Development of a temperature-based seed germination model for silverleaf nightshade (*Solanum elaeagnifolium*)

Omer Kapiluto[1] , Hanan Eizenberg[2] and Ran Nisim Lati[3]

[1]Doctoral Student, Robert H. Smith Institute of Plant Science and Genetics in Agriculture, Faculty of Agriculture, Food and Environment, Hebrew University of Jerusalem, Rehovot, Israel, and Department of Phytopathology and Weed Research, Agricultural Research Organization, Newe Ya'ar Research Center, Ramat Yishay, Israel; [2]Professor, Department of Phytopathology and Weed Research, Agricultural Research Organization, Newe Ya'ar Research Center, Ramat Yishay, Israel and [3]Researcher, Department of Phytopathology and Weed Research, Agricultural Research Organization, Newe Ya'ar Research Center, Ramat Yishay, Israel

Abstract

Silverleaf nightshade (*Solanum elaeagnifolium* Cav.) has become a highly troublesome weed in irrigated summer crops in Israel. Because herbicide-based options to control this weed are limited, the best way to improve weed control is through a study of its biology, particularly its germination dynamics. The main objective of this study was to determine the impact of temperature on the seed germination dynamics of *S. elaeagnifolium* and to develop a temperature-based (thermal) prediction model for three *S. elaeagnifolium* populations growing in different ecosystems in Israel. To this end, a laboratory study was undertaken in which the germination proportion of *S. elaeagnifolium* seeds was monitored under seven temperature regimes: 2/8, 7/13, 12/18, 17/23, 22/28, 27/33, and 32/38 C (night/day). In addition, the impact of alternating temperature regimes between night and day temperatures (of 0, 2, 4, 6, 8, and 10 C), averaged over 20 and 25 C, was determined. It was found that the three populations shared similar germination characteristics and dynamics. An alternation of ≥6 C between night and day temperatures was needed for optimal germination, with no germination taking place under constant temperatures. In all three populations, the minimal requirement for germination was a 12/18 C (night/day) regime, with the final germination proportion lying between 0.25 and 0.36. The highest final germination proportion of ≥0.8 was observed for the 17/23 C regime in all three populations. Modeling the germination rate as a function of temperature allowed us to determine cardinal temperatures for all three populations taken together, with the values being $T_b = 10.8$ C (base temperature), $T_o = 23.8$ C (optimal temperature), and $T_c = 35.9$ C (ceiling temperature). These biological parameters allowed accurate (root mean-square error < 0.06%) prediction of *S. elaeagnifolium* seed germination over the entire temperature range.

Introduction

Silverleaf nightshade (*Solanum elaeagnifolium* Cav., Solanaceae) is considered one of the most invasive weeds worldwide. It is mainly found in arid and semiarid bioclimatic regions with temperate to warm winters (Balah and Abdel Razek 2020). *Solanum elaeagnifolium* is indigenous to the western United States and northern Mexico, but has spread to other parts of the world, including Australia, Greece, Morocco, and parts of southern Europe and the Mediterranean region (Brunel 2011; Mekki 2007; Stanton et al. 2009; Uludag et al. 2016; Zernov and Mirzayeva 2016). It is a perennial weed that reproduces both sexually, through seed production, and asexually, through vegetative growth of rhizomes (Hardin et al. 1972; Knapp et al. 2017). By virtue of these characteristics, *S. elaeagnifolium* is a highly noxious weed that can colonize and thrive in various ecological niches, such as natural reservations, riverbanks, and cultivated fields (Ilçim and Behçet 2007; Krigas et al. 2021; Uludag et al. 2016). *Solanum elaeagnifolium* was introduced into Israel in the 1950s and since then has spread throughout the country, becoming a serious problem in fields of irrigated summer crops, such as cotton (*Gossypium hirsutum* L.), processing tomato (*Solanum lycopersicum* L.), and watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nikai], and often causing significant economic losses (Stanton et al. 2009).

The control of *S. elaeagnifolium* is highly challenging due to its vigorous vegetative growth and extensive root system (Qasem et al. 2019). Although glyphosate and ammonium sulfate can provide effective control (Gitsopoulos et al. 2017), the lack of selectivity of the two herbicides limits their usage for control scenarios such as preemergence and direct spraying. Other herbicides that have shown efficacy (e.g., imazapyr, aminopyralid, and picloram) are not suitable for agricultural purposes (Wu et al. 2016). Furthermore, mechanical control tools, such as tillage and cultivation, are not practicable for *S. elaeagnifolium*, because the use of mechanical

machinery can break the root system and spread the propagules throughout the field (Gitsopoulos et al. 2017; Qasem et al. 2019; Wu et al. 2016). These limitations create the need for novel ecologically based control approaches that can be integrated into the currently used control methods. However, the development of such methods will require extensive biological and ecological knowledge about the weed (Bajwa et al. 2015).

Ecological control tools are based on data about key phases in a weed's life cycle and phenology, such as the timing and magnitude of seed germination, which determine the establishment of the weed in the field (Forcella et al. 2000; Grundy et al. 2003; Rodriguez et al. 2020). Because *S. elaeagnifolium* typically produces up to 9,000 seeds per plant (Boyd and Murray 1982), effective control of young seedlings can make a significant contribution to the overall management of this weed. Seed germination is affected by various environmental conditions, with temperature being the most important of these under irrigated field conditions (Derakhshan et al. 2014; Garcia-Huidobro et al. 1982; Guillemin et al. 2013; Shrestha et al., 1999). Nonetheless, studies investigating the impact of temperature on germination in *S. elaeagnifolium* are scarce. Among those that have been conducted, Boyd and Murray (1982) evaluated the germination of *S. elaeagnifolium* under various environmental conditions. They found increased germination rates under an alternating temperature regime, with a maximal rate of 57% under a 20/30 C regime. Similar results were obtained by Balah et al. (2021), who showed optimal germination under an alternating temperature regime of 20/30 C, but at a lower rate of 33%. A slightly different germination pattern was revealed by Stanton et al. (2012), with 15/25 C as the optimal temperature regime for germination. These studies provided descriptive data about the impact of temperature on *S. elaeagnifolium* germination, but they lacked information on cardinal temperatures that could facilitate smart decision making regarding the control of this weed, for example, temperature-based germination prediction models.

Temperature measurements establish the basis for a number of weed germination predictive models, many of which use an empirical approach (Cochavi et al. 2018; Doyle 1991; Hosseini et al. 2017). The concept of these empirical models is based on thermal time units, that is, summing heat units above minimal temperature thresholds to predict the germination dynamics (Trudgill et al. 2005). The development of these predictive models is based on preliminary data about the temperature thresholds (i.e., cardinal temperatures) for weed germination, such as the base temperature (at or below which germination does not occur), the optimal temperature (which supports the maximal germination rate), and the ceiling temperature (at or beyond which germination is zero) (Goldwasser et al. 2016; Hardegree 2006; Mesgaran et al. 2017). However, no previous study has determined cardinal temperatures for *S. elaeagnifolium*, and hence there are no predictive models for *S. elaeagnifolium* seed germination. In addition, germination patterns in different *S. elaeagnifolium* populations have not been examined, and more information is needed at the local level about the variation of cardinal temperatures for *S. elaeagnifolium* populations in different climate zones in Israel.

The main objective of this study was to determine the effect of temperature on seed germination in three specific *S. elaeagnifolium* populations growing in different environments in Israel. To this end, the specific objectives of the study were: (1) to estimate the germination proportion and dynamics of *S. elaeagnifolium* under constant temperatures and under different alternating temperature regimes; (2) to determine the cardinal germination temperatures for three specific populations of *S. elaeagnifolium*; and (3) to develop a prediction model for *S. elaeagnifolium* germination dynamics and compare the germination patterns and cardinal temperatures for the three populations growing under different environmental conditions.

Material and Methods

Plant Material

Berries were collected from three populations of *S. elaeagnifolium* growing in fields located at Kibbutz Kfar Blum in the Hula Valley (33.16°N, 35.59°E), at the Newe Ya'ar Research Center in the Jezreel Valley (32.70°N, 35.18°E), and at Kibbutz Urim (31.30° N, 34.52°E) in the Negev Desert. The berries were removed from the plants and crushed, and the seeds were washed out and collected on a sieve under running water. The seeds were air-dried in a net house for 2 wk and stored at 4 C until use.

Experimental Setup

All experiments were conducted in the laboratory at the Newe Ya'ar Research Center from July to September 2019. Seed germination was evaluated by placing batches of 25 *S. elaeagnifolium* seeds in 90-mm-diameter petri dishes on filter paper (Whatman No. 1, Whatman, Maidstone, UK) presoaked for 24 h in deionized water. The photoperiod was maintained at 12 h:12 h (light:full darkness), according to Stanton et al. (2012). Germinated seeds in each petri dish were counted each day at 11:00 AM. and then removed, until no additional germinations were observed over a period of 4 d. Seeds were considered to be germinated when the observed radicle was longer than 1 mm. All experiments were performed for all three populations. Experiments were arranged in a complete randomized design with four replications of treatments for both experiments. The experiments were repeated once. There was no experiment by treatment interaction; therefore, the data from both experiments were pulled and presented as eight replications of each treatment. All statistical analyses were performed using the R statistical environment (R Core Team 2020) together with the following packages: DRC (Ritz et al. 2015) and DRCSEEDGERM (Onofri et al. 2018).

Impact of an Alternating Temperature Regime on Germination

For this experiment, different alternating (12 h/12 h) temperature regimes based on two optimal average germination temperatures, 20 and 25 C, were tested (Balah et al. 2021; Stanton et al. 2012). For each of these optimal temperatures, temperature regimes were set such that the difference between the day and night temperatures was 0, 2, 4, 6, 8, or 10 C, resulting in the following 12 regimes: 20/20, 19/21, 18/22, 17/23, 16/24, 15/25 C and 25/25, 24/26, 23/27, 22/28, 21/29, 20/30 C. The petri dishes containing the seeds were placed inside a growth chamber under these 12 alternating temperature regimes. In total, 144 petri dishes were examined (3 populations × 4 replicates × 6 temperature regimes × 2 optimal temperatures).

The data collected for each petri dish and temperature regime were used to parameterize a time-to-event model (Jensen et al. 2020). For each *S. elaeagnifolium* population, the relationship between the cumulative seed germination and time (in days) under the 12 alternating temperature regimes were analyzed using a log-logistic equation:

$$Y(t) = d/(1 + \exp\{b[\log(t) - \log(e)]\}) \qquad [1]$$

where Y is the proportion of germinated seeds at time t, d is the proportion of maximum germinated seeds when $t \rightarrow \infty$, e is the median germination time, and b is the steepness of the curve in the inflection point. Finally, the extracted d parameters were incorporated into the general linear model (GLM) with a binomial distribution and logit link. The *S. elaeagnifolium* population, average temperature (20 and 25 C), and alternating temperature range (0, 2, 4, 6, 8, and 10 C) were used as the main parameters.

Development of the Germination Model

For this experiment, the petri dishes were placed in growth chambers for 30 d under the following alternating temperature regimes: 2/8, 7/13, 12/18, 17/23, 22/28, 27/33, and 32/38 C (12 h:12 h), for a total of 168 petri dishes (3 populations × 8 replicates × 7 temperature regimes). The data collected were used to parameterize a time-to-event model for each *S. elaeagnifolium* population, in which the response of germination to the particular alternating temperature regime was estimated using a three-parameter Weibull equation:

$$Y(t) = d \exp(-\exp\{b[\log(t) - \log(e)]\}) \qquad [2]$$

where Y is the proportion of germinated seeds at time t, d is the proportion of germinated seeds when $t \rightarrow \infty$, e is the location of the inflection point, and b is the steepness of the curve at the inflection point. The Weibull equation was preferable over the log-logistic Equation 1 following Akaike information criterion (AIC) evaluation (data not shown).

Thereafter, the germination rate (GR) values (the inverse of the time needed for germination) derived from the fitted models (Equation 2) were used to develop germination prediction models. Such models use the cardinal temperatures—base temperature (T_b), optimal temperature (T_o), and ceiling temperature (T_c)—to quantify the impact of temperature on seed germination (Bradford 2002). Because GR tends to vary within populations, GRs were estimated for the different percentiles (subpopulations) of each population. Thus, in this study, GR values were estimated for the 10th, 15th, 20th, and 25th percentiles (GR_{10}, GR_{15}, GR_{20}, and GR_{25}). The lowest final germination proportion observed in our study was 0.25 in the 12/18 C regime. This proportion was therefore set as the maximal percentile of GR, and higher percentiles were omitted. As suggested by Bradford (2002), the germination data were not normalized relative to the maximal, and the absolute values were used. Additionally, Bradford observed different values of maximal GR in the different percentiles. These observations suggest the use of an addition parameter, b, which represents this maximal value. The derived GR values were used to fit a four-parameter model, as described by Mesgaran (2019):

$$\text{GR}(T, g) = \begin{cases} \left(\frac{T - T_{b(g)}}{T_{o(g)} - T_{b(g)}}\right) b_{(g)} & ; \text{if } T_b < T \leq T_o \\ \left(\frac{T_{c(g)} - T}{T_{c(g)} - T_{o(g)}}\right) b_{(g)} & ; \text{if } T_o < T \leq T_c \\ 0 & ; \text{otherwise.} \end{cases} \qquad [3]$$

where T is the temperature, subscript g represents the population percentile, T_b is the base temperature, T_o is the optimum temperature, T_c is the ceiling temperature, and b is a parameter that represents the maximal value of GR. Here, the average temperature for each regime was used for the model development (average of the

two temperatures in the interval) as an independent variable (Masin et al. 2017). This so-called segmented model facilitates the estimation of different parameter values for each percentile, g, resulting in a total number of 16 cardinal temperature parameters in this study.

Previous studies have demonstrated how the number of parameters in the prediction model can be reduced by setting the same value for some/all of the parameters across different percentiles (Ottavini et al. 2019). Similarly, Mesgaran (2019) set the cardinal temperature parameters across the percentiles to a fixed value and used the following equation to predict GR:

$$\text{GR}(T, g) = \begin{cases} \left(\frac{T - T_b}{T_o - T_b}\right) b_{(g)} & ; \text{if } T_b < T \leq T_o \\ \left(\frac{T_c - T}{T_c - T_o}\right) b_{(g)} & ; \text{if } T_o < T \leq T_c \\ 0 & ; \text{otherwise.} \end{cases} \qquad [4]$$

This model is based on a negative relationship between percentiles and GR values; thus, only the b parameter varied across percentiles. It has a total number of seven parameters.

Two additional models, both having a total number of 10 parameters, were tested in this study based on Equation 4. The first assumed a variable T_c parameter across the percentiles, according to Bradford (Bradford 2002), and the second assumed a variable T_o parameter across the percentiles (Mesgaran et al. 2017). For the sake of simplicity, we refer to the four models as follows: the 16-parameter model with different cardinal temperatures and b parameter as the "variable model," the 7-parameter model as the "fixed T_c model," and the two 10-parameter models as the "variable T_c model" and "variable T_o model," as relevant.

To compare the goodness of fit and the prediction ability of the models, two evaluation methods were used, one based on the root mean-square error (RMSE) and the other on the AIC. The RMSE represents the mean differences between the predicted values of the model and the observed values, and the AIC method integrates the reduction of the residual sum of squares (RSS) and the model complexity (Burnham and Anderson 2004):

$$\text{AIC} = 2n \ \ln\left(\frac{\text{RSS}}{n}\right) + 2k \qquad [5]$$

where n is the number of observations, and k is the number of parameters used in the model. In addition, the 95% confidence interval (CI) bounds of the cardinal temperatures were estimated.

To develop a full thermal–time germination predictive model for the different populations, the cardinal temperatures from the model that provided the best fit according to RMSE and AIC were used, and the accumulated growing degree-day (GDD) values over time (n) were estimated for each population by using the following equation (Mesgaran 2019):

$$\text{GDD} = \begin{cases} \sum_{i=1}^{n} \left(\frac{\overline{T}_i - T_b}{T_o - T_b}\right) (T_o - T_b) & ; \text{if } T_b < T \leq T_o \\ \sum_{i=1}^{n} \left(\frac{T_c - \overline{T}_i}{T_c - T_o}\right) (T_o - T_b) & ; \text{if } T_o < T \leq T_c \\ 0 & ; \text{otherwise.} \end{cases} \qquad [6]$$

where $\overline{T}_i$ is the average daily temperature for day ith, and n is the total number of days for which GDD is to be calculated. Equation 6 takes into consideration the sub- and supra-optimal temperatures ranges in the GDD accumulation.

The response of *S. elaeagnifolium* germination to GDD was analyzed using Equation 1. The RMSE value was calculated for

Table 1. Coefficients, their SEs, and P-values describing the relationship between the germination of three *Solanum elaeagnifolium* populations (Kfar Blum [KB], Newe Ya'ar [NY], and Urim [UR]) and temperature.

Population	Temperature regime	Coefficient					
	C	*b*	P-value (*b*)	*d*	P-value (*d*)	*e*	P-value (*e*)
KB	20/20	—	—	—	—	—	—
	19/21	—	—	—	—	—	—
	18/22	−6.48 (0.99)	<0.001	0.32 (0.04)	<0.001	13.97 (0.65)	<0.001
	17/23	−5.45 (0.61)	<0.001	0.90 (0.03)	<0.001	14.06 (0.53)	<0.001
	16/24	−7.28 (0.73)	<0.001	0.93 (0.02)	<0.001	10.94 (0.33)	<0.001
	15/25	−9.19 (0.86)	<0.001	0.95 (0.02)	<0.001	10.78 (0.29)	<0.001
NY	20/20	—	—	—	—	—	—
	19/21	—	—	—	—	—	—
	18/22	−5.08 (1.05)	<0.001	0.20 (0.04)	<0.001	13.11 (0.77)	<0.001
	17/23	−5.26 (0.52)	<0.001	0.91 (0.03)	<0.001	13.86 (0.50)	<0.001
	16/24	−6.59 (0.60)	<0.001	0.91 (0.02)	<0.001	11.51 (0.36)	<0.001
	15/25	−7.63 (0.68)	<0.001	0.94 (0.02)	<0.001	11.32 (0.31)	<0.001
UR	20/20	—	—	—	—	—	—
	19/21	—	—	—	—	—	—
	18/22	−5.39 (0.93)	<0.001	0.22 (0.04)	<0.001	14.15 (0.84)	<0.001
	17/23	−7.15 (0.71)	<0.001	0.87 (0.03)	<0.001	13.65 (0.36)	<0.001
	16/24	−7.11 (0.65)	<0.001	0.95 (0.02)	<0.001	11.04 (0.26)	<0.001
	15/25	−9.67 (0.87)	<0.001	0.95 (0.02)	<0.001	11.34 (0.21)	<0.001
KB	25/25	—	—	—	—	—	—
	24/26	—	—	—	—	—	—
	23/27	−4.71 (0.70)	<0.001	0.38 (0.05)	<0.001	12.46 (0.72)	<0.001
	22/28	−5.33 (0.53)	<0.001	0.80 (0.04)	<0.001	10.32 (0.36)	<0.001
	21/29	−5.66 (0.53)	<0.001	0.89 (0.03)	<0.001	9.64 (0.27)	<0.001
	20/30	−5.45 (0.49)	<0.001	0.90 (0.03)	<0.001	9.24 (0.30)	<0.001
NY	25/25	—	—	—	—	—	—
	24/26	—	—	—	—	—	—
	23/27	−5.22 (0.77)	<0.001	0.36 (0.05)	<0.001	13.15 (0.28)	<0.001
	22/28	−5.88 (0.59)	<0.001	0.80 (0.04)	<0.001	11.89 (0.35)	<0.001
	21/29	−5.67 (0.54)	<0.001	0.90 (0.03)	<0.001	10.73 (0.37)	<0.001
	20/30	−6.13 (0.53)	<0.001	0.94 (0.02)	<0.001	9.47 (0.70)	<0.001
UR	25/25	—	—	—	—	—	—
	24/26	—	—	—	—	—	—
	23/27	−5.66 (0.85)	<0.001	0.33 (0.05)	<0.001	15.25 (0.92)	<0.001
	22/28	−5.54 (0.55)	<0.001	0.77 (0.04)	<0.001	10.08 (0.36)	<0.001
	21/29	−5.00 (0.48)	<0.001	0.84 (0.03)	<0.001	11.01 (0.39)	<0.001
	20/30	−4.94 (0.47)	<0.001	0.86 (0.03)	<0.001	10.45 (0.40)	<0.001

[a]The temperature regimes were set at averages of 20 C and 25 C with an increasing alternating temperature range of 0, 2, 4, 6, 8, and 10 C between the day and night temperatures. The time-to-event-method, three-parameter log-logistic equation was used: $f[t,(b,d,e)] = d/(1 + \exp(b(\log(t) - \log(e))))$, where *d* is maximal germination; *b* is the slope at the inflection point (reflects the steepness of the curve at median germination); and *e* is the median germination time.

each population model to compare the goodness of fit (Lati et al. 2011). Finally, the cardinal temperatures were estimated for the three populations together by using the fixed T_c model, followed by the development of a separate germination prediction model for each population as described at the beginning of this section.

Results and Discussion

Impact of the Alternating Temperature Regime on Seed Germination

For all populations and for all tested temperature regimes, the log-logistic time-to-event model properly described the germination pattern of *S. elaeagnifolium* (Supplementary Figure S1), and P-values of <0.001 were obtained for all parameters, confirming the goodness of fit (Table 1). The GLM analysis that used the *d* parameter revealed that the only factor that significantly affected the germination proportion was the range of the alternating temperatures (P < 0.001). For all populations, no germination was observed under constant temperatures, whether 20 or 25 C, or at the minimal differences between alternating day and night temperatures, that is, at 19/21 or at 24/26 C (Table 1). The difference of 4 C in

alternating temperatures, that is, 18/22 and 23/27 C, gave the lowest proportions of germination (Table 1), and the highest proportions were observed for the alternating temperature differences of 6, 8, and 10 C, with the *d* parameter ranging between 0.77 and 0.95.

In terms of the time needed for 50% of the seeds to germinate, as reflected by the *e* parameter (Equation 1), the higher alternating temperature differences of 8 and 10 C resulted in lower values of this parameter than for the smaller differences of 4 and 6 C. This trend was observed in both alternating temperature ranges (based on 20 C and 25 C).

The ability of *S. elaeagnifolium* seeds to germinate over a wide range of temperatures (between 10 and 36 C) serves as an indication of the plasticity of this weed (like other invasive weeds) and its high adaptability to various climates (Brunel 2011; Mekki 2007). However, as shown in this study, temperature alternation is essential for the germination of this weed, with wider alternation ranges (6, 8, and 10 C) resulting in higher germination proportions and rates (Table 1). These results are in agreement with previous studies on *S. elaeagnifolium* populations in Egypt and Australia (Balah et al. 2021; Stanton et al. 2009, 2012). They are also in keeping with the soil temperature measurements at six locations in Israel that revealed a wide amplitude range in the main germination period
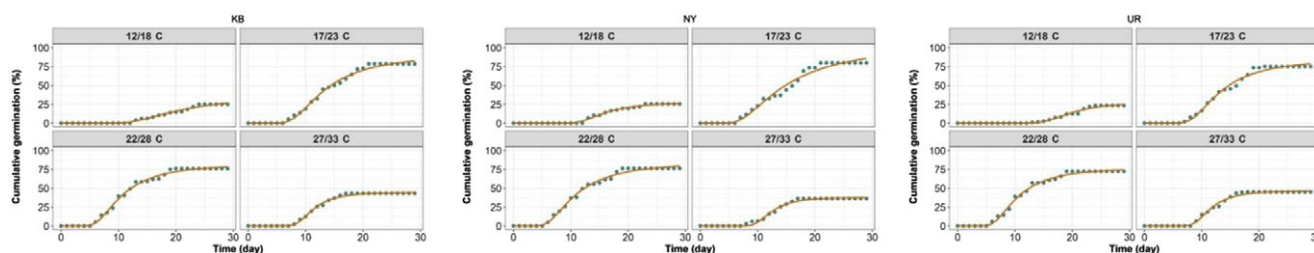
Figure 1. Time-to-event-method, three-parameter Weibull equation: $f(t, (b, d, e)) = d \left(\exp(-\exp[b(\log(t) - \log(e)]) \right)$ showing the relationship between temperature and germination of three (Kfar Blum [KB], Newe Ya'ar [NY], and Urim [UR]) *Solanum elaeagnifolium* populations. Symbols show the observed data, while lines show the fitted curves. Coefficients for the equation parameters are presented in Table 2; $n = 8$.

of *S. elaeagnifolium* (between March and May; Supplementary Figure S2). Such germination characteristics suggest that soil tillage, which will move the seeds into deeper soil layers with low-temperature amplitudes, may reduce *S. elaeagnifolium* germination and establishment and thus improve its management (Bergkvist et al. 2017; Curran et al. 1994; Hossain et al. 1999). As the average minimum/maximum temperature alternation range for all six locations in Israel was 6.6 C, an alternation value of 6.0 C between day and night temperatures was used for developing the temperature-based *S. elaeagnifolium* germination dynamics prediction model.

Germination Dynamics Model

For all populations at all tested temperatures, the Weibull time-to-event model properly described the germination pattern of *S. elaeagnifolium* (Figure 1), and P-values smaller than 0.008 were obtained for all populations and temperature regimes (Table 2). Furthermore, the germination characteristics and the critical temperature ranges were similar for all three *S. elaeagnifolium* populations. The germination proportion was zero at the low-temperature regimes (2/8 C and 7/13 C) for all three populations, whereas for the 12/18 C temperature regime, germination was observed in all three populations. For the Kfar Blum population, the final germination proportion for this regime, as reflected by parameter *d*, was 0.36, while for the Newe Ya'ar and Kibbutz Urim populations, the germination proportion fell to lower values of 0.25, and 0.26, respectively (Table 2). The highest germination proportions were observed for the 17/23 C regime in all three populations, with parameter *d* reaching values of 0.86, 0.89, and 0.80 for the Kfar Blum, Newe Ya'ar, and Kibbutz Urim populations, respectively. At the higher temperature regime (22/28 C) parameter *d* values were slightly lower, being ≥0.74, but the germination proportion was still high. The decreasing trend in the germination proportion continued in the 27/33 C temperature regime, with values falling to ~0.40 in all populations. No germination was observed for the 32/38 C regime (Table 2). The similarities in the germination characteristics among the three *S. elaeagnifolium* populations were also reflected by the *e* parameter (Equation 2), which represents the location of the inflection point. This parameter was the highest for all three populations under the 12/18 C temperature regime, with values of 20.6, 15.5, and 18.8 for the Kfar Blum, Newe Ya'ar, and Kibbutz Urim populations, respectively (Table 2). The lowest value of this parameter was observed for the 22/28 C temperature regime in all three populations, being 10.0, 10.0, and 9.9 for the Kfar Blum, Newe Ya'ar, and Kibbutz Urim populations, respectively (Table 2). These results are in agreement with previous studies that demonstrated optimal *S.*

elaeagnifolium germination occurs between 20 and 25 C (Balah et al. 2021; Stanton et al. 2012).

Modeling Germination Rate as a Function of Temperature

The fitted curves were used to derive the germination rates for the 10th, 15th, 20th, and 25th percentiles (GR_{10}, GR_{15}, GR_{20}, and GR_{25}), which were used to parameterize Equation 3 (Supplementary Figure S3). By regarding the percentile *g* as a factor and allowing different parameters for different percentiles, we reached a total number of 16 parameters. However, consistent with the literature (Bradford 2002; Rowse and Finch-Savage 2003), we tested three other modeling approaches, one with 7 parameters (Washitani 1987) and two with 10 parameters (Mesgaran et al. 2017), which adjust constant cardinal temperatures for all percentiles.

The computed RMSE values were similar for all four modeling approaches, being <1%. This trend was observed for all three populations (Table 3). However, when the AIC was used, some differences were observed between the different model approaches. As Table 3 shows, the variable model (variable T_b, T_o, T_c, and *b*) provided the worst fit with the highest AIC value for the Newe Ya'ar and Kibbutz Urim populations (Table 3). The computed AIC values for the Kfar Blum population were −127, −134, −121, and −121 for the variable model, fixed T_c, variable T_c, and variable T_o approaches, respectively. The fixed T_c approach provided the best fit with the lowest AIC values in all populations, with the extracted values being −136, −134, and −145 for the Kibbutz Urim, Kfar Blum, and Newe Ya'ar populations, respectively (Table 3).

When the computed cardinal temperatures were compared across the modeling approaches with the constant cardinal temperatures (fixed T_c, variable T_c, and variable T_o), similar values were observed, with negligible differences of 0.01 C between them. These findings coupled with the lowest AIC value observed in the fixed T_c model and the smallest number of parameters (parsimony rule) motivated us to select this model for the later stages of analysis.

When the fixed T_c model was used, the three cardinal temperatures were not significantly different between the three *S. elaeagnifolium* populations, and overlapping 95% CIs were observed (Figure 2; Table 4). For example, the estimated T_b values and their respective 95% CIs for the Kfar Blum, Newe Ya'ar, and Kibbutz Urim populations were 10.95 ± 1.31, 9.99 ± 0.45, and 10.85 ± 1.17, respectively. In addition, the *b* parameter decreased with the percentiles in all three populations, suggesting a higher GR in the lowest percentiles (Table 4). The values of the *b* parameter ranged between 0.155 to 0.117 for all populations, and for the Newe

Table 2. Coefficients, their SEs, and P-values describing the relationship between the germination of three *Solanum elaeagnifolium* populations (Kfar Blum [KB], Newe Ya'ar [NY], and Urim [UR]) under seven temperature regimes.[a]

Population	Temperature regime	Coefficient						
	C	b	P-value (b)	d	P-value (d)	e	P-value (e)
KB	2/8	—	—	—	—	—	—
	7/13	—	—	—	—	—	—
	12/18	−2.76 (0.59)	<0.001	0.36 (0.076)	<0.001	20.60 (2.01)	<0.001
	17/23	−2.99 (0.23)	<0.001	0.86 (0.033)	<0.001	11.90 (0.37)	<0.001
	22/28	−3.06 (0.23)	<0.001	0.82 (0.030)	<0.001	10.00 (0.29)	<0.001
	27/33	−5.92 (0.50)	<0.001	0.48 (0.035)	<0.001	10.62 (0.19)	<0.001
	32/38	—	—	—	—	—	—
NY	2/8	—	—	—	—	—	—
	7/13	—	—	—	—	—	—
	12/18	−5.62 (0.78)	<0.001	0.25 (0.031)	<0.001	15.51 (0.44)	<0.001
	17/23	−2.52 (0.22)	<0.001	0.89 (0.040)	<0.001	12.35 (0.49)	<0.001
	22/28	−2.97 (0.23)	<0.001	0.79 (0.032)	<0.001	10.06 (0.31)	<0.001
	27/33	−4.27 (0.42)	<0.001	0.37 (0.034)	<0.001	11.93 (0.36)	<0.001
	32/38	—	—	—	—	—	—
UR	2/8	—	—	—	—	—	—
	7/13	—	—	—	—	—	—
	12/18	−4.88 (0.75)	0.008	0.26 (0.035)	<0.001	18.82 (0.71)	<0.001
	17/23	−3.22 (0.25)	<0.001	0.80 (0.034)	<0.001	12.25 (0.36)	<0.001
	22/28	−3.11 (0.24)	<0.001	0.74 (0.033)	<0.001	9.94 (0.29)	<0.001
	27/33	−5.60 (0.49	0.001	0.46 (0.035)	<0.001	11.53 (0.23)	<0.001
	32/38	—	—	—	—	—	—

[a]The time-to-event-method, three-parameter Weibull equation: $f(t, (b, d, e)) = d \left(\exp\left(-\exp\left/[b(\log(t) - \log(e)]\right)\right.\right)$ was used, where d is maximal germination; b is the slope around the inflection point (reflecting the steepness of the curve at median germination), and e is the location parameter.

Table 3. Akaike information criterion (AIC), root mean-square error (RMSE), degrees of freedom (df), and number of parameters of the four models used (reference in parentheses) to describe the relationship between germination rate (GR) and temperature of three *Solanum elaeagnifolium* populations (Kfar Blum [KB], Newe Ya'ar [NY], and Urim [UR]).

Population		Tested model[a]			
		T_c constant (Washitani 1987)	T_c variable (Bradford 2002)	T_o variable (Mesgaran et al. 2017)	T_b, T_o, T_c variable (Parmoon et al. 2015)
		C			
KB	AIC	−134	−121	−121	−127
	RMSE	0.012	0.012	0.012	0.015
NY	AIC	−145	−139	−140	−133
	RMSE	0.008	0.008	0.008	0.012
UR	AIC	−136	−130	−130	−127
	RMSE	0.01	0.01	0.01	0.014
df		8	11	11	17
No. of parameters		7	10	10	16

[a]T_c, ceiling temperature; T_o, optimum temperature; T_b, base temperature.
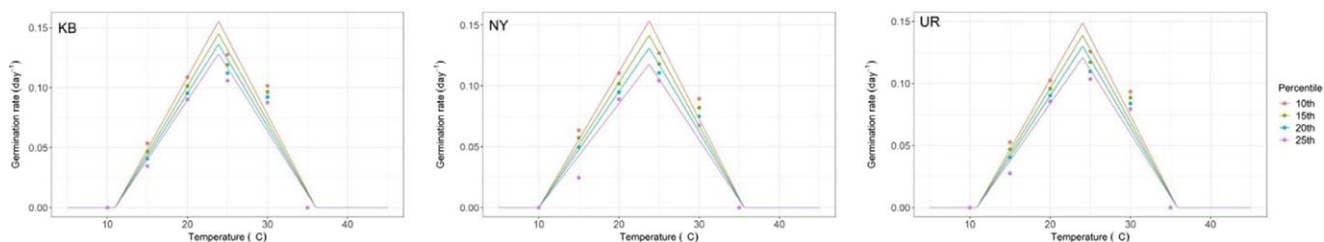

Figure 2. Relationship between germination rates (GR) of different percentiles (g) and temperature for three *Solanum elaeagnifolium* populations (Kfar Blum [KB], Newe Ya'ar [NY], and Urim [UR]). Symbols show the observed data, while lines show the fitted curves (Equation 4), with the parameters of Table 4.

Ya'ar population, the computed values of b_{10}, b_{15}, b_{20}, and b_{25} were 0.153, 0.141, 0.131 and 0.117, respectively.

The modeling approaches used in this study take into consideration the different germination characteristics of the various percentiles within the populations. These differences were reflected by the b parameter in Equation 4, which represents the maximal value of GR (Covell et al. 1986; Ordoñez-Salanueva et al. 2015; Rowse and Finch-Savage 2003). The insight gained into the

Table 4. Cardinal temperatures, namely, base temperature (T_b), optimum temperature (T_o), and ceiling temperature (T_c), and maximal germination rate (GR) value (b) of the different percentiles of three *Solanum elaeagnifolium* populations (Kfar Blum [KB], Newe Ya'ar [NY], and Urim [UR]), their SEs (in parentheses), lower and upper 95% confidence intervals (CIs), and P-values that were estimated from the Washitani model (Washitani 1987) in Equation 4.

Population	Parameter	Estimate	Lower CI	Upper CI	P-value
KB	T_b (C)	10.95 (1.31)	8.17	13.72	<0.001
	T_o (C)	23.87 (0.70)	22.38	25.37	<0.001
	T_c (C)	36.04 (0.64)	34.68	37.40	<0.001
	b (10th)	0.155 (0.01)	0.128	0.182	<0.001
	b (15th)	0.145 (0.01)	0.118	0.171	<0.001
	b (20th)	0.136 (0.01)	0.109	0.162	<0.001
	b (25th)	0.128 (0.01)	0.101	0.154	<0.001
NY	T_b (C)	9.99 (0.45)	9.02	10.96	<0.001
	T_o (C)	23.75 (0.40)	22.91	24.60	<0.001
	T_c (C)	35.61 (0.42)	34.71	36.50	<0.001
	b (10th)	0.153 (0.01)	0.136	0.17	<0.001
	b (15th)	0.141 (0.01)	0.124	0.158	<0.001
	b (20th)	0.131 (0.01)	0.114	0.147	<0.001
	b (25th)	0.117 (0.01)	0.101	0.134	<0.001
UR	T_b (C)	10.85 (1.17)	8.36	13.33	<0.001
	T_o (C)	24.03 (0.61)	22.73	25.34	<0.001
	T_c (C)	35.85 (0.53)	34.73	36.97	<0.001
	b (10th)	0.148 (0.01)	0.126	0.171	<0.001
	b (15th)	0.138 (0.01)	0.116	0.161	<0.001
	b (20th)	0.130 (0.01)	0.107	0.152	<0.001
	b (25th)	0.120 (0.01)	0.1	0.142	<0.001

germination dynamics of different *S. elaeagnifolium* percentiles can facilitate optimal decision making regarding control activities. Revealing such dynamics enables control activity to be targeted to the time when most of the population has emerged and prevent early or late applications. These nonoptimal timings may result in uncontrolled germination flashes or highly developed weeds that are not adequately controlled, respectively. However, no significant differences were observed in the percentiles of the different populations, which suggests similar germination patterns.

The fixed T_c model allowed accurate prediction of *S. elaeagnifolium* germination across the entire temperature range with a high level of accuracy (Figure 3). It takes into consideration the decreased germination rate above the optimal temperatures (22/28 C) and is thus superior to the so-called linear models that exhibit limited prediction accuracy for the optimal temperature range (Cochavi et al. 2016). These models take into consideration a wide range of temperatures (Parmoon et al. 2015) to provide a robust tool for describing weed germination dynamics for various weed species (Forcella et al. 2000; Mesgaran et al. 2017). Prediction models can be employed to improve decision making regarding the nature and timing of weed control tools. For example, the results of any control tactic (e.g., herbicides, cultivation, or flaming) are affected by weed growth stage and density at the time of application (Lati et al. 2012).

Development of the Solanum elaeagnifolium Germination Dynamics Model

To develop a thermal time model for estimating cumulative *S. elaeagnifolium* germination, data from all temperature regimes were combined. For each population separately, the chronological time (days) was converted to thermal time (GDD) by using Equation 6 and the computed cardinal temperatures. As Figure 3 and Table 5 show, the three-parameter log-logistic equation adequately described the germination dynamics of all *S. elaeagnifolium* populations, with P-values <0.001. The resulting RMSE values for all three populations were <0.07%, and the P-values for the three parameters, b, d, and e, were highly significant

(P < 0.001). Furthermore, the values of the estimated parameters were similar for the three populations. The approximate difference of 10 GDD units in the value of the e for the Newe Ya'ar population is negligible, being equivalent to half a day under spring–summer temperatures (Table 5).

Finally, by virtue of the lack of significant differences between the *S. elaeagnifolium* populations in terms of cardinal temperatures and predictive models, all data were pooled. The cardinal temperatures were then re-estimated using the fixed T_c model and were used for development of the prediction model. Here, the estimated cardinal temperatures were 10.82, 23.86, and 35.9 C for T_b, T_o, and T_c, respectively. As Figure 3 shows, the log-logistic equation adequately described the germination dynamics of all three populations taken together (P < 0.001), with the RMSE value being similar, 0.064%, compared with the values computed for each population separately. These results indicate the accurate germination prediction ability offered by the cardinal temperatures that were evaluated by the fixed T_c model, with the computed cardinal temperatures not being significantly different between the three populations (Table 4). They also provide support for the similarity of the germination patterns of the three examined populations, which were collected from various regions in Israel, over a 250-km range from the north (Kfar Blum) to the south (Kibbutz Urim). Despite the fact that Kibbutz Urim is located in what is considered to be an arid region, Supplementary Figure S4 shows that, in terms of temperature, Kfar Blum, Newe Ya'ar, and Kibbutz Urim share similar values and that the average temperatures between March and May (main germination period of *S. elaeagnifolium*) are similar. Kfar Blum has a cooler autumn–winter season (September to February) than Kibbutz Urim, with a temperature difference of approximately 4 C. Nonetheless, this difference in environmental conditions was not reflected in a lower T_b, and even the 95% CIs for the temperature ranges of these two populations were similar, lying between 8 and 14 C. The lack of differences in the cardinal temperatures offers an agronomic advantage. Any decision making regarding the control of this weed that is based on these temperatures will be identical for all regions. However, the three locations do differ in amounts of precipitation, with

Table 5. Estimated parameters of the three-parameter log-logistic equation describing the germination dynamics of *Solanum elaeagnifolium* in relation to growing degree days (GDD): $f(GDD, (b, d, e)) = d/(1 + \exp(b(\log(GDD) - \log(e))))$, where *d* is maximal germination, *b* is the steepness of the curve at the inflection point, and *e* is the median germination GDD.

Population	Parameter[a]	Estimate	P-value
KB	*d*	0.84 (0.03)	<0.001
	b	−3.25 (0.28)	<0.001
	e	125.14 (5.36)	<0.001
	RMSE	0.071	
NY	*d*	0.92 (0.04)	<0.001
	b	−2.79 (0.19)	<0.001
	e	134.18 (6.08)	<0.001
	RMSE	0.057	
UR	*d*	0.77(0.02)	<0.001
	b	−3.49 (0.26)	<0.001
	e	128.03 (4.34)	<0.001
	RMSE	0.061	

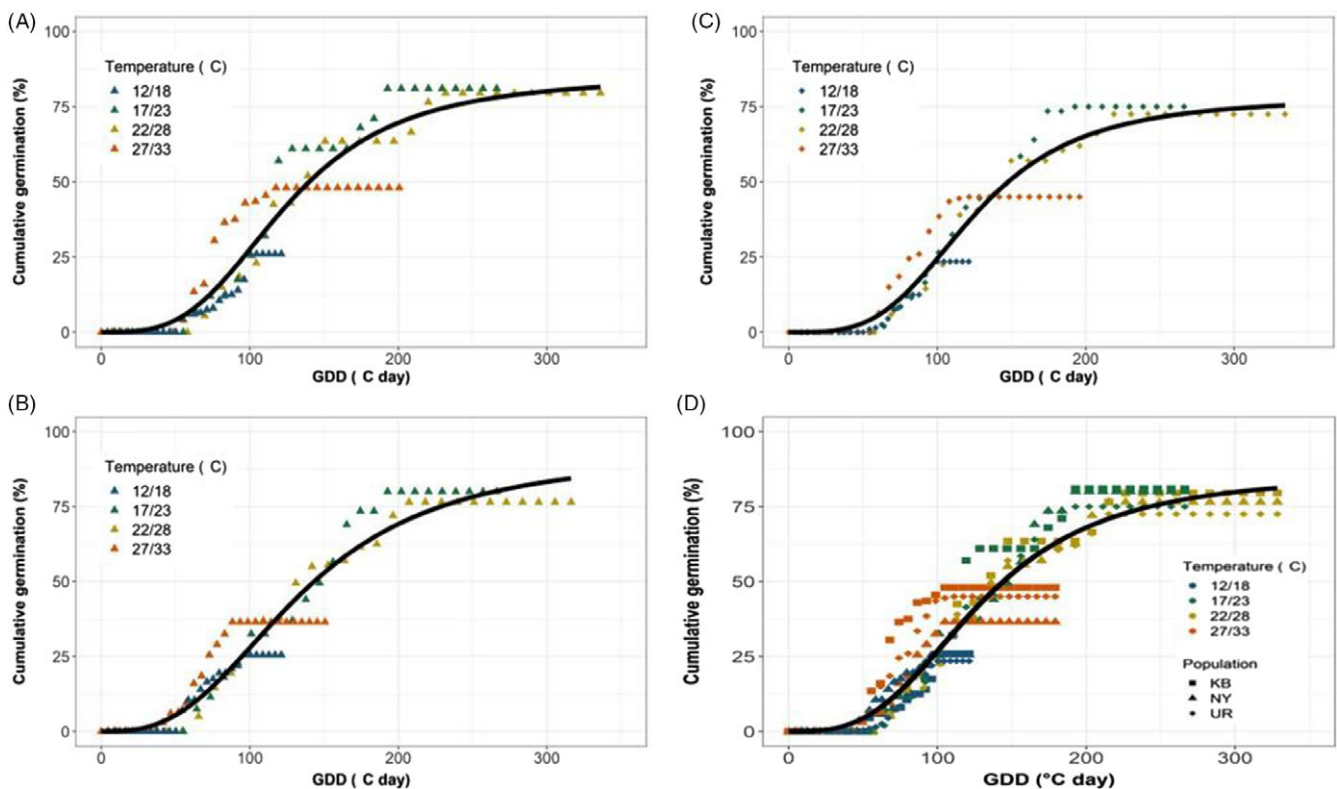[a]RMSE, root mean-square error.

Figure 3. Germination dynamics of *Solanum elaeagnifolium* in relation to growing degree days (GDD) using log-logistic three parameters: cumulative germination (%) = $d/(1 + \exp(b(\log(GDD) - \log(e))))$, where *d* is maximal germination, *b* is the steepness of the curve at the inflection point, and *e* is the median germination GDD. The model was fit for all three populations separately, namely: (A) Kfar Blum (KB), (B) Newe Ya'ar (NY), and (C) Urim (UR); and (D) for all three populations for all the temperature regimes. The evaluated parameters (*d*, *b*, and *e*), the cardinal temperatures (base temperature [T_b], optimum temperature [T_o], and ceiling temperature [T_c]), P-value, and root mean-square error (RMSE) value were: $d = 0.85$, $b = −3.06$, $e = 129.3$, $T_b = 10.82$ C, $T_o = 23.86$ C, $T_c = 35.9$ C, $p < 0.001$, and RMSE = 0.064.

Kibbutz Urim having significantly lower rainfall than the other two locations. As this environmental parameter plays a crucial factor in seed germination (Jami Al-Ahmadi and Kafi 2007), future research will have to develop a hydrothermal germination dynamics model (Alvarado and Bradford 2002; Mesgaran et al. 2017; Onofri et al. 2018). Such a model would be relevant for nonirrigated fields, natural reserves, and other niches where water is a limiting factor that may inhibit seed germination.

To best of our knowledge, this is the first study to estimate cardinal temperatures for *S. elaeagnifolium* germination. The estimated temperatures are in agreement with those for other weed species originating from the southern United States and Central America that are associated with warm and dry climates. For example, the T_b value (10.82 C) revealed in our study is within the range of other typical "summer" weeds, between 7.5 C (common purslane [*Portulaca oleracea* L.]) and 16.9 C (Palmer amaranth [*Amaranthus palmeri* S. Watson]) (Cochavi et al. 2018). Furthermore, the optimal germination temperature of 23.8 C and high ceiling temperature of 35.9 C, which are typical for the Israeli early and midsummer, respectively, can explain the

adoption of this weed over wide areas in the Mediterranean region. However, our results were driven by controlled conditions, and further validation under field conditions with a varying range of temperature fluctuations are needed to ensure robustness.

In conclusion, *S. elaeagnifolium* is a troublesome weed that poses a threat to agricultural summer crops and natural ecological niches in Israel and other parts of the world (Boyd et al. 1984; Mekki 2007; Qasem et al. 2019; Travlos 2013). Herbicide-based options to control *S. elaeagnifolium* are limited (Wu et al. 2016); thus, extensive biological knowledge about this weed is a prerequisite for improving its control. The main objectives of this study were therefore to determine the cardinal temperatures for the germination of this weed and to develop a prediction model for its germination. It was found that the seed germination characteristics of the three examined local *S. elaeagnifolium* populations were similar, including the impact of alternating temperature regimes on cumulative germination (proportion and rate) and cardinal temperatures. *Solanum elaeagnifolium* germination will not occur under constant temperatures, and an alternation range of ≥6 C is needed for optimal germination. The cardinal temperatures for seed germination of *S. elaeagnifolium* were found to be 10.8, 23.8, and 35.9 C for the base, optimal, and ceiling temperatures, respectively. These biological parameters can be used to accurately predict *S. elaeagnifolium* seed germination under different temperature regimes. The biological data presented here regarding the impact of temperature on *S. elaeagnifolium* germination can be used to improve the control of this weed through smart decision making regarding tilling, timing of weed control, and weed control tool(s).

References

Alvarado V, Bradford KJ (2002) A hydrothermal time model explains the cardinal temperatures for seed germination. Plant Cell Environ 25:1061–1069

Bajwa AA, Mahajan G, Chauhan BS (2015) Nonconventional weed management strategies for modern agriculture. Weed Sci 63:723–747

Balah MA, AbdelRazek GM (2020) Pesticidal activity of *Solanum elaeagnifolium* Cav. Leaves against nematodes and perennial weeds. Acta Ecol Sin 40:373–379

Balah MA, Hassany WM, Mousa EA (2021) Response of invasive *Solanum elaeagnifolium* Cav. seed germination and growth to different conditions and environmental factors. Biologia 76:1409–1418

Bergkvist G, Ringselle B, Magnuski E, Mangerud K, Brandsæter LO (2017) Control of *Elymus repens* by rhizome fragmentation and repeated mowing in a newly established white clover sward. Weed Res 57:172–181

Boyd JW, Murray DS (1982) Growth and development of silverleaf nightshade (*Solanum elaeagnifolium*) Weed Sci 30:238–243

Boyd JW, Murray DS, Tyrl RJ (1984) Silverleaf nightshade, *Solanum elaeagnifolium*, origin, distribution, and relation to man. Econ Bot 38:210–217

Bradford KJ (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Sci 50:248–260

Brunel S (2011) Pest risk analysis for *Solanum elaeagnifolium* and international management measures proposed. EPPO Bull 41:232–242

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Cochavi A, Goldwasser Y, Horesh A, Igbariya K, Lati RN (2018) Impact of environmental factors on seed germination and emergence of wild poinsettia (*Euphorbia geniculata* Ortega). Crop Prot 114:68–75

Cochavi A, Rubin B, Achdari G, Eizenberg H (2016) Thermal time model for Egyptian broomrape (*Phelipanche aegyptiaca*) parasitism dynamics in carrot (*Daucus carota* L.): field validation. Front Plant Sci 7:1–11

Covell S, Ellis RH, Roberts EH, Summerfield RJ (1986) The influence of temperature on seed germination rate in grain legumes: I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. J Exp Bot 37:705–715

Curran WS, Werner EL, Hartwig NL, Curran WS, Werner EL, Hartwig NL (1994) Effectiveness of herbicides and tillage on quackgrass (*Elytrigia repens*) control in corn. Weed Sci 8:324–330

Derakhshan A, Gherekhloo J, Vidal RA, De Prado R (2014) Quantitative description of the germination of littleseed canarygrass (*Phalaris minor*) in response to temperature. Weed Sci 62:250–257

Doyle CJ (1991) Mathematical models in weed management. Crop Prot 10: 432–444

Forcella F, Benech Arnold RL, Sanchez R, Ghersa CM (2000) Modeling seedling emergence. Field Crop Res 67:123–139

Garcia-Huidobro J, Monteith JL, Squire GR (1982) Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.): I. Constant temperature. J Exp Bot 33:288–296

Gitsopoulos TK, Damalas CA, Georgoulas I (2017) Chemical options for the control of silverleaf nightshade (*Solanum elaeagnifolium*). Planta Daninha 35:1–8

Goldwasser Y, Miryamchik H, Rubin B, Eizenberg H (2016) Field dodder (*Cuscuta campestris*)—a new model describing temperature-dependent seed germination. Weed Sci 64:53–60

Grundy AC, Peters NCB, Rasmussen IA, Hartmann KM, Sattin M, Andersson L, Mead A, Murdoch AJ, Forcella F (2003) Emergence of *Chenopodium album* and *Stellaria media* of different origins under different climatic conditions. Weed Res 43:163–176

Guillemin JP, Gardarin A, Granger S, Reibel C, Munier-Jolain N, Colbach N (2013) Assessing potential germination period of weeds with base temperatures and base water potentials. Weed Res 53:76–87

Hardegree SP (2006) Predicting germination response to temperature. I. Cardinal-temperature models and subpopulation-specific regression. Ann Bot 97:1115–1125

Hardin JW, Doerksen G, Herndon D, Hobson M (1972) Pollination ecology and floral biology of four weedy genera in southern Oklahoma. Southwestern Naturalist 16:403–412

Hossain A, Ishimine Y, Akamine H, Murayama S (1999) Effect of burial depth on emergence of *Panicum repens*. Weed Sci 47:651–656

Hosseini P, Ahmadvand G, Oveisi M, Morshedi P, Gonzalez-Andujar JL (2017) A modelling approach for predicting the initial phase of Egyptian broomrape (*Phelipanche aegyptiaca*) parasitism in potato. Crop Prot 100:51–56

Ilçim A, Behçet L (2007) *Solanum elaeagnifolium* Cav in Turkey. Turk J Botany 31:577–579

Jami Al-Ahmadi M, Kafi M (2007) Cardinal temperatures for germination of *Kochia scoparia* (L.). J Arid Environ 68:308–314

Jensen SM, Wolkis D, Keshtkar E, Streibig JC, Ritz C (2020) Improved two-step analysis of germination data from complex experimental designs. Seed Sci Res 30:194–198

Knapp S, Sagona E, Carbonell AKZ, Chiarini F (2017) A revision of the *Solanum elaeagnifolium* clade (*Elaeagnifolium* clade; subgenus *Leptostemonum*, Solanaceae). PhytoKeys 2017:1–104

Krigas N, Tsiafouli MA, Katsoulis G, Votsi NE, van Kleunen M (2021) Investigating the invasion pattern of the alien plant *Solanum elaeagnifolium* Cav. (silverleaf nightshade): environmental and human-induced drivers. Plants 10:805

Lati RN, Filin S, Eizenberg H (2011) Temperature- and radiation-based models for predicting spatial growth of purple nutsedge (*Cyperus rotundus*). Weed Sci 59:476–482

Lati RN, Filin S, Eizenberg H (2012) Effect of tuber density and trifloxysulfuron application timing on purple nutsedge (*Cyperus rotundus*) control. Weed Sci 60:494–500

Masin R, Onofri A, Gasparini V, Zanin G (2017) Can alternating temperatures be used to estimate base temperature for seed germination? Weed Res 57:390–398

Mekki M (2007) Biology, distribution and impacts of silverleaf nightshade (*Solanum elaeagnifolium* Cav.). EPPO Bull 37:114–118

Mesgaran MB (2019) Modeling Weed Seed Germination and Seedling Emergence. https://rpubs.com/mbmesgaran/495385

Mesgaran MB, Onofri A, Mashhadi HR, Cousens RD (2017) Water availability shifts the optimal temperatures for seed germination: a modelling approach. Ecol Modell 351:87–95

Onofri A, Benincasa P, Mesgaran MB, Ritz C (2018) Hydrothermal-time-to-event models for seed germination. Eur J Agron 101:129–139

Ordoñez-Salanueva CA, Seal CE, Pritchard HW, Orozco-Segovia A, Canales-Martínez M, Flores-Ortiz CM (2015) Cardinal temperatures and thermal time in *Polaskia* Backeb (Cactaceae) species: effect of projected soil temperature increase and nurse interaction on germination timing. J Arid Environ 115:73–80

Ottavini D, Pannacci E, Onofri A, Tei F, Jensen Kryger P (2019) Effects of light, temperature, and soil depth on the germination and emergence of *Conyza canadensis* (L.) Cronq. Agronomy 9:533

Parmoon G, Moosavi SA, Akbari H, Ebadi A (2015) Quantifying cardinal temperatures and thermal time required for germination of *Silybum marianum* seed. Crop J 3:145–151

Qasem JR, Al Abdallat AM, Hasan SM (2019) Genetic diversity of *Solanum elaeagnifolium*, an invasive problematic weed in Jordan. Weed Res 59:222–234

R Core Team (2020) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing

Ritz C, Baty F, Streibig JC, Gerhard D (2015) Dose-response analysis using R. PLoS ONE 10:1–13

Rodriguez S, Kruk BC, Satorre EH (2020) Modelling *Chloris virgata* germination and emergence under different temperature and light quality conditions. Weed Res 60:287–296

Rowse HR, Finch-Savage WE (2003) Hydrothermal threshold models can describe the germination response of carrot (*Daucus carota*) and onion (*Allium cepa*) seed populations across both sub- and supra-optimal temperatures. New Phytol 158:101–108

Shrestha A, Roman ES, Thomas AG, Swanton CJ, Thomas AG (1999) Modeling germination and shoot-radicle elongation of *Ambrosia artemisiifolia*. Weed Sci 47:557–562

Stanton R, Heap JW, Carter R, Wu H (2009) *Solanum elaeagnifolium* Cav. Pages 274–293 *in* Panetta FD, ed. The Biology of Australian Weeds. Volume 3. Meredith, Australia: R.G. and F.J. Richardson

Stanton R, Wu H, Lemerle D (2012) Factors affecting silverleaf nightshade (*Solanum elaeagnifolium*) germination. Weed Sci 60:42–47

Travlos IS (2013) Responses of invasive silverleaf nightshade (*Solanum elaeagnifolium*) populations to varying soil water availability. Phytoparasitica 41:41–48

Trudgill DL, Honek A, Li D, Van Straalen NM (2005) Thermal time—concepts and utility. Ann Appl Biol 146:1–14

Uludag A, Gbehounou G, Kashefi J, Bouhache M, Bon MC, Bell C, Lagopodi AL (2016) Review of the current situation for *Solanum elaeagnifolium* in the Mediterranean Basin. EPPO Bull 46:139–147

Washitani I (1987) A convenient screening test system and a model for thermal germination responses of wild plant seeds: behaviour of model and real seeds in the system. Plant Cell Environ 10:587–598

Wu H, Stanton R, Lemerle D (2016) Herbicidal control of *Solanum elaeagnifolium* Cav. in Australia. Crop Prot 88:58–64

Zernov AS, Mirzayeva SN (2016) *Solanum elaeagnifolium* Cavara, a new invasive species in the Caucasus. Wulfenia 23:253–256