany). The oven was allowed to stabilize for 1 h at each temperature before samples were heated. In total there were 19 treatments in one run (6 temperatures × 3 exposure times = 18 treatments + control treatment). The soil was divided into three subsamples (250 g), and each subsample was considered a replicate of a treatment, giving a total of 57 samples in one experiment. The soil samples were sieved through a 0.2-cm mesh and spread in a 2-cm-thick layer on a metal plate (25 by 55 cm) before being placed in the laboratory oven. The control treatment contained the soil sample that was not subjected to the heat treatment. This non-disinfected soil was used to isolate weed seeds and determine the quantity, composition, and germination of *A. retroflexus* and *S. pumila* seeds in the natural seedbank. After soil disinfection was completed for each treatment, the soil and the seeds it contained were allowed to cool to room temperature for 24 h before seed extraction was performed.

Seed Extraction from the Soil

The soil seedbank was analyzed separately for each of the 114 samples (57 samples × 2 runs) of the heat-treated soil. Each subsample was pretreated with 20 g of sodium hexametaphosphate ($Na_6[(PO_3)_6]$, Sigma-Aldrich Chemie 68915-31-1, Steinheim, Germany) in 500 ml of tap water (20 C) for 20 min to dissolve the structural aggregates (Malone 1967). Seed extraction was performed using the sieve technique. The subsamples were washed with running water through a system of four sieves (3, 1.25, and 1 mm and 630 µm). A vibrating sieve machine (AS 200 Basic, Retsch, Haan, Germany) was used for sieving, with the shaking time set to 5 min at an amplitude of 1.2 mm. After the soil was washed, the residue in the sieve was placed on filter paper sheets so weed seeds could be isolated and identified under a magnifying glass.

Germination Test

Isolated seeds of *A. retroflexus* and *S. pumila* exposed to the studied temperatures and exposure times were placed in 9-cm-diameter

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glass petri dishes lined with two Whatman No. 1 filter papers (Sigma-Aldrich, Steinheim, Germany) and moistened with 4 ml of distilled water. The petri dishes were sealed with Parafilm® (The Paul Marienfeld GmbH & Co. KG, Lauda-Königshofen, Germany) to prevent evaporation and placed in a climate chamber (HCP 108, Memmert, Schwabach, Germany) at a constant temperature of 24 C with 70% humidity and a 12-h day/12-h night photoperiod. The light intensity in the chamber was 40 to 50 µmol m^{-2}. Germination was recorded 2 wk after sowing. The seeds were considered germinated when the radicle was 1 mm in size. The tetrazolium test was not performed, as it was not possible to remove or pierce the seed coat of *A. retroflexus* without destroying the embryo (Dahlquist et al. 2007; Vidotto et al. 2013).

Statistical Analysis

Statistical data analyses were performed in the R software and environment v. 4.1.1 (R Core Team 2022). The relative seed mortality (RSM) was determined using the following calculation (adapted from Hoyle and McElroy 2012):

$$RSM = 100 - \left(\frac{\%germ\ treat}{\%germ\ control}\right) \times 100 \quad [1]$$

where % germ treat is the germination measured after heat treatment, and % germ control is the germination measured for seed extracted from the nontreated soil.

The data were the mean of two runs, and there was no significant difference between two experimental runs. A two-way ANOVA was performed to analyze the effect of temperature and exposure time on seed mortality. Data were checked for normality and homogeneity of variance by graphical inspection of residuals and Levene's test. Transformation did not improve the homogeneity of variance; therefore, original values were subjected to further analysis. To compare the effect of heat treatment on RSM, estimated marginal means (Searle et al. 1980) were generated using the R package EMMEANS (Lenth 2023), and means were separated with Tukey's honestly significant difference (HSD) test at $P \leq 0.05$.

To estimate the lethal temperature parameters (LT_{50} and LT_{90}), the data were subjected to dose–response analysis using R package DRC (Ritz et al. 2015). RSM (%) at different temperatures and exposure times was fit to a three-parameter Weibull function (W1.3 and W2.3). The Akaike information criterion (AIC) was used to select the best model (lowest AIC score). The goodness of fit of all selected models was determined using the R^2 and root mean-square error (RMSE) values. The 95% confidence intervals for LT_{50} and LT_{90} at different exposure times were determined using a bootstrap method (Efron 1979). The LT_{50} and LT_{90} values were compared according to criterion of overlap of the 95% confidence intervals. If there was no overlap of the confidence intervals, the difference was determined to be significant.

Results and Discussion

Composition of the Soil Seedbank

Analysis of the soil seedbank taken from the field previously sown with soybean revealed the presence of seeds of nine different weed species, including the two studied species, *A. retroflexus* and *S. pumila*. A total density of 15,768 seeds m^{-2} at the 5-cm depth were isolated in the experiment, of which 13,756 were seeds of *A. retroflexus* and 1,346 were seeds of *S. pumila*.

Table 1. The results of the two-way ANOVA for the relative seed mortality (%) of *Amaranthus retroflexus* and *Setaria pumila* at different temperatures (40, 50, 60, 80, 100, and 120 C) and exposure times (30, 60, and 90 min) of the seeds

		F_{exp}/PR > F % Relative seed mortality (RSM)	
Sources of variability	*n*–1	*Amaranthus retroflexus*	*Setaria pumila*
Temperature (T)	5	242.6579***	1,104.007***
Exposure times (ET)	2	9.6387**	49.744***
T × ET	10	2.2017*	22.306 ***
Residuals	54		

*P = 0.05.
**P = 0.01.
***P < 0.001.

Other species were present in smaller quantities (number of seeds per square meter indicated in parentheses), such as barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] (441), spotted ladysthumb (*Polygonum persicaria* L.) (77), common ragweed (*Ambrosia artemisiifolia* L.) (72), birdeye speedwell (*Veronica persica* Poir.) (34), jimsonweed (*Datura stramonium* L.) (26), black bindweed [*Polygonum convolvulus* L.] (11), and prostrate knotweed (*Polygonum aviculare* L.) (5).

Initial germination of seeds isolated from the control soil sample without prior heat treatment showed germination of 58.6% of *S. pumila* seeds and 40.3% of *A. retroflexus* seeds. The percentage of germination of the two species analyzed and the amount of seed isolated from the soil provide information about the age of the seedbank in the soil. The field from which the soil samples were taken is an experimental field that has been continuously infested for the last 12 yr.

RSM

The results of the two-way ANOVA showed that both temperature and exposure time influenced mortality of *A. retroflexus* and *S. pumila* seeds (Table 1). In general, all temperature treatments reduced RSM of the weed species *A. retroflexus*, with overall RSM ranging from 18.0% to 100.0% (Figure 1). The lowest RSM was determined at a temperature of 40 C (18.0% to 19.8%). Starting at 50 C for 30 min, there was a significant difference in RSM compared with all time intervals of exposure at 40 C. The RSM increased with the exposure time from 49.6% for 30 min to 70.2% for 90 min. At 60 C for 90 min, RSM of *A. retroflexus* was 80%, but not significantly different from the treatments at 80 C in all intervals. RSM was 100% for all durations at 100 and 120 C, with no significant differences between temperature and exposure time.

Similar results have been reported by other authors for *A. retroflexus*. Ye and Wen (2017) studied the effects of high temperatures on two *Amaranthus* spp. in the temperature range of 30 to 95 C. Germination of Joseph's coat (*Amaranthus tricolor* L.) was reduced by 60% to 70% after treatment at 60 C for 30 min. In contrast, the viability of spiny amaranth (*Amaranthus spinosus* L.) was unaffected under the same conditions (60 C for 30 min), indicating the different sensitivities to high temperatures, even among species belonging to the same family and genus and having a similar seed structure. A similar pattern can be observed in species belonging to the Asteraceae family. Wen (2015) found that only 40% of the seeds of tree marigold [*Tithonia diversifolia* (Hemsl.) A. Gray; Asteraceae] germinated at 60 C for 30 min, while no seeds survived at 65 C or above. In contrast, Yuan and Wen (2018) studied the effect of heat from 30 to 95 C on the

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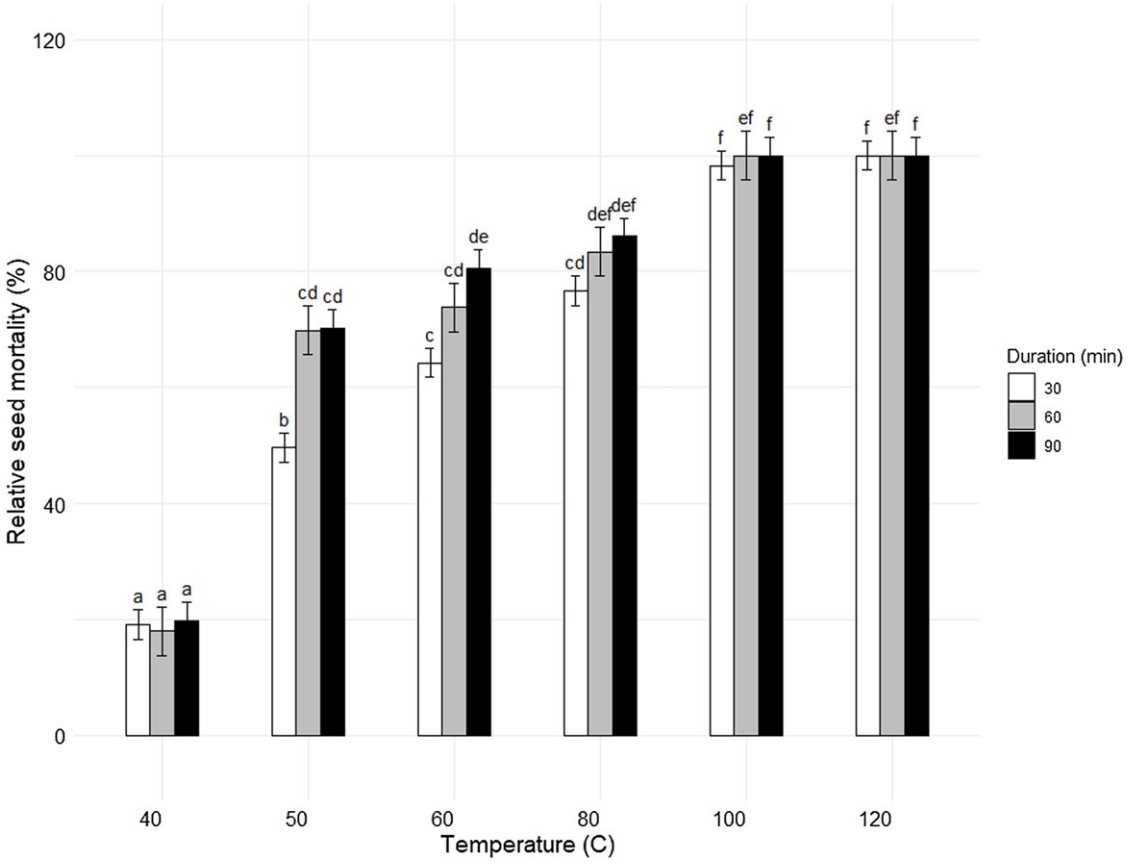

Figure 1. Effect of temperature (40, 50, 60, 80, 100, and 120 C) and exposure time (30, 60, and 90 min) on relative seed mortality (RSM) of *Amaranthus retroflexus*. The same letters indicate means are not significantly different ($P < 0.05$) when tested with Tukey's honestly significant difference (HSD) test.

seeds of three Asteraceae species, redflower ragleaf [*Crassocephalum crepidioides* (Benth.) S. Moore], Canadian horseweed [*Conyza canadensis* (L.) Cronquist], and tropical whiteweed (*Ageratum conyzoides* L). All seeds failed to germinate after being heated to 55 C (for *C. crepidioides* and *C. canadensis*) or 60 C (for *A. conyzoides*) and above for 30 min.

Temperature and duration of exposure had less effect on *S. pumila* seeds (Figure 2) compared with *A. retroflexus* seeds (Figure 1). RSM at temperatures of 40, 50, and 60 was minimal for all exposure durations. The only exception was the treatment at 90 min at 60 C causing a maximum of 16.17% RSM, which was not significantly different from seeds that were exposed for 30 or 60 min at 80 C. However, a significantly higher percentage of RSM was observed at 80 C for 90 min (64.6%). At temperatures ≥100 C, RSM was ≥93.3%. Germination for both species was nil at 100 and 120 C for all exposure durations.

There is a lack of studies investigating the effects of high temperatures on the seeds of *S. pumila*. However, similar studies were conducted for other species belonging to the Poaceae family. Dahlquist et al. (2007) reported 100% germination reduction of *E. crus-galli* exposed for 17 min at 70 C and concluded that *E. crus-galli* is much more susceptible to heat treatment compared with black nightshade (*Solanum nigrum* L.), common purslane (*Portulaca oleracea* L.), and tumble pigweed (*Amaranthus albus* L.). In contrast, Vidotto et al. (2013) and Bàrberi et al. (2009) observed that *E. crus-galli* is less susceptible to heat treatment than *A. retroflexus* and *P. oleracea*. Clark and French (2005) investigated the response of 22 Poaceae species to heat by studying germination after exposure to three temperatures of 40, 80, and 120 C for 2 min in a gravity convection oven. The results showed no pattern between the Poaceae species. However, in most of the species studied, germination increased upon exposure to higher temperatures. Similarly, González-Rabanal and Casal (1995) studied the effect of high temperature on 10 species, including three Poaceae: bristlegrass (*Agrostis curtisii* Kerguelen), bentgrass (*Agrostis delicatula* Pourr. ex Lapeyr.), and *Avenula marginata* (Lowe) Holub. at two temperatures (80 and 110 C) for 5 min. The germination of these species was slightly (2% to 10% compared with the control) or not at all affected when exposed to the aforementioned temperatures. In both studies, species were exposed to high temperatures for only a short time (2 and 5 min). In our study, the RSM of *S. pumila* at 80 C for 90 min (64.6%) was significantly different from RSM at the same temperature and shorter exposures (30 and 60 min; 8.8% and 18.9%, respectively). Similarly, Smith et al. (1999) exposed the seeds of two grass species, compact needlegrass [*Austrostipa compressa* (R.Br.) S.W.L. Jacobs & J. Everett] and perennial veldtgrass (*Ehrharta calycina* Sm.), to 70, 80, or 90 C for 10, 20, 30, or 60 min. At 90 C, 37% of *A. compressa* seeds survived 30 min of heat, but only 4% germinated after 60-min exposure. Similarly, in our study, 30 min of exposure to 80 C caused 76.6% RSM of *S. pumila*. The seeds of *E. calycina* survive at 70 or 80 C for up to 60 min, as did *S. pumila* seeds in our study, for which 100% RSM was observed only for 60 min exposure at 100 C.

Lethal Temperature Model

The temperature at which seed mortality was reduced by 50% and 90% at different exposure times was estimated using the fitted

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Table 2. Estimated lethal temperatures required for 50% (LT_{50}) and 90% (LT_{90}) of seed mortality and model performance metrics (coefficient of determination [R^2] and root mean-square error [RMSE]) for the seeds of the species *Amaranthus retroflexus* (AMARE) and *Setaria pumila* (SETPU) at different exposure times

Weed species	Exposure time (min)	LT_{50} (±SE)	±95% CI[a]	LT_{90} (±SE)	±95% CI[a]	R^2	RMSE
AMARE	30	54.9 (2.8)	5.9	113.4(19.2)	40.0	0.95	6.06
	60	46.1 (1.4)	2.9	65.3 (6.8)	14.2	0.88	9.84
	90	46.6 (0.9)	1.9	65.7 (4.2)	8.7	0.94	6.99
SETPU	30	91.3 (1.1)	2.3	98.8 (1.3)	2.7	0.99	0.99
	60	84.5 (1.0)	2.0	95.0 (3.1)	6.5	0.99	0.99
	90	75.2 (0.9)	1.8	90.3 (1.8)	3.6	0.99	0.99

[a]CI, confidence interval.

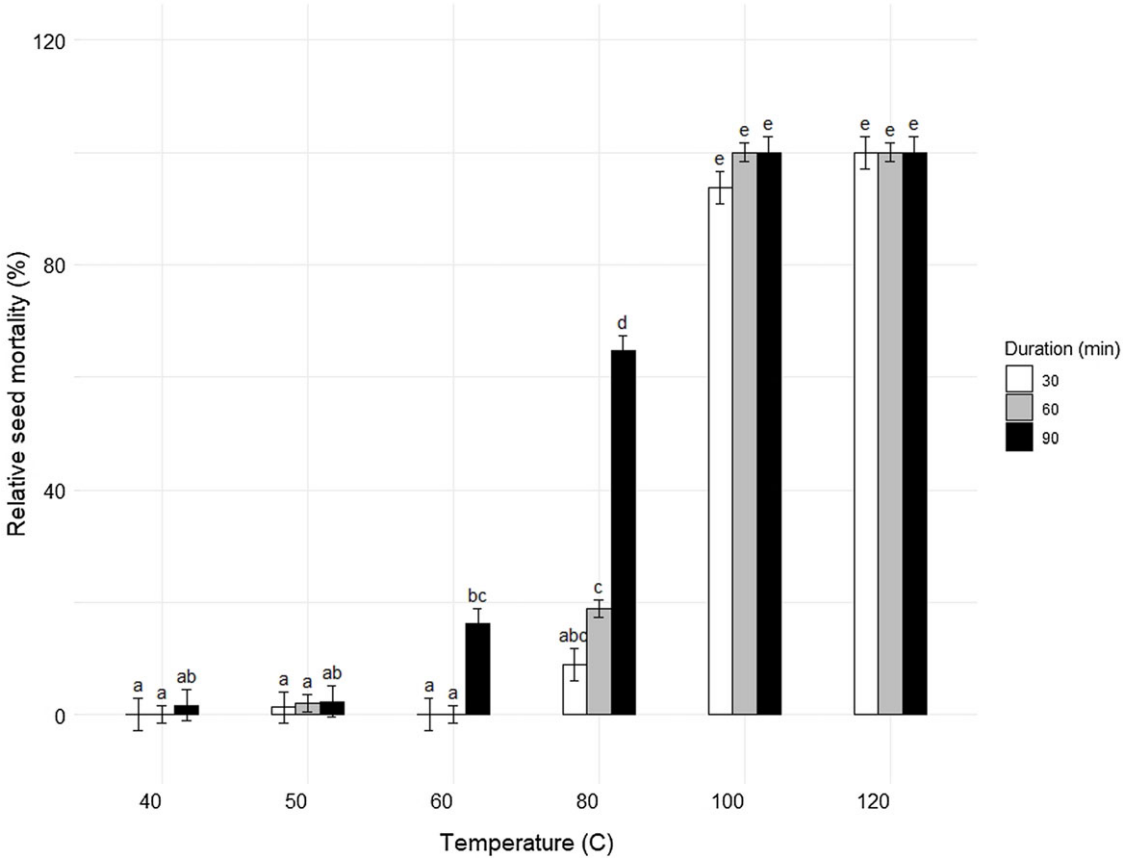

Figure 2. Effect of temperature (40, 50, 60, 80, 100, and 120 C) and exposure time (30, 60, and 90 min) on relative seed mortality (RSM) of *Setaria pumila*. The same letters indicate means are not significantly different ($P < 0.05$) when tested with Tukey's honestly significant difference (HSD) test.

three-parameter sigmoid model. Separate models were created for each exposure time (30, 60, and 90 min) and temperature (40, 50, 60, 80, 100, and 120 C).

For *A. retroflexus*, overlap was found between the estimated LT_{50} and LT_{90} temperature at different exposure times in the 95% confidence intervals between LT_{50} at 60 and 90 min of exposure (46.1 ± 1.4 and 46.3 ± 0.9 C). In addition, the estimated LT_{90} values at 60 and 90 min (65.3 ± 6.8 and 65.7 ± 4.2 C) of exposure also overlapped in the 95% confidence intervals, so that no statistical difference was found at these lethal temperatures (Table 2). Vidotto et al. (2013) estimated the LT_{99} for *A. retroflexus* to be 70.9 C. Compared with the other species included in the study, *A. retroflexus* was found to be the second most sensitive species to high temperatures, while *E. crus-galli* and green foxtail [*Setaria viridis* (L.) P. Beauv.] were found to be less sensitive, with estimated LT_{99} values of 79.6 and 75.8 C, respectively.

The estimated LT_{50} temperatures for *S. pumila* at 30, 60, and 90 min ranged from 75.2 ± 0.9 to 91.3 ± 1.1 C, with the temperature increasing as the exposure time was shortened (Table 2). Statistical difference was found between the estimated temperature of LT_{50} at different exposure times. In contrast, the estimated temperatures for LT_{90} at three exposure times ranged from 90.3 ± 1.8 to 98.8 ± 1.3 C and overlapped in the 95% confidence intervals, so no statistical difference was found between these temperatures. In Vidotto et al. (2013) estimated the temperature needed for 99% germination reduction for the closely related species *S. viridis* to be 75.8 C, which is lower than the temperatures estimated for *S. pumila* in this study.

The temperature differences needed for a 50% germination reduction have even been found in different populations of the same species. For example, Bitarafan et al. (2022) estimated 50% and 90% seed mortality of four *E. crus-galli* populations in the

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range of 62 to 68 C and 76 to 86 C, respectively, during soil steaming (0.5, 1.5, 3, and 9 min). They found no effect of duration on seed mortality. In addition, Wang et al. (2018) found that the differences between three populations of the grass species Japanese foxtail (*Alopecurus japonicus* Steud.) at the estimated temperature for 50% germination reduction (5-min heat shock with soaked seed) were 72, 95, and 104 C, respectively. Similarly, Bolfrey-Arku et al. (2011) estimated the temperature for 50% germination reduction of two Philippine populations of itchgrass [*Rottboellia cochinchinensis* (Lour.) W.D. Clayton] to be 145 and 151 C. Also, Weller et al. (2019) estimated the temperature difference for 50% germination reduction between seeds of the annual weed red sprangletop [*Dinebra panicea* var. *brachiata* (Steud.) P.M. Peterson & N. Snow] collected in two different years (2015 and 2016) to be 93 and 99 C, respectively. Temperatures needed for 50% germination reduction were also estimated by Fernando et al. (2016) for another grass weed, feather fingergrass (*Chloris virgata* Sw.). The estimated temperature for 50% germination reduction was 88 C for presoaked seeds and 119 C for dry seeds. Differences between dry and presoaked seeds in terms of lethal temperature were also observed for the annual winter grass Tausch's goatgrass (*Aegilops tauschii* Coss.), where the temperature for 50% germination was 110 C for dry seeds and 70 C for presoaked seeds.

The heat sensitivity of the two species studied is different, with *A. retroflexus* showing greater susceptibility to high temperatures than *S. pumila*. According to the cited sources, the differences in temperature sensitivity were explained by various factors, such as seed size, seed structure, and protein content. Moonen et al. (2002) reported that seed size does not seem to play a role in heat sensitivity. Several authors (Andreasen et al. 2018; Jakobsen et al. 2019; Vidotto et al. 2013) found that large seeds are less sensitive to heat than small seed species. In addition, Bitarafan et al. (2022) investigated the sensitivity of four Norwegian and one Polish population of *E. crus-galli* and found that the Norwegian population, which had the smallest seed (1,000-seed weight: 0.97 g), was more sensitive to temperature than the other three populations (1,000-seed weight: 1.11 to 2.57 g). The seeds of *A. retroflexus* and *S. pumila* used in this study have dimensions (length by width) of 1.15 by 0.90 and 3.30 by 2.06 mm, and 1,000-seed weights of 0.48 and 3.09 g, respectively (unpublished data). It is evident that the seeds of *A. retroflexus* are smaller than those of *S. pumila*, which could explain the higher sensitivity of *A. retroflexus* to temperature. Apart from seed size, the protein content of seeds could also play a role in sensitivity to high temperatures.

Further research should focus on harmonizing the methodology while investigating the effects of heat on weed seeds. Currently, there are various approaches, such as placing the seeds in bags and burying them in the soil (Bitarafan et al. 2022; Fernando et al. 2016; Wang et al. 2018, 2020); placing the seeds in aluminum plates and directly in the oven (Mahmood et al. 2016; Weller et al. 2019); placing the seeds in triangular flasks and water baths (Wen 2015; Ye and Wen 2017; Yuan and Wen 2018); and removing the soil from the field, exposing it to high temperatures in the oven, and then allowing the seeds to emerge in the greenhouse (Melander and Jørgensen 2005; Read et al. 2000). In contrast to the majority of studies, the seeds analyzed in this study were sourced from the natural soil seedbank and extracted directly from the soil from a depth of 5 cm. In accordance with physical methods of weed control such as flaming, soil steaming, and soil solarization, the heat that penetrates the soil decreases with depth, and thus the mortality decreases with depth (Melander and Jørgensen 2005). Therefore, knowledge of the heat sensitivity of certain species is in practice more useful for the seeds in the upper soil layer. This approach enables more accurate simulation of field heat application and the observation of its effects on the natural soil seedbank under controlled laboratory conditions. The translation of temperature and exposure time to the practical application depends on the technology used, for example, soil steaming can cause faster soil heating than soil solarization. According to Horowitz et al. (1983), the temperature at a depth of 5 cm under the transparent films used for soil solarization increased the average soil temperature of 9.3 C compared with the soil without film cover. The temperature at a depth of 5 cm reached between 39.7 and 49.5 C, depending on the type of polythene film. At a depth of 15 cm, the temperature did not exceed 36 C, regardless of the type of polythene film. In contrast, temperatures of up to 100 C were recorded for about 10 min at a depth of 15 cm when the soil was steamed (Raffaelli et al. 2002). The valuable information here is therefore the sensitivity of the seed to high temperatures at different exposure times, which gives insight into the effect a certain physical weed control technique could have on some weed species.

The results of this study could be useful to predict the efficacy of soil heating to reduce the weed seedbank. Because *A. retroflexus* and *S. pumila* had the highest emergence from the 2-cm-thick layer (Dowsett et al. 2018; Khan et al. 2022), using the estimated lethal temperature should provide good results for seeds in this topsoil layer.

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