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Field Dodder (*Cuscuta campestris*)—A New Model Describing Temperature-Dependent Seed Germination

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The members of the genus *Cuscuta* (common name: dodder) are obligate holoparasitic plants that are found throughout the agricultural regions of the world. Of all of the species of dodder, field dodder (*Cuscuta campestris*) causes the most damage to crops. This species parasitizes the shoots of broadleaf plant crops and weeds. We conducted a series of field dodder seed germination tests in controlled-temperature chambers, in order to describe the effect of temperature on field dodder germination and develop a germination model based on the obtained data. The best fit was obtained when temperature data and time were transformed to thermal time using the beta-function model. The field dodder germination model can serve as a tool for knowledge-based predictions of germination and emergence timing, to allow for the implementation of effective mechanical and chemical management measures.

Nomenclature: Field dodder; *Cuscuta campestris* Yuncker.

Key words: Germination analysis, management, parasitic plants, weed control.

Plants belonging to the genus *Cuscuta* (common name: dodder) are obligate holoparasitic plants. There are over 170 different species of this genus distributed throughout the world (Dawson et al. 1994; Holm et al. 1997). Field dodder, often called "witch's hair," is the most agriculturally damaging dodder species, parasitizing shoots of broadleaf plants, including weeds, field crops, vegetables, and ornamentals throughout most of the agricultural regions of the world. The rootless, leafless parasite coils around the shoot of the host plant and produces haustoria that penetrate host stems and leaves, attach to the xylem and phloem, and extract water and assimilates from the host plant, leading to severe reduction in host growth and yield (Dorr 1987). The wide geographical distribution of dodder species and their wide range of hosts place them among the most damaging of all parasitic plants (Holm et al. 1997).

Field dodder seed control by physical means is extremely difficult due to their hard seed coats and the fact that these seeds can remain viable in soil for a long time and continue to germinate and emerge throughout the warm seasons. Furthermore, field dodder control is highly problematic due to the nature of attachment and association between host and parasite, which requires highly selective means to destroy the parasite without damaging the crop. Several different methods for field dodder control in crops have been reviewed (Cudney et al. 1992; Dawson et al. 1994; Parker and Riches 1993), but, in most cases, options for effective control are limited or nonexistent.

Keith and Tingey (1968) examined the germination of scarified field dodder seed from Utah on filter paper in petri dishes in fixed-temperature growth chambers and nonscarified seed placed in cans during two seasons in the field. In the growth-chamber study, field dodder seeds did not germinate at temperatures of less than 7 C. At 10 C, 7% of the seeds germinated; at 15 C, 31% germinated; at 21 C, 23% germinated; and at 35 C, 22% germinated. In the field, dodder started to germinate in March or April when daily average soil temperatures reached 10 C, and maximum germination was observed in May or June when daily average soil temperatures reached 20 C. Hutchinson and Ashton (1980) reported that scarified field dodder seeds from California that were placed on a filter paper in petri dishes placed on a temperature-gradient bar or on a laboratory mechanical convection oven did not germinate at 15 C or at temperatures of 39 C or above. Maximum germination of 68% occurred at 30 and 33 C. Nir et al. (1996) found that scarified Israeli field dodder seeds placed on moist filter paper in petri dishes placed in controlled constant-temperature chambers began germinating at temperatures between 10 and 15 C, and reached a maximum

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germination rate of 90% at 30 C. At 40 C, germination decreased to 10%. Benvenuti et al. (2005) reported a sigmoid-curve pattern for the germination of scarified field dodder seeds from Italy on filter paper in petri dishes placed in constant-temperature growth chambers. In that study negligible germination was recorded at temperatures of 5 to 10 C and maximum germination of 90% was observed at 30 C, whereas 50% germination was recorded at 18 C. The differences in germination rates reported by the different researchers could be attributed to differences between local biotypes and differences in the ages of the seeds, storage conditions, and the treatments to which they were subjected.

The thermal-unit concept proposes that the sum of the heat units between a minimal and a maximal temperature threshold can serve as robust parameter for estimating the time required for phenological events such as seed germination or seedling emergence (Leblanc et al. 2003). The most common method for computing thermal time is the growing degree days (GDD) equation and the use of this equation for the prediction of the parasitism dynamics of the root parasitic plant broomrape (*Phelipanche* and *Orobanche* spp.) has been proposed previously (Eizenberg et al. 2004, 2005, 2012a, Ephrath and Eizenberg 2010, Ephrath et al. 2012).

This method may be used in situations in which a model is examined at temperatures between the minimum and maximum threshold for plant development. However, if the temperatures are outside of this range, the sine-wave method is more appropriate (Allen 1976). The sine-wave method proposes that the daily temperature curve can be described as a sine wave. The nonlinear beta-function model may be used to describe situations in which organisms experience out-of-range temperatures that inhibit phenological events (Yin and Kropff 1996). The beta-function model has been used to quantify the effect of temperatures on plant phenological processes but, to the best of our knowledge, has not been employed for plant seed germination.

Nonlinear equations (e.g., Weibull, sigmoid, and logistic) have been employed to describe the relations of thermal time and the parasitism dynamics of broomrape (*Orobanche* and *Phelipanche* spp.). These regressions successfully describe the temperature-dependent phases of the parasite life cycle, including germination, attachment, tubercle development, and shoot emergence (Ephrath and Eizenberg 2010; Eizenberg et al. 2004, 2005, 2012b).

The aim of this study was to develop a thermal-time model for field dodder seed germination under controlled conditions.

Materials and Methods

Field Dodder Seeds. The field dodder seeds used in the experiments conducted in 2010 were collected from a heavily infested chickpea (*Cicer arietinum* 'Yarden' L.) field in Saar in the western Galilee in Israel (33.03°N, 35.11°E) in June 2002. Mature, dry field dodder capsules were carefully removed from plants, air-dried, threshed, cleaned, and stored at 4 C until use. Before seeding in petri dishes, field dodder seeds were scarified by a 1-h treatment with sulphuric acid, washed thoroughly with sterile water, and air-dried**.** Scarification of seeds is a common procedure and a must for field dodder laboratory germination tests, as nonscarified seeds germinate very poorly**.** This procedure is similar to the procedure seeds gradually undergo under natural conditions. Seed scarification reduces the germination variability within a field dodder population and thus may increase model accuracy. In preliminary seed germination tests that were conducted before each experiment, we observed 80 to 100% field dodder seed germination following seed scarification.

Germination Chambers. Twenty scarified field dodder seeds were placed in 90-mm plastic petri dishes lined with No. 1 Whatman filter paper moistened with 1.5 ml of ionized sterile water. Field dodder seeds were placed on the filter paper in each petri dish with five replications (petri dishes) per treatment (temperature). Petri dishes were sealed carefully with Parafilm and the dishes were placed in a 27-cm-diam aluminium canister lined with moist paper towels and sealed with masking tape. The canisters were placed in forced-air germination chambers, set at fixed temperatures of 5, 10, 15, 20, 25, 30, 35 and 40 C, $\pm$ 0.5 C. Canisters were opened daily and field dodder seed germination was evaluated in a dark room. The filter paper in the petri dishes and the paper towels in the canisters were replenished with water as needed, to ensure adequate moisture for maximal seed germination. The growth-chamber studies were repeated twice under identical conditions.

Field dodder seeds were determined to be germinating once the length of the emerging shoot was equal to the diameter of the seed. The experiment was terminated after 24 d (experiment 1) and 27 d

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(experiment 2), the time at which all germination ceased at all temperatures.

Statistical Analysis. All experiments were conducted in a completely randomized design with five replicates (petri dishes with 20 field dodder seeds) per treatment. The statistical analysis was carried out as described by Onofri et al. (2010). The response of field dodder germination to the examined temperatures was evaluated relative to the four-parameter Weibull equation, using nonlinear regression:

$$f(x) = a \times \left[1 - \exp\left(-\left(\frac{GDD - lag}{b}\right)^{c}\right)\right] \quad [1]$$

where a is the maximal field dodder germination, c is the shape parameter that determines the skewness and kurtosis of the equation, and b is the scale parameter regardless of the shape value. Nonlinear regressions and beta-function analyses were performed using SAS PROC NLMIXED (ver. 9.2, SAS Institute, Cary, NC) and SigmaPlot (ver. 11, SAS).

Results and Discussion

Field Dodder Germination in Temperature Chambers. In the seed germination experiments, there were no experiment by temperature regime interactions; therefore, the results of the two experiments were combined and analyzed as 10 replications. A strong relationship was observed between temperature and the time required for seed germination (Figure 1). Field dodder seeds started to germinate 3 d after seeding (DAS) at all of the examined temperatures, except for 5 C. The relationship between temperature and seed germination is described as a four-parameter Weibull equation for all temperature regimes. The estimated parameters for the eight equations associated with the temperature regimes are presented in Table 1. Parameter a represents the maximal asymptote for final accumulated field dodder germination. At 5 C, 6.25% of all field dodder seeds germinated; whereas between 10 and 35 C, 96.4 to 100% germinated and, at 40 C, 62.11% of the seeds germinated.

The four-parameter Weibull equation can be used to estimate the lag phase for field dodder germination. The significance of the lag phase lies in its ability to allow us to estimate the first day of field dodder seed germination. The duration of the lag phase was between 2 and 3 DAS for all of the temperature treatments, except for the 5 C regime, in which it was 5 DAS. The scale parameter b represents the day by which 63% of the seeds had germinated. The use of this parameter enables us to compare the germination rates observed under different temperature regimes. The results of this experiment show that at temperatures between 15 and 35 C, the value of scale parameter b was between 0.29 and 1.19 DAS. However, for the two extreme temperature regimes (5 and 40 C), the values of the scale parameters were 1.63 and 3.18 DAS, respectively. The root mean square error (RMSE) values of all the temperature regimes (presented in Figure 1 and Table 1) were between 1.00 and 4.40, representing a strong association between germination dynamics and temperature regime.

The data presented in Figure 1 and Table 1 were combined over thermal time and fitted to the GDD model using the four-parameter Weibull equation. The T_{base} value (i.e., the computed minimal temperature for germination) calculated by the model was 2 C. The a parameter, representing the upper asymptote (maximal accumulated germination), was estimated as 90.3 $\pm$ 2.5% SE. The inflection point of the logistic equation (i.e., the point at which 50% of maximal germination was observed) was estimated as 80.0 $\pm$ 4.7%. The RMSE for the three-parameter log logistic equation was 21.74.

At temperatures of 20 to 35 C, maximal germination of 93 to 100% was observed at 11 DAS. At 15 C, the rate of germination was slower than that observed for the 20 to 35 C group, but did reach 96.5% by the end of the experiments. At 35 C, germination was fastest and reached 93% after only 3 d. At 40 C the germination curve was about 60% of that of the 20 to 35 C group, eventually reaching 60% at the end of the experiments. At 5 C, germination was slowest and seeds started to geminate only after 7.5 d, reaching a low maximal germination rate of 6% at the end of the experiments. Field dodder seed germination at 10 C was slow, started only at 3 DAS and reached only 55% by the end of the study. The germination rate of field dodder seeds and the final germination percentage were optimal between 26 and 35 C, minimal at 5 C, and reached 40 and 60% at temperatures of 15 C and 40 C, respectively.

Development of the Field Dodder Germination Model. In order to develop a thermal time model for predicting cumulative field dodder germination, field dodder germination data from all of the temperature regimes were combined. Temperatures were converted to thermal time (GDD) using

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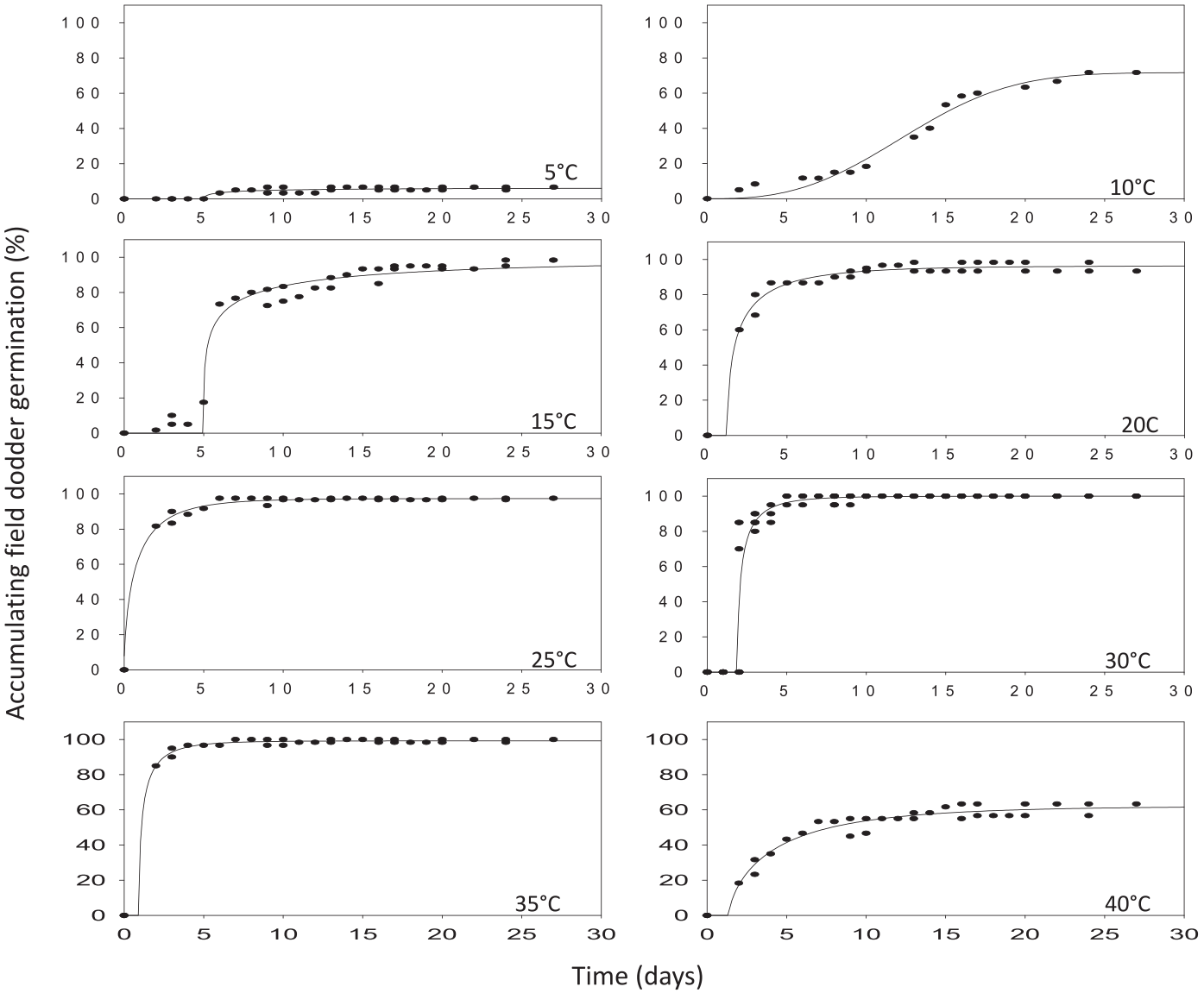


Figure 1. Effect of temperature on the rate of field dodder germination. Nonlinear, four-parameter Weibull regression (F(GDD) = a × [1 − exp(−{[(GDD − lag)/b]^c})]) (Eizenberg et al. 2012b) coefficients for cumulative field dodder germination are presented in Table 1.

Table 1. Nonlinear, four-parameter Weibull regression ($Y = a \times [1 - \exp(-\{[(x - lag)/b]^c\})]$) (Eizenberg et al. 2012b) coefficients for cumulative field dodder germination in petri dishes under different temperature regimes.

Temperature (constant)	Coefficient parameters[a]								Regression	
C	a	P(a)	b	P(b)	c	P(c)	lag	P(lag)	P	RMSE
5	6.25	0.042	1.63	0.66	0.44	0.73	5.00	0.35	0.0001	1.00
10	100	0.402	25.31	0.32	1.92	0.08	0	1	0.0001	12.64
15	100	0.001	0.79	0.031	0.32	0.03	4.99	0.001	0.0001	4.40
20	96.40	0.001	0.78	0.12	0.51	0.0091	1.25	0.032	0.0001	2.72
25	97.36	0.001	0.83	0.14	0.63	0.0017	0	1	0.0001	1.41
30	100	0.001	1.19	0.014	0.79	0.0001	0	1	0.0001	1.03
35	99.21	0.001	0.29	0.56	0.51	0.107	0.93	0.373	0.0001	1.18
40	62.11	0.001	3.18	0.001	0.69	0.0019	1.36	0.0260	0.0001	3.31

[a] Abbreviations: a, maximal field dodder germination; b, scale parameter regardless of the shape value; c, shape parameter that determines the skewness and kurtosis of the equation; lag, estimate of the time required for the germination of the first seedling; RMSE, root mean square error.

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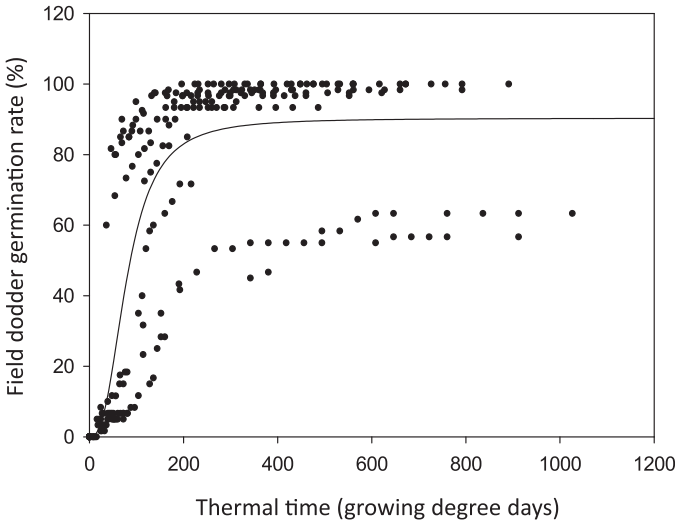


Figure 2. Three-parameter, logistic nonlinear regression of the rate of field dodder germination and growing degree days (Base temperature = 2 C). Root mean square error = 21.74.

Equation 2; T_{base} = 2 C:

$$GDD = \sum_{i}^{n}\left[\frac{(T_{max}+T_{min})}{2} - T_{base}\right] \qquad [2]$$

where T_{max} is the maximum daily temperature, T_{min} is the minimum daily temperature, and T_{base} is the base temperature (Ephrath and Eizenberg 2010; Leblanc et al. 2003; McMaster and Wilhelm 1997).

A three-parameter sigmoid equation (Equation 3) indicated the presence of a significant relation between thermal time and the germination of field dodder seeds (P = 0.001, RMSE = 21.74; Figure 2). The nonlinear regressions included, among other things, a three-parameter logistic function (Equation 3; Brown and Mayer 1988, Eizenberg et al. 2009; previously used to describe the effects of thermal time on other parasitic weeds (i.e., broomrape).

$$Y = \frac{a}{1+\left(\frac{x}{x_{50}}\right)^{b}} \qquad [3]$$

where Y represents the number of field dodder seedlings, a represents the upper asymptote (maximal field dodder germination), x_{50} represents the GDD value at which the germination is 50% of maximal, and b represents the slope at x_{50} (Ephrath et al. 2012).

When the thermal time was greater than 200 GDD, two groups of data points were observed (as shown in Figure 2). One group of points collapsed around the range of 80 to 100% cumulative field dodder germination and the second group collapsed around 40 to 60% cumulative germination. The main source of the high degree of variation in cumulative germination above 200 GDD was associated with the 40 C temperature regime. Therefore, the 40 C temperature-regime germination data were omitted and the remaining data were refitted to thermal time based on the sigmoid equation (T_{base} = 2 C, T ≤ 35 C).

The refitting of the thermal time equation over 200 GDD reduced the amplitude of the points from 45 to 100% to 90 to 100% (Fig. 3). In addition, the RMSE was decreased by 41% from 21.74 to 15.35. The difference between the observed data and the predicted equation results under 200 GDD is big, and thus there is a need to improve the equation in order to reduce this difference.

The next step in the development of the model was to include the data for the 35 to 40 C temperature regimes and to reduce the error under 200 GDD. Among several equations that were tested to correct the thermal time transformation, the beta-function equation (Yin and Kropff 1996) was found to be the most accurate. The new GDD (GDD_{beta}) describes the effect of thermal time on accumulated field dodder germination at temperatures between 5 and 40 C (Figure 4). This function is unique as it can describe an asymmetric shape of the relation between thermal time and cumulative field dodder germination.

If $T_b < T < T_m$, *then*:

$$R = k\left\{\left(\frac{T-T_b}{T_o-T_b}\times\frac{T_m-T}{T_m-T_o}\right)^{\left(\frac{T_m-T_o}{T_o-T_b}\right)}\right\}^{a} \qquad [4]$$

If $T \leq T_b$ *or* $T \geqslant T_m$, *then*:

$$R = 0$$

where T_{base} represents the base temperature, the temperature at or below which no field dodder seed can germinate; T_o represents optimum temperature, the temperature at which germination proceeds most quickly; T_m represents the ceiling or maximum temperature, at or beyond which germination is zero. Parameter k represents the maximum germination rate (R) that occurs at T_o and a is the shape parameter of the equation that gives more flexibility to the model (Figure 4).

$$TT = GDD_{beta} = \sum R(T_0 - T_b) \qquad [5]$$

New GDD_{beta} is computed by summing the products of R and (T_o − T_b), where R is the daily rate of

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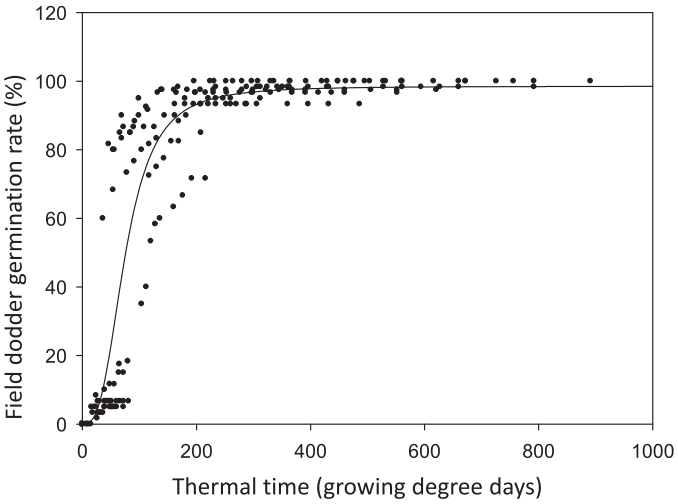


Figure 3. Three-parameter, logistic nonlinear regression of the rate of field dodder germination and growing degree days (Base temperature = 2 C), without the data collected for the 40 C temperature treatment. Root mean square error = 15.35.

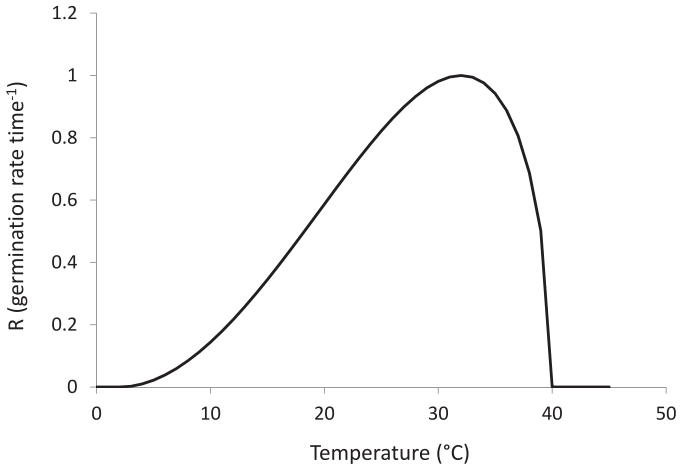


Figure 4. Beta function (Equation 2) describing the relationship between germination rate (R) and temperature (T).

germination at any temperature, T_{base} represents the base temperature (i.e., the temperature at or below which no field dodder seed can germinate) and T_o represents optimal temperature (the temperature at which germination takes place most rapidly).

The observed data collapsed excellently around the curve computed by the sigmoid equation and GDD_{beta}, reducing the RMSE almost twofold from 15.35 to 8.17 (Figure 5). The computed coefficients for the beta-function equation that were incorporated into the model were the following: T_{base} = 2 C (base temperature); T_o = 32 C (optimal temperature); and T_m = 40 C (ceiling or maximal temperature, at or beyond which no germination occurs).

The relationships between seed germination or emergence and thermal time have been expressed using sigmoid, logistic, Weibull, and Gompertz equations (Alvarado and Bradford 2002; Brown and Mayer 1988; Ephrath and Eizenberg 2010; Ephrath et al. 2012; Grundy 2003; Izquierdo et al. 2009; Kebreab and Murdoch 1999). A three-parameter sigmoid equation was previously used to describe the relationship between GDD and the parasitism of Egyptian broomrape (*Phelipanche aegyptiaca* Pers.) on tomato (*Solanum lycopersicon* L.) (Ephrath et al. 2012). In the current study, this equation is used to describe the relationship between GDD and field dodder seed germination.

The relationship between field dodder seed germination and time was initially described by us using the Weibull equation consisting of a lag phase, an acceleration phase, and a maximal phase (Figure 1). The maximal asymptote (parameter a) was around 100% at 10 to 35 C (Table 1). Similar patterns of seed germination have been reported by Rowse and Finch-Savage (2003) for the germination of carrot (*Daucus* carota) and onion (*Allium cepa*) seeds, by Steinmaus et al. (2000) for the germination of the seeds of nine different weed species, and by Ephrath et al. (2012) for the germination of sunflower broomrape (*Orobanche cumana* Wallr.) and Egyptian broomrape.

The strong relationship between seed germination and temperature observed in the current study was used to develop a thermal-time model of field dodder seed germination. Thermal-time models have been developed to describe the germination of crop seeds (Aiken 2005; Stenmause et al. 2000) and weed seeds (Grundy 2003). These kind of models have also been developed for the root parasitic weeds common broomrape (*Orobanche minor* Sm.), sunflower broomrape and Egyptian broomrape in red clover (*Trifolium pratense* L.), sunflower (*Helianthus annuus*), and tomato, respectively, as the only option to predict their hidden subsoil developmental stages (Eizenberg et al. 2005, Ephrath et al. 2012).

In all of the studies listed above, the cumulative degree days were computed using a linear equation (Equation 1). However, when this equation was used in the current study, the RMSE was high (21.74; Figure 2) and the model failed to predict the germination of field dodder. Two groups of points (observations) could be observed, one above the regression line (overestimations) and one below it (underestimations). When the data for the highest temperature (40 C) were omitted, the RMSE was reduced to 15.35; that is, the accuracy of the model increased considerably (Fig. 3).

The employment of a beta function for computing the GDD to estimate the germination rate of

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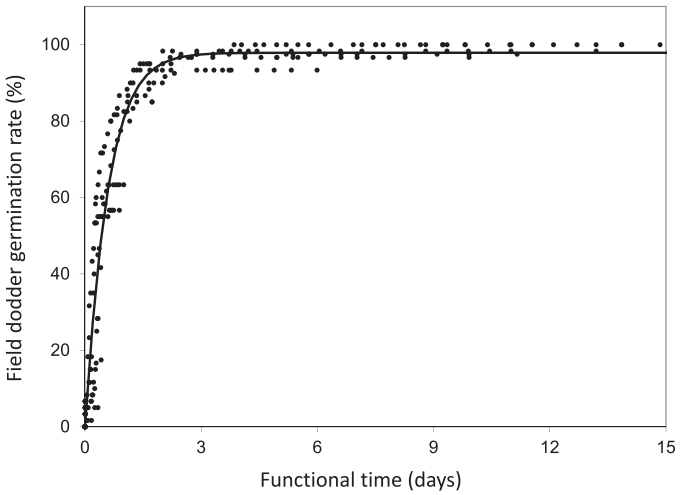


Figure 5. Three-parameter, nonlinear regression of field dodder germination rate and thermal time (Base temperature = 2 C) based on the new beta-function growing degree days D_{beta} computed by summing the products of the daily rate of germination and (T_o – T_{base}). Root mean square error = 8.17.

field dodder as related to thermal time allows the use of data obtained from the entire examined range of temperatures (Yin and Kropff 1996). When the beta function was used to compute GDD and the data were fitted to field dodder germination, a good fit was achieved (RMSE = 817). To the best of our knowledge, this is the first time a beta function has been used to predict field dodder germination based on thermal time.

The germination responses of field dodder seeds to different temperatures observed in our study resemble the results obtained by Nir et al. (1996). This is not surprising as the seeds are from the same geographical area with similar climatic conditions, although they were collected from different fields and in different years.

The climatic conditions required for field dodder germination and emergence in the field correspond with the conditions needed for the emergence of susceptible host plants, ensuring the further development and completion of the life cycle of this obligate parasite. Predicting the time of field dodder germination in the field is crucial for the timing of control measures. We propose that control measures should be concentrated during the short period during which the parasite seedling is independent and has not yet connected with a host. At this stage, the parasite is small, with restricted resources, and more vulnerable to different control measures.

To optimize herbicide use and insure a logical framework for weed management, information on the critical period of weed interference is crucial. There are two recognized components of the critical period. The first component is the timing of control measures and the length of time weed control practices must be continued to prevent crop yield loss. The second component is the window of time during which weeds can remain in the field before they interfere with crop growth and ultimately reduce yield (Swanton and Weise 1991). Herbicide efficacy is greatly affected by weed developmental stage and density at the time of application and, when herbicides are applied under optimal conditions, low rates can provide maximal control (Lati et al. 2012).

The critical period for weed control (CPWC) is the period in the crop growth cycle during which weeds must be controlled to prevent yield loss. This concept has been studied for many weeds and many crops and reviewed by Knezevic et al. (2002). Knowing the CPWC is useful for making smart decisions regarding the need for and timing of weed control and in maximizing the efficacy of herbicide applications, from both a biological and an economic perspective (Knezevic and Datta 2015).

The CPWCs for dodder species are unique and different from those for nonparasitic weeds, since there is no direct competition between the weed and crop at the early emergence stage. Therefore, we assume that the critical period for dodder management is dependent mainly on parasite germination and not crop development. Validation of our thermal-time model for field dodder control under field conditions is presently under way.

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