

Time and Temperature Requirements for Weed Seed Thermal Death

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Mortality of weed seeds at temperatures of 39, 42, 46, 50, 60, and 70 C was recorded through time under controlled laboratory conditions similar to those of soil solarization for six weed species: annual sowthistle, barnyardgrass, black nightshade, common purslane, London rocket, and tumble pigweed. Time and temperature requirements for thermal death varied considerably among the species studied. Barnyardgrass, London rocket, and annual sowthistle were more susceptible to heat treatment than black nightshade, common purslane, and tumble pigweed. Temperatures of 50 C and above were lethal for seeds of all species. Common purslane seeds were unaffected at 46 C and below, tumble pigweed and barnyardgrass seeds were unaffected at 42 C and below, and black nightshade seeds were unaffected at 39 C. Nonlinear models for mortality as a function of duration of heat treatment were developed for each species at each temperature at which mortality occurred. These models provide an empirical relationship for the construction of field-applicable decision models that could predict the accumulation of time and temperature combinations for effective solarization of weed seeds.

Nomenclature: Annual sowthistle, *Sonchus oleraceus* L. SONOL; barnyardgrass, *Echinochloa crus-galli* (L.) Beauv. ECHCG; black nightshade, *Solanum nigrum* L. SOLNI; common purslane, *Portulaca oleracea* L. POROL; London rocket, *Sisymbrium irio* L. SSIYR; tumble pigweed, *Amaranthus albus* L. AMAAL.

Key words: Soil solarization, methyl bromide alternatives.

Soil solarization is a hydrothermal process of soil disinfection that reduces populations of weed seeds and other pest organisms in the soil (Stapleton and DeVay 1986). It is used commercially on a limited but increasing scale in warmer areas around the world (Stapleton 2000). Most commercial growers currently using solarization in California are organic or small farm producers, whereas larger acreage growers tend to rely on the use of fumigant chemicals as soil disinfectants. Reliance on fumigants is due in part to solarization being a knowledge-based rather than a product-based technology, with a resulting lack of technical support and reliable treatment guidelines compared with chemical fumigation (Stapleton et al. 2000). Although the California Department of Food and Agriculture has recently approved treatment guidelines for solarization as a nematicidal treatment for container nursery plants (CDFA 2002), treatment guidelines for solarization in the field are currently limited to a general recommendation of 3 to 6 wk treatment during hot summer months (Stapleton 2000).

To develop reliable treatment guidelines for solarization, data are needed to determine the temperatures and duration of treatment required for control of specific pests. Insufficient accumulation of heat may result in inadequate control, as weed seed thermal death occurs above a threshold temperature that varies for each species and may be influenced by environmental factors such as soil moisture and depth of seeds. Field evaluations of solarization have shown that soil temperatures above 45 C can reduce emergence of seeds of annual weed species such as common purslane (Horowitz et al. 1983) and annual bluegrass (*Poa annua* L.) (Peachey et al. 2001). Soil temperatures may exceed the threshold temperature for weed seed thermal death for only a few hours each day, and so the effects of high temperatures are accumulated in short, repeated events (Horowitz and Taylorson 1983). The cumulative number of hours at which soil temperatures exceed the threshold can be calculated to estimate the duration of

treatment necessary for control. For example, Peachey et al. (2001) found that over a solarization period of 24 d, a cumulative total of 66 h of temperatures above 45 C effectively reduced survival of annual bluegrass seed. This method provides a rough estimate that can be obtained from field experiments, but specific time and temperature data obtained under controlled environmental conditions are necessary to develop models that can be used for treatment guidelines.

Limited information exists on specific time and temperature requirements for control of soilborne pests with solarization. Time and temperature data have been determined for seeds of some weed species at selected lethal temperatures, although laboratory conditions such as exposure to moisture vary among studies (Egley 1990; Hesketh 1984; Horowitz and Taylorson 1983; Rubin and Benjamin 1984). However, these data have not been incorporated into models that could be used to predict weed seed mortality under temperatures reached during solarization. Thermal death curves (log time vs. temperature) have been developed for the fungal pathogens *Verticillium dahliae*, *Pythium ultimum*, *Rhizoctonia solani*, and *Thielaviopsis basicola* (Pullman et al. 1981). Models relating weed seed mortality to temperature using thermal degree hours have been generated for the weed species sterile oat (*Avena sterilis* L.), riggut brome (*Bromus diandrus* Roth), and wild mustard (*Sinapis arvensis* L.) (Economou et al. 1998). Also, a model has been developed that uses the Richards function (Causton et al. 1978) to describe the effects of alternating temperatures on sprouting of purple nutsedge (*Cyperus rotundus* L.) tubers (Miles et al. 2002).

We conducted thermal death studies on six weed species at constant temperatures. Our objectives were to (1) determine percentage mortality of seeds at a range of time and temperature values for each weed species and (2) develop models predicting percentage mortality as a function of time and temperature.

Materials and Methods

Laboratory experiments were conducted to determine the duration of heat treatment required for seed mortality of six

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weed species at six constant temperatures. Temperatures were chosen to reflect the range of temperatures reached during solarization (Stapleton 2000). The six weed species studied were barnyardgrass, London rocket, common purslane, black nightshade, annual sowthistle, and tumble pigweed. These species were selected to represent a range of thermal sensitivities and responses to solarization (Hesketh 1984) as well as to include summer and winter growth habits. Two species, London rocket and annual sowthistle, are pests of fall and winter crops. Barnyardgrass, common purslane, tumble pigweed, and black nightshade are problematic in spring and summer crops. Common purslane can be particularly problematic as the seeds are heat tolerant (Egley 1990) and can survive some solarization treatments.

Preparation of Seed for Treatment. All seeds were collected in 1997 from plants growing wild around Fresno, CA, and all experiments were conducted at the University of California Kearney Agricultural Center in Parlier, CA. Seeds were placed in nylon organdy packets of 3.5 cm diam, which were closed with wire twist ties. A short length of cotton string was attached to each bag to facilitate sample removal. Each bag contained the number of seeds required for 10 seeds to germinate, determined from the percentage germination of seed lots of each species. The number of seeds in each bag was 10 for barnyardgrass, 11 for London rocket, 15 for annual sowthistle, 10 for black nightshade, 10 for tumble pigweed, and 13 for common purslane. To simulate moist field conditions before treatment by solarization, the packets of seeds were submerged for 5 s in deionized water and then placed between moist paper towels in a plastic box to imbibe water for 24 h before the heat treatment. The only exception was common purslane, which was submerged 2 h before heat treatment, to prevent premature germination. The shortened imbibition time for common purslane ensured that common purslane did not germinate before the heat treatments. Seeds of London rocket were surface-sterilized with 0.5 % bleach before imbibing water.

Packets were buried at a depth of 7 cm in 0.47-L microcosms, one species per microcosm. Microcosms consisted of 0.47-L mason-type canning jars, 8.5 cm diam, and 12.5 cm height, filled with 30-grit silica sand wetted to field capacity (10.4% moisture) with deionized water. To simulate field conditions during solarization, the tops of the jars were covered with pieces of clear plastic film (Rubin and Benjamin 1984) and secured with the metal outside ring of the jar lids. The number of seed packets in each microcosm varied from three to eight depending on the number of time intervals to be studied at each temperature.

Heat Treatments. Seeds were treated at constant temperatures of 39, 42, 46, 50, 60, and 70 C. Microcosms were heated in water baths (Rubin and Benjamin 1984) using immersion circulators.^{1,2} At each temperature, several separate experiments were conducted for each species. Six microcosms (replications) per species were heated in each experiment, whereas three unheated microcosms per species were kept in a water bath at room temperature (21 C) as experimental controls and sampled concurrently with the temperature treatments.

The water baths were covered with a piece of plastic film for insulation. One packet was recovered from each

microcosm at each sampling time interval, which varied depending on species' susceptibility to heat. At all temperatures below 60 C, packets were recovered at four or more sampling times. Only three sampling times were used for each species at 60 C because removing packets at shorter intervals would not allow the temperature within the microcosms to return to the treatment temperature before the next sampling. Temperature inside the packets was monitored with thermistors attached to data loggers.³ Treatment duration was calculated beginning from the time that the treatment temperature was achieved, which was consistently about 30 min after the microcosms were placed in the water bath. The microcosms were removed from the water bath to recover the packets and immediately returned to the water bath.

At 70 C, the method was modified because sampling times were shorter than the half-hour required for the samples to reach the treatment temperature. The microcosms filled with moistened sand were sealed and placed in the water baths before adding the packets. The packets were buried in the microcosms when the sand reached 70 C and allowed to equilibrate for 6 min before starting the treatment intervals.

Germination Tests. After removal from the microcosms, seeds were taken out of the packets and placed in 100 by 15-mm petri dishes on 7-cm-diam Whatman #1 filter paper moistened with 1.4 ml of deionized water. The petri dishes were incubated in a growth chamber⁴ on a cycle of 8 h at 20 C in darkness and 16 h at 30 C with a fluorescent grow light (Standifer et al. 1984). Cumulative germination percentages were determined for each dish after 14 d of incubation (Hesketh 1984). Deionized water was added to the petri dishes as needed to maintain the original moisture level during the 14 d. Seeds were counted as germinated if the radicle had emerged and the plumule had emerged to a length of 3 mm. The percentage germination from each bag of seeds was divided by the average percentage germination of the three controls to correct for any variables besides temperature. Seeds with intact seed coats that had not germinated were stained with triphenyl tetrazolium chloride to verify that they were dead and not dormant (Moore 1973). Seeds were incubated at 30 C in triphenyl tetrazolium chloride for 6 h at 0.25% (wt vol⁻¹) for barnyardgrass, for 6 h at 1% (wt vol⁻¹) for annual sowthistle, for 5 h at 1% (wt vol⁻¹) for London rocket, and for 24 h at 1% (wt vol⁻¹) for black nightshade. Seeds with embryos stained red were considered viable. Tetrazolium tests were not feasible on common purslane and tumble pigweed because their seed coats were impermeable to tetrazolium, and it was not possible to remove or pierce the seed coat without destroying the embryo.

Data Analysis. Our experimental design was a randomized block with temperature and duration as the two independent variables. Differences among species in thermal susceptibility were analyzed using a general linear model. The dependent variable, percentage mortality, from each combination of time and temperature values was calculated for each replication using the initial germination percentage. Assumptions for use of a general linear model were tested using a univariate procedure with procedure options set for all plots in SAS.⁵

Mortality data for each species at each temperature where mortality occurred were analyzed using nonlinear regression (Myers 1986) and a model specified as follows:

Table 1. Temperature and duration of heat treatment required to achieve 100% mortality for each species.

Weed species	Temperature (C)					
	70	60	50	46	42	39
	duration for 100% mortality (h)					
Annual sowthistle	0.17	0.25	4	15 ^a	96 ^d	672 ^d
Barnyardgrass	0.17	0.25	9	16		
London rocket	0.17	0.25	6	24	96 ^a	^b
Common purslane	0.67	3	56 ^a	^c	^d	^d
Black nightshade	0.67	2	71	213	384 ^d	^d
Tumble pigweed	0.67	1	113	312	^d	^d

^a 100% mortality not obtained because of a few heat-resistant individuals in each sample.

^b Could not be evaluated because of fungal infection.

^c Seeds germinated inside packets.

^d Species not affected at this temperature.

$$m = C / \{1 + e^{[-b_1(d-b_0)]}\} \quad [1]$$

where m is mortality expressed as a percentage, d is duration in hours, C is a constant value of 1 (1.16 for black nightshade and tumble pigweed), and b_0 and b_1 are estimated parameters, with b_0 estimating the 50th percentile for mortality and b_1 as the rate at which mortality occurs. Models with an overall significance of $P < 0.001$ were selected. Pseudo R^2 values were calculated for each model using the following formula:

$$R^2 = 1 - (\text{residual sum of squares}) / (\text{corrected total sum of squares}) \quad [2]$$

Results and Discussion

Complete Mortality at Each Temperature. The time to complete mortality varied considerably among species at each temperature studied (Table 1). In general, barnyardgrass, London rocket, and annual sowthistle were much more susceptible to heat treatment than black nightshade, common purslane, and tumble pigweed. Observed duration of heat treatment required to kill 100% of weed seeds (LD_{100}) values ranged from 0.17 h at 70 C for three species (barnyardgrass, London rocket, and annual sowthistle) to 672 h at 39 C for annual sowthistle. The LD_{100} for each species and temperature was considered to be the shortest treatment interval at which all seeds at that time and temperature were dead.

At 60 C, seeds of all species were dead within 3 h. At 50 C, LD_{100} values ranged from 4 h for annual sowthistle to 113 h for tumble pigweed. An LD_{100} value was not obtained for common purslane because some relatively heat-tolerant seeds survived 56 h of heat treatment, but an LD_{90} was obtained in 23 h.

At 46 C, LD_{100} values ranged from 15 h for annual sowthistle to 312 h for tumble pigweed. Common purslane could not be studied at this temperature because it began to germinate inside the packets during the heat treatment. At 42 C, barnyardgrass, tumble pigweed, and common purslane germinated inside the microcosms during treatment. London rocket and annual sowthistle were dead at 96 h, and black nightshade was dead within 384 h.

Seeds of barnyardgrass, tumble pigweed, and common purslane were not studied at 39 C, because heat treatment at 42 C had no effect on their germination. London rocket seeds were not studied because of fungal infection, despite surface

Table 2. Subsample of intact seed tested for viability using tetrazolium after heat treatment.

Species	Temperature (C)			
	60	50	46	42
	viability (%)			
Annual sowthistle	^a	0	0	0
Barnyardgrass	0	0	0	^b
London rocket	0	2	9	4
Black nightshade	1	0	0	4

^a No intact seeds after heat treatment.

^b Species not affected at this temperature.

sterilization with 0.5% bleach. Black nightshade seeds did not germinate in the microcosms but still germinated once removed from 672 h of heat treatment. Annual sowthistle seeds remained alive without germinating for at least 384 h in the microcosms but were dead and infected with fungus by 672 h.

Evaluation of Seed Viability and Dormancy. Over 90% of all nongerminated seeds evaluated in tetrazolium tests were not viable (Table 2). At 60 C, nongerminated seeds of annual sowthistle and tumble pigweed had cracked seed coats and were assumed dead without a tetrazolium test. All nongerminated seeds of barnyardgrass and annual sowthistle, at all temperatures studied, either had cracked seed coats or were determined to be nonviable by tetrazolium tests (Table 2). According to tetrazolium tests, 0 to 9% of intact, nongerminated seeds of London rocket were viable, and 0 to 4% of intact, nongerminated black nightshade seeds were viable (Table 2). However, because these tests were only done on intact seeds, the percentage of viable nongerminated seeds out of all seeds in the experiment was $< 1\%$ except for London rocket at 46 C. These results indicated that nongerminated seeds were dead and not dormant. Nongerminated, viable seeds were not accounted for in thermal death models because they represented a very small percentage of the total seeds in each experiment. Tetrazolium tests were not feasible on common purslane and tumble pigweed because it was difficult to remove or pierce the seed coat without destroying the embryo.

Thermal Death Models. The thermal susceptibility of each species was described using Equation 1. Separate models were constructed for each temperature, and models that converged are summarized in Table 3. Percentage mortality was plotted vs. duration of treatment for each species at each temperature having lethal effects (Figures 1–6). Percentage mortality was calculated at 42, 46, and 50 C for annual sowthistle (Figure 1); 46 and 50 C for barnyardgrass (Figure 2); 42, 46 and 50 C for London rocket (Figure 3); 50 and 60 C for common purslane (Figure 4); 42, 46, 50, and 60 C for black nightshade (Figure 5); and 46, 50, and 60 C for tumble pigweed (Figure 6). Thermal susceptibility for all species increased rapidly as temperature increased, with a marked increase in mortality at 60 C.

Thermal susceptibility varied among species. London rocket, barnyardgrass, and annual sowthistle were more susceptible to heat than the other three species; these species did not survive long enough at 60 C to fit a model to the data (Table 3). Parameter values for b_0 , the estimated time to 50% mortality, can be used to compare susceptibility to heat

Table 3. Nonlinear models describing the relationship of duration of heat treatment to mortality using the equation $m = C / \{1 + e^{[-b_1(d-b_0)]}\}$, where m is mortality, C is a constant with $C = 1$ except for black nightshade and tumble pigweed at 60 C, where $C = 1.16$, d is duration of exposure at a specific temperature, and b_0 and b_1 are estimated parameters. All models were significant at $P = 0.0001$. Confidence intervals (CI) are for 95%.

Species	Temp	b_0	b_0 SE	b_0 lower CI	b_0 upper CI	b_1	b_1 SE	b_1 lower CI	b_1 upper CI
	C								
Annual sowthistle	42	29.459	0.833	27.794	31.123	0.129	0.023	0.084	0.174
	46	9.109	0.280	8.549	9.670	0.525	0.096	0.334	0.717
	50	1.313	0.054	1.205	1.42	2.665	0.297	2.073	3.256
Barnyardgrass	46	10.47	0.207	10.060	10.891	1.036	0.229	0.577	1.495
	50	3.631	0.095	3.442	3.821	1.257	0.155	0.949	1.566
London rocket	42	53.771	1.886	50.009	57.533	0.075	0.011	0.0533	0.0963
	46	14.902	0.387	14.128	15.676	0.340	0.057	0.226	0.454
	50	2.882	0.065	2.753	3.011	1.929	0.227	1.476	2.381
Common purslane	50	10.857	0.398	10.068	11.646	0.275	0.208	0.208	0.343
	60	0.449	0.048	0.354	0.544	2.571	0.372	1.829	3.312
Black nightshade	42	294.8	3.233	288.3	301.4	0.048	0.007	0.034	0.061
	46	169.1	2.254	164.6	173.6	0.080	0.012	0.057	0.104
	50	55.388	2.087	53.225	57.550	0.332	0.091	0.150	0.513
	60	1.061	0.592	0.128	0.404	1.902	0.2677	1.368	2.436
Tumble pigweed	46	235.2	2.244	230.7	239.7	0.066	0.0113	0.0437	0.0888
	50	78.435	1.380	75.685	81.185	0.077	0.010	0.056	0.097
	60	-1.543	0.796	-2.241	0.119	0.477	0.146	0.274	1.085

among species, with higher values indicating greater susceptibility to heat. At 50 C, the only temperature with models for all species, the order of susceptibility as determined by b_0 was annual sowthistle, London rocket, barnyardgrass, common purslane, black nightshade, and tumble pigweed, from most to least susceptible (Figure 7). Estimated values for b_0 for the three least susceptible species at 50 C (black nightshade, common purslane, and tumble pigweed) were 3 to 60 times as great as for the three most susceptible species (annual sowthistle, London rocket, and barnyardgrass) (Table 3). The confidence intervals of the three most-susceptible species did not overlap with the three least-susceptible species (Figure 7). This pattern also occurred at 46 C, with the exception of common purslane, which was not affected.

The LD₉₀ values calculated from the nonlinear models also demonstrate that annual sowthistle, London rocket, and barnyardgrass were the most susceptible to heat (Table 4). Annual sowthistle, London rocket, and barnyardgrass succumbed at least three times faster than the other species (Table 4). Ranking common purslane, black nightshade, and

tumble pigweed for susceptibility was difficult. Common purslane was not affected at 46 C, but black nightshade and tumble pigweed were affected. Tumble pigweed survived at least 40% longer than the other two species at 50 C, but at 60 C, black nightshade survived longest. Winter annuals (annual sowthistle and London rocket) and the only grass species tested expressed greater susceptibility to heat than spring and summer annuals, suggesting there may be differential thermal susceptibility between winter annual and spring and summer annual weed species. Proteins in seeds appear to be involved in protection from heat (Coca et al. 1994; Medina and Cardemil 1993), and these heat shock proteins may be more prevalent in species likely to experience high temperatures during germination.

Application of the Models to Field Conditions. Thermal models greatly simplify the accumulation of heat by holding time and temperature constant. In field conditions under

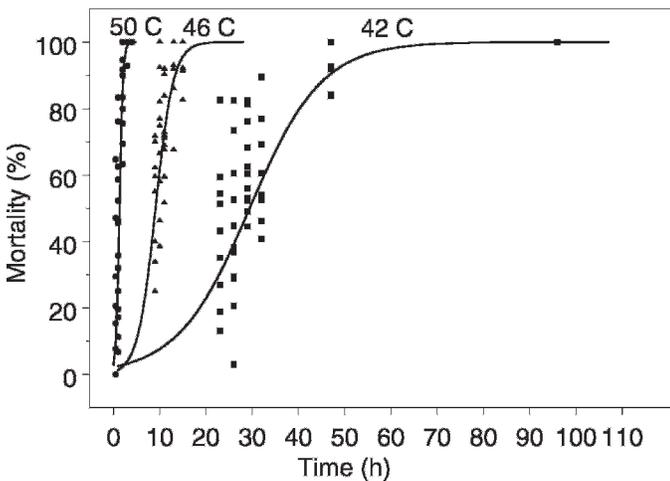


Figure 1. Annual sowthistle percentage mortality vs. time at constant temperatures. At 42 C, % mortality = $1 / \{1 + e^{[-0.129(d - 29.459)]}\}$, pseudo $R^2 = 0.93$; at 46 C, % mortality = $1 / \{1 + e^{[-0.525(d - 9.109)]}\}$, pseudo $R^2 = 0.96$; at 50 C, % mortality = $1 / \{1 + e^{[-2.665(d - 1.313)]}\}$, pseudo $R^2 = 0.96$, where d = duration of exposure at each temperature.

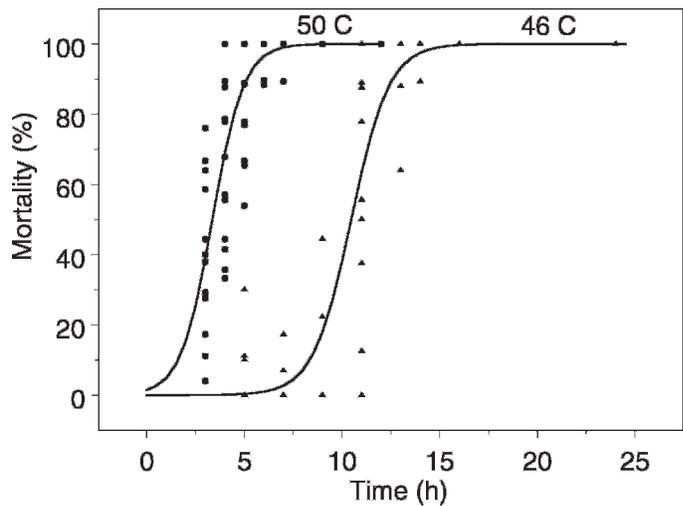


Figure 2. Barnyardgrass percentage mortality vs. time at constant temperatures. At 46 C, % mortality = $1 / \{1 + e^{[-1.036(d - 10.47)]}\}$, pseudo $R^2 = 0.94$; at 50 C, % mortality = $1 / \{1 + e^{[-1.257(d - 3.631)]}\}$, pseudo $R^2 = 0.97$, where d = duration of exposure at each temperature.

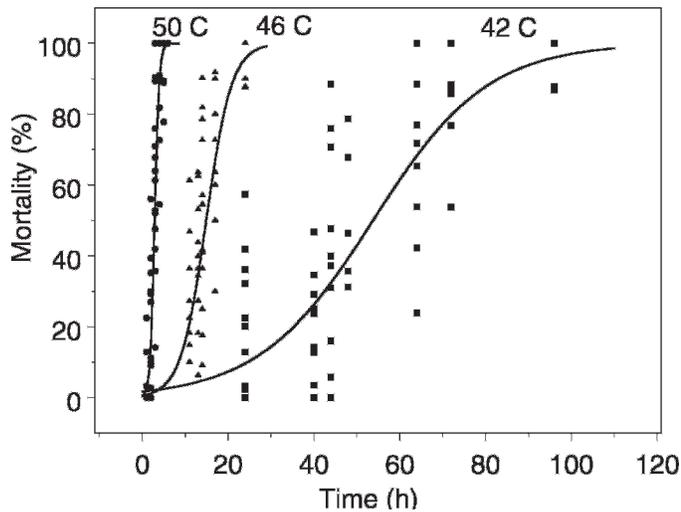


Figure 3. London rocket percentage mortality vs. time at constant temperatures. At 42 C, % mortality = $1/(1 + e^{[-0.075(d - 53.771)])}$, pseudo $R^2 = 0.89$; at 46 C, % mortality = $1/(1 + e^{[-0.34(d - 14.902)])}$, pseudo $R^2 = 0.91$; at 50 C, % mortality = $1/(1 + e^{[-1.929(d - 2.882)])}$, pseudo $R^2 = 0.95$, where d = duration of exposure at each temperature.

solarization, the duration of heat treatment varies with daily temperature fluctuations. Models that account for this can be generated from laboratory experiments using diurnal temperature fluctuations. However, construction of these models is more difficult because it is necessary to account for each discrete temperature and time increment along the mortality curve. Although models based on thermal experiments are simplified, they describe the susceptibility of target weed species to heat at specific temperatures and can be used to develop simplified treatment guidelines.

Models generated from thermal data, such as the ones described in this article, can be applied to temperature and duration combinations within the range of data in the study for validation under field conditions. For a conservative estimate of mortality, the duration of heat treatment in the field can be estimated using the cumulative number of hours above a threshold temperature (Peachey et al. 2001).

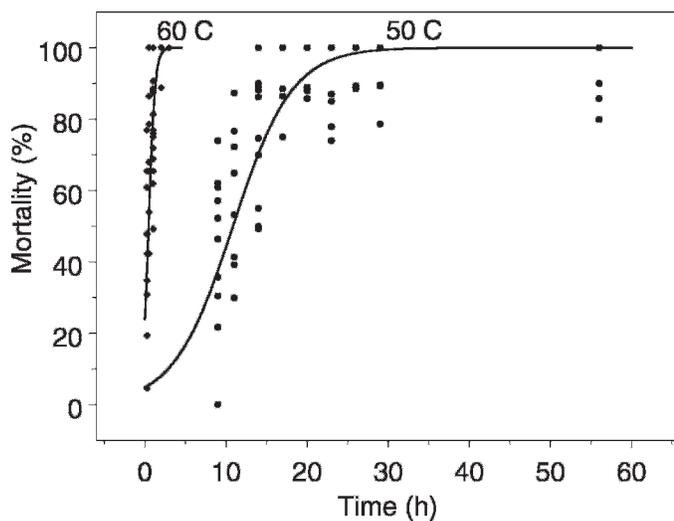


Figure 4. Common purslane percentage mortality vs. time at constant temperatures. At 50 C, % mortality = $1/(1 + e^{[-0.275(d - 10.857)])}$, pseudo $R^2 = 0.996$; at 60 C, % mortality = $1/(1 + e^{[-2.571(d - 0.449)])}$, pseudo $R^2 = 0.96$, where d = duration of exposure at each temperature.

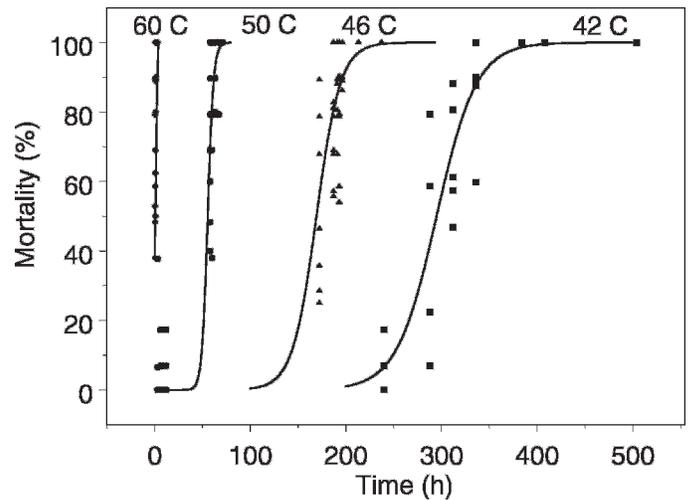


Figure 5. Black nightshade percentage mortality vs. time at constant temperatures. At 42 C, % mortality = $1/(1 + e^{[-0.048(d - 294.8)])}$, pseudo $R^2 = 0.98$; at 46 C, % mortality = $1/(1 + e^{[-0.08(d - 169.1)])}$, pseudo $R^2 = 0.98$; at 50 C, % mortality = $1/(1 + e^{[-0.332(d - 55.388)])}$, pseudo $R^2 = 0.97$; at 60 C, % mortality = $1.16/(1 + e^{[-0.68(d - 1.061)])}$, pseudo $R^2 = 0.98$, where d = duration of exposure at each temperature.

However, that does not account for increasing mortality as the temperature increases above the threshold. Increasing mortality at higher temperatures can be accounted for in models constructed from thermal data by using thermal degree hours, or degrees accumulated above a threshold temperature (Economou et al. 1998). The thermal models generated in the present study could use time and temperature data measured at discrete intervals to calculate the percentage mortality at each interval for which a lethal temperature is reached. Mortality values from each interval could then be summed to obtain a cumulative percentage mortality, with the assumption that the accumulation of heat is additive. Alternatively, time and temperature measurements could be summed over a given interval of time and then used to calculate mortality. As a result, a greatly simplified heat accumulation model can be provided to end users of

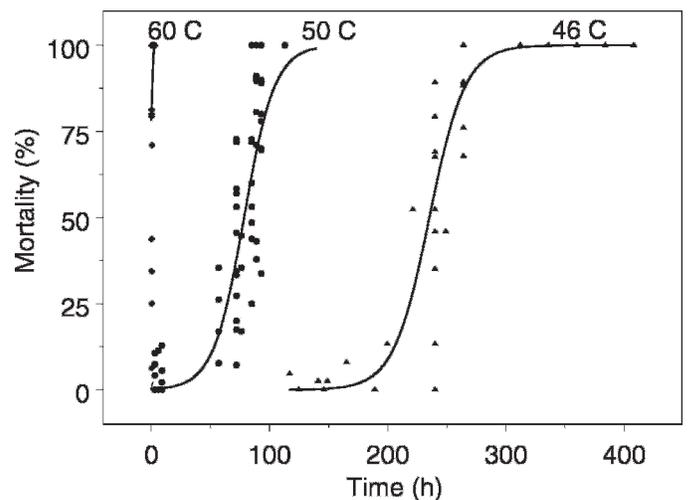


Figure 6. Tumble pigweed percentage mortality vs. time at constant temperatures. At 46 C, % mortality = $1/(1 + e^{[-0.066(d - 235.2)])}$, pseudo $R^2 = 0.98$; at 50 C, % mortality = $1/(1 + e^{[-0.077(d - 78.435)])}$, pseudo $R^2 = 0.93$; at 60 C, % mortality = $1.16/(1 + e^{[-0.477(d + 1.543)])}$, pseudo $R^2 = 0.97$, where d = duration of exposure at each temperature.

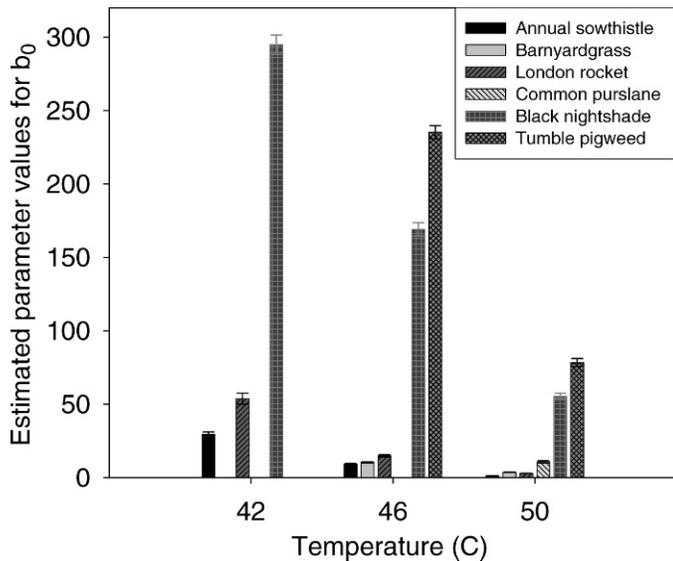


Figure 7. Estimated time to 50% mortality (b_0) for six weed species estimated from the equation $m = C/(1 + e^{-b_1(d-b_0)})$, where m is mortality, C is a constant with $C = 1$ except for black nightshade and tumble pigweed at 60 C where $C = 1.16$, d is duration of exposure at a specific temperature and b_0 and b_1 are estimated parameters. Error bars indicate 95% confidence intervals.

solarization to aid in their decisions regarding ongoing solarization treatments in the field. Validation trials of three species (common purslane, black nightshade, and tumble pigweed) have already been conducted in solarized container soils using diurnal temperature changes rather than constant temperatures (Stapleton et al. 2002). Seeds of all three species failed to germinate following exposure to 1 hour above 50 C and 2 h above 60 C. These results fall within the approximate range of the laboratory time and temperature data. Further validation trials are needed to account for diurnal temperature fluctuations in soil and variation in temperature at different depths.

The duration of heat treatment with solarization required to kill weed seeds in the field would depend on the weed species present and the temperatures reached during solarization. If temperatures are cooler during solarization, common purslane would be the problematic species. However, when higher temperatures (50 to 60 C) are achieved, duration of treatment should be calculated using the model for tumble pigweed because it survived longest at 50 C, and survival of species at 60 C differed by only 2 h. Additional work on integrating across these temperature-specific models will be

Table 4. Number of hours required to kill 90% of seeds (LD_{90}) calculated from nonlinear models.

Weed species	Temperature (C)			
	60	50	46	42
	h			
Annual sowthistle	— ^a	2.1	13.3	46.5
Barnyardgrass	— ^a	5.4	12.6	na ^b
London rocket	— ^a	4.0	21.4	83.1
Common purslane	1.3	18.8	na ^b	na ^b
Black nightshade	2.9	62.0	196.6	340.6
Tumble pigweed	1.1	107.0	268.5	na ^b

^a Model did not converge, and seeds died quickly.

^b Species not affected at this temperature.

required to accurately assess when solarization has killed seeds in soil.

The effects of soil solarization on weed populations may include other factors in addition to thermal death of weed seeds. Laboratory tests measured the effects of heat treatment on seeds that had begun the process of germination but had not yet emerged as seedlings. However, temperatures reached under solarization may affect seedlings as well as seeds, because seeds located below a lethal temperature zone in the soil may germinate and succumb as the seedling moves upward through soil heated to a lethal temperature (Rubin and Benjamin 1984). This was observed for one species in the present study. Common purslane germinated inside the treatment microcosms at 46 C, resulting in seedling death. This temperature was excluded from analysis because there was no lethal effect on the seed itself. However, mortality of field populations might be greater than predicted by the model if seedling mortality is a significant component of control. Sublethal effects of high temperature, such as increased susceptibility to microbial infection, may also contribute to weed control under solarization (Rubin and Benjamin 1984). Time and temperature requirements developed under semisterile laboratory conditions would not reflect the possible contribution of antagonistic soil organisms or release of chemical toxicants in heated field soils to seed or seedling mortality (Stapleton and DeVay 1986; Stapleton 2000). Consequently, the models constructed in the present study are expected to overestimate the time necessary for weed seed death.

The high temperatures reached during solarization may affect dormancy induction and release in weed seed populations. This could be a concern for summer annuals, which may be induced to enter secondary dormancy by high temperatures. Winter annuals, by contrast, are released from dormancy by high temperatures (Forcella et al. 2000). However, other environmental factors, such as soil moisture, can affect dormancy induction (Grundy 2003). For example, low soil water potentials in the spring are related to induction of secondary dormancy in some summer annuals (Benech-Arnold et al. 2000). The practice of irrigating soil before solarization could also influence induction of secondary dormancy, as well as avoiding dormancy induction altogether by causing seeds to germinate before exposure to high temperatures. However, seeds in secondary dormancy before solarization might not be induced to germinate unless soil water potential triggered release from dormancy. Solarization could also affect dormancy release by altering temperature fluctuations, which terminate dormancy in many species (Benech-Arnold et al. 2000). In barnyardgrass seeds, secondary dormancy is thought to be induced by constant temperatures and low soil water content, whereas fluctuating temperatures release seeds from dormancy regardless of soil water potential (Martinez-Ghersa et al. 1997). The interactions of dormancy induction and release with solarization would vary depending on weed species and environmental conditions before and during treatment.

Although further work is required to apply the models developed in this study to solarization in the field, the models are a first step in developing improved treatment guidelines for solarization based on data for individual weed species. Further efforts should include generating time and temperature data for additional weed species, evaluating environmental factors affecting weed seed thermal death under field

conditions, and the development of user-friendly guidelines integrating time, temperature, and environmental factors for each weed species.

Sources of Materials

¹ Immersion circulator, Isotemp, model 730, Fisher Scientific, Pittsburgh, PA.

² Immersion circulator, model FTE10A, Techne Ltd., Duxford, Cambridge, UK.

³ Data logger, HOBO XT, Onset Computer Corp., Bourne, MA.

⁴ Growth chamber, model BOD50A14, Revco Scientific, Inc., Asheville, NC.

⁵ SAS version 9.1, SAS Institute, Cary, NC.

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