Weed Science 2012 60:57–63

Use of Logistic Equation for Detection of the Initial Parasitism Phase of Egyptian Broomrape (*Phelipanche aegyptiaca*) in Tomato

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The dynamics of the host–parasite relationship between tomato cv. Brigade and Egyptian broomrape is temperature-related. This relationship was utilized for the development of an equation on the basis of thermal time (as measured by growing degree days, GDD, C) to predict the parasitism dynamics of Egyptian broomrape in tomato. To obtain a reliable prediction from thermal time values, studies based on a wide range of temperatures are essential. Four temperature-regime treatments and five levels of infestation with Egyptian broomrape seeds were tested in a multiclimate greenhouse (phytotron) and a temperature-controlled greenhouse, respectively. The day/night temperature regimes were 20/12 C, 23/15 C, 26/18 C, and 29/21 C and the infestation levels were 0 (noninfested control), 1, 5, 10, and 25 mg of Egyptian broomrape seeds per liter of soil. As expected, increasing temperature or infestation levels resulted in faster appearance and higher rate of attachments, respectively. The relation between development of attachments and GDD was described as a three-parameter logistic curve. In both temperature-regime and infestation-level experiments, the development of attachments began 200 GDD after planting and the maximal number of attachments was recorded 800 GDD after planting. A significant reduction in the aboveground biomass of the tomato plants due to increased Egyptian broomrape biomass was recorded only for the 26/18 C and 29/21 C day/night treatments and the three highest infestation levels (5, 10, and 25 mg L^{-1} soil). The ability to predict the start of parasitism can be used to develop a climate-based system for Egyptian broomrape control with herbicides.

Nomenclature: Egyptian broomrape, *Phelipanche aegyptiaca* Pers. (syn. *Orobanche aegyptiaca*); tomato, *Lycopersicon esculentum* L.

Key words: Growing degree days (GDD), simulation, phytotron.

Broomrapes (*Orobanche* and *Phelipanche* spp.) are chlorophyll-lacking holoparasites that parasitize the roots of many dicotyledonous species worldwide and cause severe damage to vegetable and field crops (Joel et al. 2007; Parker 2009; Parker and Riches 1993). Egyptian broomrape and branch broomrape (*Phelipanche ramose*) are annual plants that germinate and parasitize tomato in the early spring and scatter seeds in the summer, at the end of the tomato growing season. In the Mediterranean basin, specifically in Italy, Greece, Turkey, Iran, and Israel, this parasitic plant is considered to be a major pest of tomato in the field and in greenhouses (Hershenhorn et al. 2009; Joel et al. 2007; Parker 2009).

A chemical control approach was proposed to manage Egyptian broomrape in processing tomato using sulfonylurea herbicides (Eizenberg et al. 2004a, 2006, 2009; Hershenhorn et al. 1998, 2009). Sunflower (*Helianthus annuus* L.) dry biomass grown under field conditions was reduced by sunflower broomrape infection before broomrape shoot emergence (Grentz et al. 2008). Similar results were obtained for faba bean (*Vicia faba* L.) parasitized by crenate broomrape (*O. crenata*) (Grentz et al. 2005). The reduction in dry weight of red clover (*Trifolium pratense* L.), grown under controlled conditions, occurred at 1,500 growing degree days (GDD) prebroomrape shoot emergence (Eizenberg et al. 2005). Therefore, to develop an efficient control strategy, it is essential to overcome the inability to detect onset of the underground parasitism and initial developmental stages of the root parasites. Accordingly, a modeling approach was proposed on the basis of the use of thermal time units for predicting subsurface developmental stages of of small broomrape (*O. minor*) in red clover and sunflower broomrape (*O. cumana*) in sunflower (Eizenberg et al. 2004b, 2005; Ephrath and Eizenberg 2010). Temperature may affect synchronization of the development between host and parasite. Several studies have shown that *Orobanche* and *Peliphanche* germination is accelerated at high temperatures, whereas low temperatures delay the dynamics of the parasitism (Sauerborn et al. 1989; van Hezewijk 1994). Kebreab and Murdoch (1999) determined that maximum germination of nonconditioned Egyptian broomrape seeds occurs in a temperature range of 21/15 C day/night. Sunflower broomrape parasitism in sunflower was positively correlated to temperature in the germination, attachment, and tubercle-production stages (Eizenberg at al. 2003). Temperature also affected small broomrape parasitism in red clover (Eizenberg et al. 2004b). In this latter case, the dependence between temperature and development was used to create a degree-day model to predict the parasitism. This model was validated under field conditions (Eizenberg et al. 2005). Thermal time was also effectively used to predict the parasitism of sunflower broomrape and Egyptian broomrape in sunflower (Ephrath and Eizenberg 2010).

In field studies and under controlled conditions, Egyptian broomrape infection in tomato and eggplant (*Solanum melongena* L.) increases with temperature (Eizenberg et al. 1998). However, the relationship between temperature and Egyptian broomrape parasitism on tomato in the soil subsurface have never been investigated. This knowledge is essential for the development of a climate-based system for controlling this parasite in tomato. Therefore, the main objective of this study was to detect the precise timing of the initial attachments' appearance as affected by (1) thermal time and (2) infestation level.

DOI: 10.1614/WS-D-11-00070.1

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Materials and Methods

The experiments were conducted in a controlled-temperature phytotron located at the Agricultural Research Organization (ARO) in Bet-Dagan, Israel, and in a temperature-controlled greenhouse located at the ARO's Newe Ya'ar Research Center.

Tomato transplants ('Brigade', 40 d old) were used in all experiments. Egyptian broomrape inflorescences were collected from tomato parasitized by Egyptian broomrape in the year before the experiments. Seeds were separated from the dry inflorescences on 300-mesh sieves, and stored in a dark environment at 4 C until use. Germination test under standard conditions (25 C; 10 ppm GR-24 applied after 12 d of preconditioning) was performed before the experiments, resulting in germination rates of 82% for Egyptian broomrape (Eizenberg et al. 2003).

Four temperature-regime treatments were used in a multiclimate sunlight greenhouse (phytotron), with an average of 12 h of daylight. The day/night temperature regimes, which were held constant throughout the experiment, were: 20/12 C, 23/15 C, 26/18 C, and 29/21 C. Temperatures were recorded hourly with temperature data loggers (HOBO data logger, Onset Computer Corporation, Bourne, MA). Growing degree days (GDD) were calculated (Equation 1) during the period between planting date and harvest according to McMaster and Wilhelm (1997):

$$\mathrm{GDD} = \sum \left[(T_{\max} + T_{\min})/2 - T_{base} \right] \qquad [1]$$

where $T_{\max}$ and $T_{\min}$ are the maximum and minimum daily temperatures (C), respectively. T_{base} (Scholberg et al. 2000) is the base temperature (C), which has been defined as 10 C for tomato (Van Der Ploeg and Heuvelink 2005; Wolf et al. 1986). Since the base temperature of the broomrape is 4.9 C (Kebreab and Murdoch 1999), which is lower of that of the host (10 C) and the development of the parasite from that point on depends mainly on the development of the host, we used 10 C as the base temperature.

Parasitism dynamics under different infestation levels was studied in a temperature-controlled greenhouse. The day/night temperature regime throughout the experiment was 32/20 C. Temperatures were recorded hourly with the same equipment used for the phytotron experiment and GDD was calculated as described above (Equation 1). The tomato plants were grown for 80 d (April through June), and the development of Egyptian broomrape attachments and biomass was monitored at 100 GDD intervals until the conclusion of the experiment at 1,800 GDD.

In both experiments, tomato plants were grown in 2-L (18-cm-diam) pots containing soil and vermiculite (1 : 1 by vol). Plants were drip-irrigated and fertigated with sufficient 20–20–20 (N–P–K) fertilizer to prevent water or nutrient stress. Egyptian broomrape seeds (10 mg L^{-1} soil, 10 ppm) were mixed with the soil in a cement mixer to homogeneity. The same procedure was used to produce infested soil at levels of 1, 5, 10, or 25 mg of Egyptian broomrape seeds per liter of soil (1, 5, 10, and 25 mg L^{-1} soil, respectively). No Egyptian broomrape seeds were present in the control treatment. To monitor Egyptian broomrape development, soil was carefully removed from the pots, tomato roots were washed under tap water over a screen, and the number of attachments was counted. The Egyptian broomrape attachments or shoots were carefully removed from the tomato roots, oven-dried (60 C, 72 h), and their dry weight recorded.

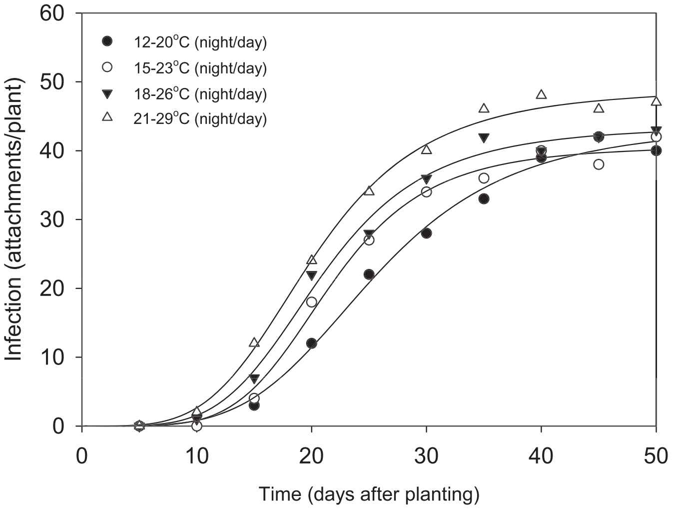

Figure 1. Effect of four temperature regimes on attachment dynamics of Egyptian broomrape on tomato grown in pots.

Statistical Analysis. Statistical analysis was performed following Onofri et al. (2009). The phytotron experiment was conducted in full factorial design with two factors: infestation (infested or noninfested) and temperature (four temperature regimes). The treatments were replicated five times and the experiments were repeated twice with similar results. Number of Egyptian broomrape attachments (above 1 mm) and their biomass were regressed linearly to temperature and nonlinearly to GDD. The nonlinear regression included a three-parameter logistic function (Equation 2) (Brown and Mayer 1988, Eizenberg et al. 2009; Ephrath and Eizenberg 2010):

$$Y = a / \left[1 + (x/x_{50})^{b} \right] \qquad [2]$$

where Y represents the number of attachments or their biomass, a represents the upper asymptote (maximum Egyptian broomrape attachment number or biomass), x_{50} represents the GDD when Y is 50% of maximum, and b represents the slope at x_{50}.

Two-segmental linear regression (Soltani et al. 2006) was computed (Equation 3):

$$\begin{aligned} &(\text{if } \mathrm{TT} \leq \mathrm{TT_c} \text{ then } Y = [a + b]\mathrm{TT_c}; \\ &\text{if } \mathrm{TT} > \mathrm{TT_c} \text{ then } Y = [a + b]\mathrm{TT}) \end{aligned} \qquad [3]$$

TT represents the time (days or GDD) and $\mathrm{TT_c}$ is the estimated time (days) for the first day of yield reduction to estimate the reduction in aboveground tomato plant biomass under different infestation levels or temperature regimes.

Nonlinear regressions were conducted using Sigma plot® (SigmaPlot, version 11.01, SPSS Inc., Chicago, IL).

Results

Temperature affected Egyptian broomrape parasitism on tomato (Figure 1), with increasing temperature resulting in a higher rate, and earlier appearance, of attachments. The first attachments appeared 10 d after planting in the 23/15 C, 26/18 C, and 29/21 C day/night treatments, whereas in the 20/12 C day/night treatment, the first attachments were observed 5 d later. Saturation in the number of attachments (a,

Table 1. No-linear three-parameter logistic regression ($Y = a/(1 + [x/x_{50}]^{b})$ coefficients for the comparison of accumulation of Egyptian broomrape attachments on tomato grown in pots under different temperature regimes.

	Coefficient parameters									Regression	
Temperature (night/day)	a[a]	SE(a)	P(a)	b[b]	SE(b)	P(b)	x_{50}[c]	SE(x_{50})	P(x_{50})	P	RMSE[d]
C											
12/20	43.8	1.8	0.0001	−4.2	0.5	0.0001	25.6	0.8	0.0001	0.0001	13.6
15/23	40.67	1.1	0.0001	−5.0	0.6	0.0001	21.6	0.5	0.0001	0.0001	15.5
18/26	43.5	1.3	0.0001	−4.5	0.5	0.0061	20.9	0.6	0.0001	0.0001	18.9
21/29	49.1	1.1	0.0001	−4.1	0.3	0.0161	20.2	0.4	0.0001	0.0001	10.4

[a] Maximum asymptote represents maximal attachments.

[b] Slope at inflection point.

[c] Inflection point represents the time required for 50% accumulation of attachments.

[d] Abbreviation: RMSE, root mean square error.

Table 1) occurred in the 23/15 C, 26/18 C, and 29/21 C day/night treatments 35 d after planting. In the 20/12 C day/night treatment, attachments continued developing until the end of the experiment. The highest number of attachments was measured in the 29/21 C day/night treatment (Figure 1, Table 1). No differences were recorded between the other temperature treatments (Table 1).

The relationship between development of attachments and GDD is described as a three-parameter logistic curve (Figure 2). Attachments started to appear 200 GDD after planting and the maximal number of attachments was recorded 800 GDD after planting (Figure 2). The effect of temperature regime on the parasitism dynamics of Egyptian broomrape on tomato could be described by one curve.

The effect of temperature on Egyptian broomrape biomass development during the experiment is presented in Figure 3 and Table 2. Under all temperature regimes, a difference was measured in the biomass as the temperature increased (Table 2). The differences between the various treatments began 20 d after planting.

A reduction in the aboveground biomass of the tomato plants paralleled the increase in biomass of Egyptian broomrape attachments (Figure 4, Table 3). No difference in the aboveground tomato plant biomass was determined between the 20/12 C and 23/15 C day/night treatments. With the 26/18 C and 29/21 C day/night treatments, however, a difference was measured as the growing season progressed. Analyzing the effects of GDD on the aboveground tomato biomass revealed no effect of Egyptian broomrape development up to 490 GDD after planting (Figure 5). As the infection levels increased with increasing GDD, a linear and constant reduction in the aboveground biomass of the host plants was computed and presented as a two-segmental linear regression ($a = -0.11 \pm 0.005$; $TT_c = 510.15 \pm 19.51$; $R^2 = 0.96$; $P < 0.00019$), where TT_c is the point when tomato biomass starts to reduce as response to GDD. Maximal reduction (relative to the noninfested control) was 86%, occurring 1,240 GDD after planting (Figure 5).

The effect of thermal time was examined at four Egyptian broomrape infestation levels and could be described as a three-parameter logistic curve (Figure 6, Table 4). As expected, increasing the infestation rate resulted in more attachments per plant (Figure 6, Table 4). However, as determined with the different temperature regimes using one infestation level of 10 mg L^{-1} soil (Figure 2), the attachments began to appear at 200 GDD, irrespective of infestation level (Figure 6). The effect of infestation level on damage to the host tomato plants was described as the reduction in dry aboveground biomass of the tomato plants as related to the noninfested control (Figure 7). A reduction in biomass was measured at the upper three levels of infestation (5, 10, and 25 mg L^{-1} soil, Figure 7, Table 5) The reduction in biomass started 500 GDD after planting in the 25 mg L^{-1} soil treatment and 600 GDD in the 5 and 10 mg L^{-1} soil treatments. No difference

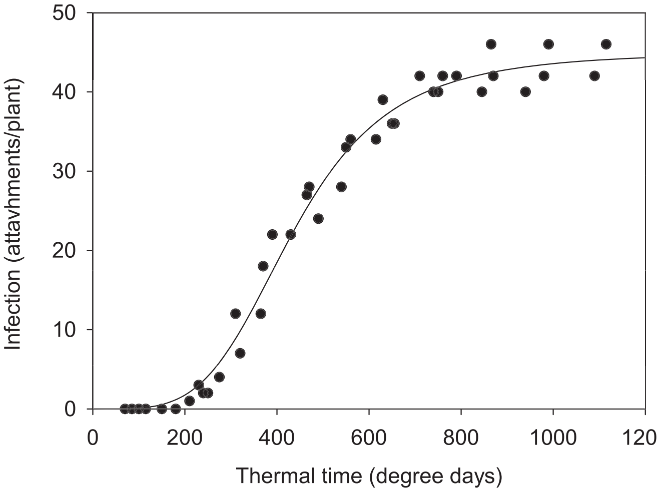

Figure 2. Three-parameter logistic nonlinear regressions between attachment of Egyptian broomrape on tomato grown in pots and thermal time, measured in growing degree days ($y = 45.0/(1+[x/436.8]^{-4.1})$; $R^2 = 0.99$; $P < 0.0001$).

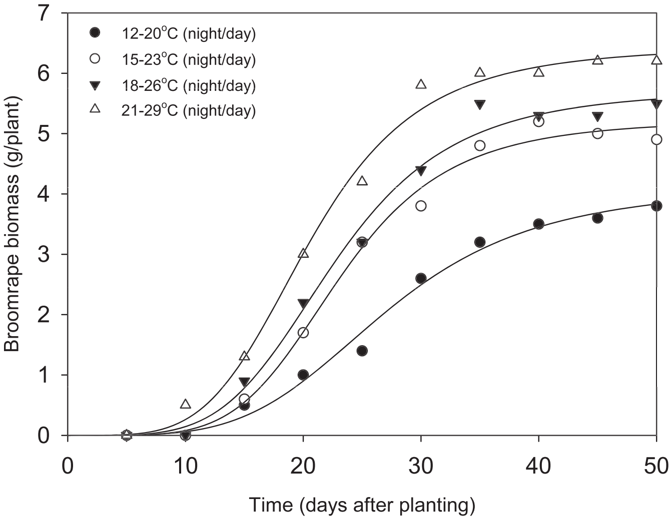

Figure 3. Effect of four temperature regimes on biomass of Egyptian broomrape parasitizing tomato grown in pots.

Table 2. Nonlinear three-parameter logistic regression ($Y = a/(1 + [x/x_{50}]^b)$) coefficients for the comparison of accumulation of Egyptian broomrape dry biomass (g) on tomato grown in pots under different temperature regimes.

	Coefficient parameters									Regression	
Temperature (night/day)	a[a]	SE(a)	P(a)	b[b]	SE(b)	P(b)	x_{50}[c]	SE(x_{50})	P(x_{50})	P	RMSE[d]
C											
12/20	4.12	0.3	0.0001	−4.2	0.6	0.0001	27.1	1.2	0.0001	0.0001	0.2
15/23	5.2	0.2	0.0001	−4.9	0.6	0.0001	23.1	0.6	0.0001	0.0001	0.3
18/26	5.7	0.2	0.0001	−4.4	0.6	0.0001	22.6	0.7	0.0001	0.0001	0.4
21/29	6.4	0.2	0.0001	−4.4	0.5	0.0001	20.6	0.6	0.0001	0.0001	0.4

[a] Maximum asymptote represents maximal dry biomass.
[b] Slope at inflection point.
[c] Inflection point represents the time required for 50% accumulation of dry biomass.
[d] Abbreviation: RMSE, root mean square error.

was measured between the control and the 1 mg L^{-1} soil treatment, but both were significantly different from the other infestation levels (Figure 7, Table 5). Tomato biomass at the end of the experiment, after 1,200 GDD, was reduced by 83, 58, 30, and 0% in the 25, 10, 5, and 1 mg L^{-1} soil treatments, respectively.

Discussion

The aim of this study was to define the timing of the initial attachments' appearance as affected by thermal time and by different infestation levels. Increasing temperature resulted in acceleration of Egyptian broomrape development as expressed by the number of attachments and the rate of their appearance (Figures 1 and 2, Table 1). The value of x_{50} (Table 1), which describes the number of days from planting to the appearance of 50% of the attachments, decreased significantly from 25.6 d in plants growing under temperature regime of 20/12 C day/night to about 20 d in plants that were subjected to a temperature regime of 15 C to 29 C. Except for the 20/12 C day/night treatment, attachments appeared on the tomato roots 10 d after planting (Figure 1).

Temperature accelerates broomrape parasitism dynamics by increasing the number of attachments and their biomass. This phenomenon has been demonstrated in small broomrape parasitizing red clover (Eizenberg et al. 2004b), crenate broomrape in faba beans (Mesa-García and García Torres 1986; van Hezewijk 1994), sunflower broomrape in sunflower (Castejon-Munoz et al. 1993), and sunflower broomrape parasitizing sensitive sunflower varieties (Ephrath and Eizenberg 2010). However, in resistant sunflower, high temperature reduced the parasitism dynamics (Eizenberg et al. 2003; Serghini et al. 2001). In carrots, high temperature has also been found to inhibit the parasitism of Egyptian broomrape and crenate broomrape as compared with low temperature (Eizenberg et al. 2001). The effect of temperature on the parasitism of Egyptian broomrape in tomato is similar to that reported in sensitive sunflower (Castejon-Munoz et al. 1993), red clover (Eizenberg et al. 2004b), and faba bean (Grenz et al. 2005). This acceleration by increasing temperatures can be utilized for the development of a thermal time equation to predict the parasitism in the soil subsurface.

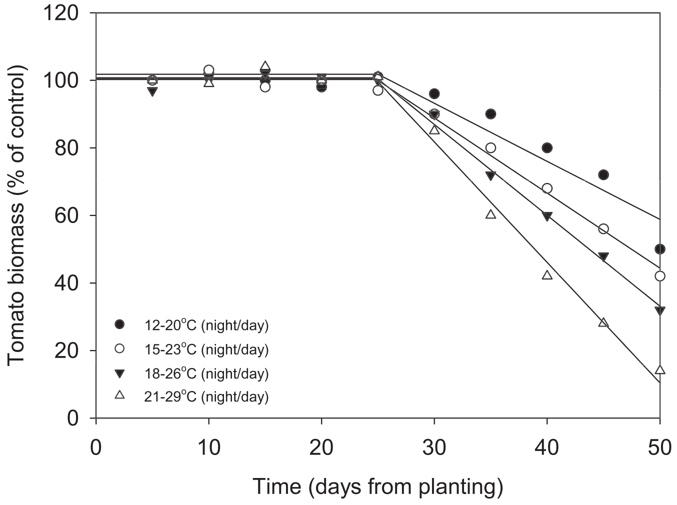

Figure 4. Dry-weight biomass of pot-grown tomato under four temperature regimes in response to parasitism by Egyptian broomrape over time. The relationship between dry-weight biomass reduction (% of noninfested control) of tomato plants and time is described by a linear regression for each of the four temperature regimes (see Table 3 for coefficients).

The use of thermal time can robustly predict phonological events, such as germination or biomass accumulation, to different temperature regimes (Eizenberg et al. 2005). In this study, calculating the development of Egyptian broomrape with thermal time (GDD) associated the development of the parasite to a specific host, tomato. The calculation of the GDD also takes into account physiological characteristics, such as the host's base temperature. The minimal growth threshold temperature of tomato plants has been examined in several studies (Van Der Ploeg and Heuvelink 2005; Wolf and Rudich 1988; Wolf et al. 1986) and determined to be 10 C. Kebreab and Murdoch (1999) reported that the base temperature of Egyptian broomrape is 4.9 C. Joel et al. (2007) and Plakhine et al. (2009) reported that there is a preconditioning period for the development of broomrape seeds, from the start of the germination process until the

Table 3. Two-segmental linear regression (if $TT \leq TT_c$ then $Y = [a + b]TT_c$; if $TT > TT_c$ then $Y = [a + b]TT$) coefficients and standard error (SE) values of the coefficients of the reduction in aboveground tomato plant biomass due to increase of Egyptian broomrape dry biomass under the various temperature regimes (Table 2). TT is the time (days) and TT_c is the estimated time (days) for the first day of yield reduction (see Figure 4 for details).

Temperature (night/day)	Slope, a	SE	TT_c	SE	R^2	P
C						
12/20	−3.56	0.13	24.66	0.80	0.99	< 0.0001
15/23	−2.68	0.10	25.02	0.87	0.98	< 0.0001
18/26	−1.72	0.31	24.86	0.91	0.93	< 0.0001
21/29	−0.11	0.005	25.1	3.30	0.96	< 0.0001

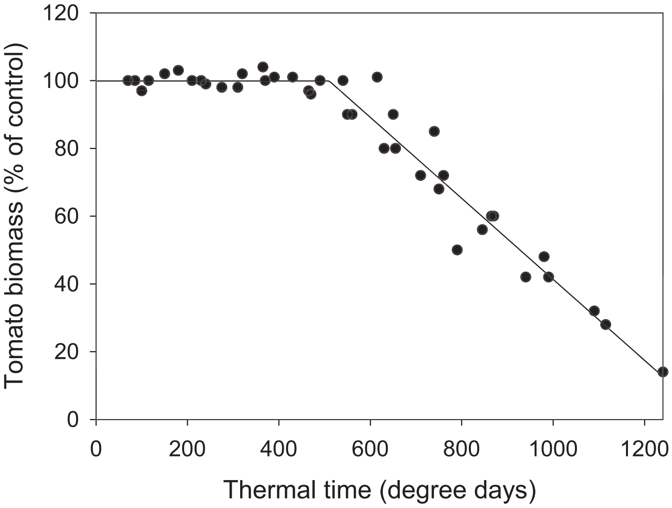

Figure 5. Dry-weight biomass of pot-grown tomato under four temperature regimes in response to Egyptian broomrape parasitism over thermal time, measured in growing degree days (GDD). The relationship between dry-weight biomass reduction (% of noninfested control) of tomato plants and time is described by a linear regression (see text for equation and coefficients).

haustorium emerges from the seed, which varies between 7 d under optimal conditions and about 12 d under suboptimal conditions. A few more days are needed for haustorium growth until it meets the host root. The base temperature for *P. aegyptiaca* seed germination is 4.9 C (Kebreab and Murdoch 1998). We hypothesized that this base temperature is required only for seed germination and preattachment developmental stage, but not for further stages. As base temperature of tomato is 10 C (higher than that of Egyptian broomrape), *P. aegyptiaca* can germinate and parasitize tomato; however, after parasitizing its host further growth depends on the host; therefore the base temperature of 10 C is used for both host and parasite.

In our study, Egyptian broomrape attachments developed on roots of tomato plants growing under a temperature range between 15 C and 29 C 200 GDD after planting (Figure 2). Lower growth temperatures (12/20 C) resulted in a ca. 50 GDD delay in Egyptian broomrape attachments. Infection saturation occurred about 650 GDD after planting (Figure 2). Under field conditions, Grenz et al. (2008) reported a delay in sowing date associated with an increase in parasite number and oilseed sunflower yield losses. A positive relationship between parasitism and thermal time was determined, supporting our results (Grenz et al. 2005, 2008). In this study, nonlinear regression equations were developed to describe the relationship between parasitism and thermal time.

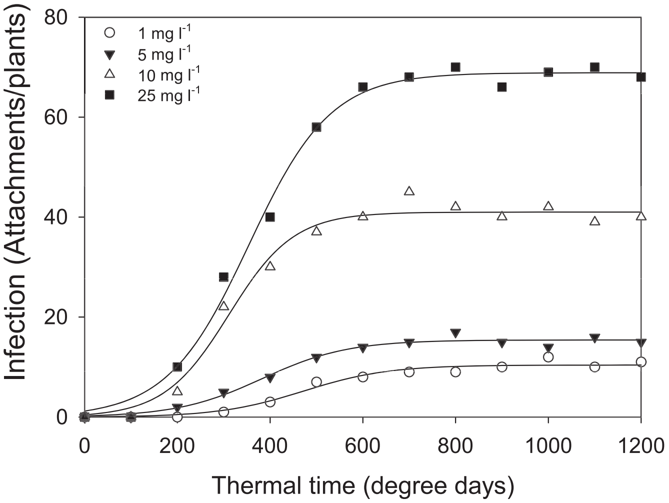

Figure 6. Effect of four infestation levels on attachment dynamics of Egyptian broomrape on tomato grown in pots.

The difference in final number of attachments was only between the 29/21 C day/night treatment and the other treatments (Figure 1). However, the increase in Egyptian broomrape biomass with increasing temperature (Figure 3, Table 2) produced differences in biomass between all temperature-regime treatments. Similar results have been reported for small broomrape, i.e., a poor relationship between attachment number and biomass (Lins et al. 2007).

Damage to tomato is demonstrated by a reduction in dry biomass (Figure 4). As seen in Figure 3, Egyptian broomrape biomass was positively correlated to increased temperature over time. In parallel to this increase, there was a reduction in the tomato biomass (Figure 4). This can be explained by diversion of dry matter to the parasite (Hibberd et al. 1998). Although the increase in Egyptian broomrape started 10 d after planting, the damage to the tomato plants started only 30 d after planting. At this stage, the increase in Egyptian broomrape biomass was relatively small and the reduction in tomato biomass was high (Figure 4, a in Table 3). This initial stage (10 to 30 d after planting) is characterized by a small number of attachments that can be supported by the relatively large tomato plants. However, as the season progresses and attachments become larger and more demanding, the host translocates larger amounts of photosynthates to the parasite, resulting in reduced rates of tomato biomass accumulation.

To determine whether the initial appearance of attachments occurs after 200 GDD from planting under a wide range of environmental conditions, we also tested the effect of infestation levels on the parasitism dynamics. Temperature

Table 4. Nonlinear three-parameter logistic regression ($Y = a/(1 + [x/x_{50}]^b)$) coefficients for the comparison of accumulation of Egyptian broomrape attachments on tomato grown in pots under different infestation levels.

	Coefficient parameters									Regression	
IL[a]	a[b]	SE(a)	P(a)	b[c]	SE(b)	P(b)	x_{50}[d]	SE(x_{50})	P(x_{50})	P	RMSE
mg L^{-1} soil											
25	68.9	0.1	0.0001	88.2	7.4	0.0001	354.2	8.5	0.0001	0.0001	53.1
10	40.1	0.8	0.0001	69.9	13.3	0.0001	311.2	11.9	0.0001	0.0001	49.0
5	15.4	0.4	0.0001	92.0	12.1	0.0001	383.2	14.0	0.0001	0.0040	6.7
1	10.4	0.5	0.0001	91.1	17.8	0.0001	472.1	20.7	0.0001	0.0001	6.5

[a] Abbreviation: IL, infestation level; RMSE, root mean square error.
[b] Maximum asymptote represents maximal infestation.
[c] Slope at inflection point.
[d] Inflection point represents the time required for 50% accumulation of attachments.

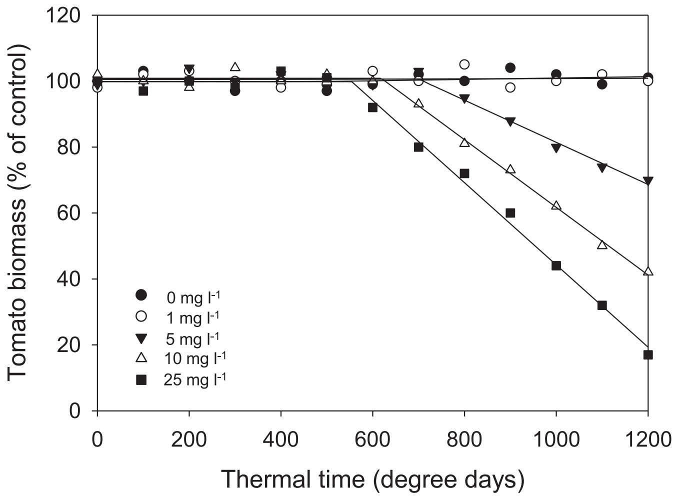

Figure 7. Dry-weight biomass of pot-grown tomato under four infestation levels in response to Egyptian broomrape parasitism over thermal time, measured in growing degree days (GDD). The relationship between dry-weight biomass reduction (% of noninfested control) of the tomato plants and time is described by a linear regression (see Table 5 for coefficients).

was kept at a constant 32/20 C day/night. As had been determined for the different temperature regimes (Figures 1 and 2), infection was initially detected 200 GDD after planting at all infestation levels (Figure 6). It is obvious that as the rate of infestation increases the number of infections will increase. However, despite the large differences in the final number of attachments per plant, the time of infection saturation occurred at about 600 GDD after planting in all treatments. As shown for the temperature treatments (Figure 4), the increasing number of attachments per plant resulted in increased damage to the plants (Figure 6), which was only measured 500 GDD after planting. The damage to the host increased as the infestation levels increased (a, Table 5).

The ability to predict the initiation of parasitism can serve to develop a climate-based system for Egyptian broomrape control with herbicides. Furthermore, the choice of specific herbicide can be associated with the developmental stage of the parasite. For example, sulfonylurea herbicides have been found to effectively control Egyptian broomrape in processing tomato (Eizenberg et al. 2004a; Hershenhorn et al. 2009), but in those studies, the authors raised the issue of lack of knowledge of the developmental stage of the parasite. This knowledge is essential because sulfonylurea herbicides such as rimsulfuron (Eizenberg et al. 2004a; Goldwasser et al. 2001); Hershenhorn et al. 2009) effectively control broomrape when applied at the preattachment stage in tomato and potato. On the other hand, other acetolactate synthase-inhibiting herbicides belonging to the imidazolonone group are highly effective in broomrape control when applied on host foliage at the postattachment stage for sunflower broomrape (imazapic) in sunflower (Aly et al. 2001; Eizenberg et al. 2009), crenate broomrape and Egyptian broomrape (glyphosate and imazapic) in parsley (Goldwasser et al. 2003), and small broomrape (imazamox) in red clover (Lins et al. 2005; Eizenberg et al. 2005*)*. The imidazolinone herbicides are translocated from the leaves to the parasite, which is a strong sink. In these cases, it is also important to detect the developmental stages of the parasitism in the soil subsurface for safe herbicide application at a stage at which the parasite is sensitive to the herbicide.

Table 5. Linear regression ($Y = ax+b$) coefficients of the slopes, standard error (SE) values of the slopes, and probability (P) of the reduction in the aboveground tomato plant biomass due to increasing Egyptian broomrape dry biomass at the various infestation levels (Table 4) (see Figure 7 for details).

IL[a]	Slope, *a*	SE	P	R^2	RMSE
mg L^{-1} soil					
25	−0.120	0.0040	< 0.0001	0.99	49.5
10	−0.100	0.0059	< 0.0001	0.98	61.5
5	−0.040	0.0074	0.0007	0.87	139.7
1	−0.040	0.0033	0.3000	0.17	27.9
0*	0.001	0.0040	0.8800	0.01	36.7

[a] Abbreviations: IL, infestation level; RMSE, root mean square error.

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Received May 3, 2011, and approved August 29, 2011.