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Comparison of degree-day distribution models for predicting emergence of the cabbage aphid on canola

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ABSTRACT

Cabbage aphid, *Brevicoryne brassicae* (L.), is a serious pest on canola, *Brassica napus* L. Estimation of required degree-days for 50% emergence of the population is of special interest for controlling this aphid. To precisely predict 50% emergence of aphid populations as a function of accumulated degree-days, eight distribution models were tested. Models were evaluated statistically and validated with a separate data set collected from three canola fields. Observed cumulative emergence of the aphid was well described by three models. The sigmoid model proposed by Brown and Mayer was recommended to describe 50% emergence of the cabbage aphid population, because the model is simple and the parameter *b* denotes the accumulated degree-days at 50% emergence. The selected model could be used to better time insecticide applications and to more efficiently forecast aphids in canola fields.

1. Introduction

Weather plays a major role in development of aphid populations (Gutierrez et al., 1974a, 1974b) and temperature is often the most important single factor for the development of aphids (Campbell et al., 1974; Harrington et al., 2007; Ro et al., 1998; Worner, 1992). The principle of using temperature and time to describe development of poikilothermic organisms has long been recognized (Higley et al., 1986). Campbell et al. (1974) reported thermal requirements for some species of aphids and their parasitoids, and discussed the importance of temperature on their biological parameters. Fathipour et al. (2005) studied the effect of temperature on biological parameters of the cabbage aphid, *Brevicoryne brassicae* (L.), and reported 25 °C as the optimal temperature. Fathipour et al. (2006) determined the foraging behavior of the parasitoid wasp, *Diaeretiella rapae* (McIntosh), on the cabbage aphid and found it an efficient natural enemy. A study on the development time, survival and reproduction rates of cabbage aphid showed that the optimum temperature range for growth of the aphid on white cabbage, *Brassica oleracea* var. *capitata*, was 20 to 25–30 °C (Satar et al., 2005).

Many studies have determined the appropriate development rate function for a phenological or general population model that can be used to predict important events in insect life cycles or insect abundance, and for control purposes (Worner, 1992). Applications of degree-day models for predicting the development of insects have been well documented (e.g., Pruess, 1983; Welch et al., 1978; Worner, 1992), including for aphids (e.g., Hochberg et al., 1986; Ro et al., 1998). Limited information is available on the biological aspects of the cabbage aphid concerning its phenology in central Iran. A recent study showed that the aphid significantly prefers upper parts of canola (*Brassica napus* L.) plants (i.e., 10–15 cm upper parts of stems), and the highest aphid density was found in mid stem elongation stage and afterwards it decreased gradually (Nematollahi et al., 2014a). Another study indicated that population growth rate of the aphid is closely related to accumulated degree-days, and the production of alates was density-dependent (Nematollahi et al., 2015). Several studies were conducted on the temperature-dependent development of the cabbage aphid, regarding temperature threshold (Campbell et al., 1974; Deloach, 1974), and on the influence of temperature on biological parameters (Fathipour et al., 2006; Vasicek et al., 1994). Distribution

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emergence pattern of the aphid, as a function of accumulated degree-days, has not been modeled yet.

Cumulative emergence models represent the interaction between accumulated degree-days and cumulative emergence, and in fact represent the distribution emergence pattern. These models are usually based on the degree-days at 50% cumulative emergence of the population and a given biofix (Ahn et al., 2012). Various models can be fitted to these data, and many were reviewed by Landsberg (1977). These models have been used for various insects (e.g., Ahn et al., 2012; Kim and Lee, 2010; Kim et al., 2004; Welch et al., 1978), but only a few studies have been conducted on aphids. For example, Celini and Vaillant (2004) determined the temporal trend for emergence of the cotton aphid, *Aphis gossypii* Glover, by means of a polynomial exponential regression. Generally, polynomial models are rarely used, because they cannot asymptote and therefore cannot provide a satisfactory description of data sets (Brown and Mayer, 1988). Therefore, the present study did not examine polynomial models.

The cabbage aphid feeding on canola plants can weaken the plants and reduce the quality and quantity of seeds (Khanjani, 2005). Damage due to the cabbage aphid is usually serious that crops often require insecticide treatments to ensure profitable production and reduce economic damage (Khanjani, 2005; Nematollahi et al., 2014a,b). Farmers usually spray a range of broad-spectrum insecticides including organophosphates and carbamates, and some selective insecticides such as pymetrozine. These applications are calendar-based, usually once in late winter (at the end of rosette stage) and 2–4 additional times in the spring (at stem elongation stage). Understanding the timing of critical events of insect pests in the field is paramount to develop a sustainable pest management strategy. Determining appropriate timing for insecticide application or release of beneficial insects is, therefore, critical to reduce economic damage by the cabbage aphid. The aim of the study was to develop a model based on degree-days for predicting 50% emergence of the cabbage aphid population in canola fields.

2. Materials and methods

2.1. The study area and sampling procedure

Study was conducted at two sites in Isfahan province, central Iran (site 1: Isfahan 32° 30′ 34″ N and 51° 49′ 57″ E at 1547 m altitude, and site 2: Alavije 33° 04′ 56″ N and 51° 11′ 08″ E at 1814 m altitude) for three growing seasons, 2011–2014. In each site, the canola variety Okapi was planted into two fields (each 500 m^2), and no insecticide was applied on or around the fields. For all experimental fields, sampling began at plant emergence; sampling unit was a whole plant, and 20 plants were sampled weekly during a 32-week period, from plant emergence (mid-October) to crop harvest (late May). The average plant growth stages of the crop were recorded using the key provided by Harper and Berkenkamp (1975) with minor modifications, thus stem elongation was used instead of bud. Sampling involved uprooting or cutting plants at ground level and placing them individually into plastic bags. In the laboratory, heat extracting and sub-sampling were used to estimate the number of apterous (1st–4th instars and adults) and alates (4th instars and adults) and then the sum of apterous and alates in each sample (Nematollahi et al., 2014a).

For heat extraction, plant samples were placed in an oven preheated up to 60–70 °C for 20–30 min. Heating caused the aphids to take their stylets out of plant tissues, so they could be easily shaken off onto a tray (Raworth et al., 1984). In samples containing more than 3000 aphids, counts were estimated using a sub-sampling technique and ratio estimation, as described by Raworth et al. (1984) with some modifications. Briefly, plant samples were shaken off into a glassy beaker containing diluted alcohol (EOH 70%). After removing plant debris, three 1-ml aliquots (sub-samples) were taken from the solution and placed in graduated cylinders. After 5 min, when all the aphids were settled down at the bottom of the cylinders and beaker, the volume of aphids in the sub-samples and original sample were determined. Finally, the total number of aphids was estimated by counting all aphid individuals in sub-samples and multiplying it by the ratio of volumes.

2.2. Degree-day accumulation

Pruess (1983) recommended that all degree-day methods with practical application in pest management should be reported using standardized thresholds, either actual degree-days or sin wave estimates, use air temperatures obtained with equipment and locations comparable to temperature reported by national weather services, and should clearly state the biofix. Thus, the base temperature of 5 °C was used for the aphid (Campbell et al., 1974) and degree-days were accumulated for each site from mid-October, i.e., approximate date of plant emergence. Temperature data were obtained from meteorological stations located less than 2 km from the experimental fields. Sampling weeks were converted to degree-days (*DD*) using a half-day sin wave method (Higley et al., 1986) as follows:

$$DD = \left(\frac{T_{max} + T_{min}}{2}\right) + \left(\frac{T_{max} - T_{min}}{2}\right)\sin(-1.5708 + 0.2618j) \tag{1}$$

where T_{max} is the maximum daily temperature, T_{min} is the minimum daily temperature, and j is the number of hours passes the minimum for that day. Accumulated degree-days over the first 12 h were calculated from that day's minimum and maximum air temperatures, and for the next 12 h were calculated from that day's maximum temperature and the next day's minimum temperature (Young and Young, 1998). Sites selected for monitoring the cumulative emergence of the cabbage aphid population are described in Table 1.

2.3. Distribution model development

To develop a distribution model, proportional emergence for total population (sum of apterous and alates) of the aphid was calculated, and then emergence by sampling dates, from plant emergence (mid-October) to crop harvest (late May), was cumulated. This proportion was analyzed relative to accumulated degree-days using eight nonlinear regression models (Table 2) using SPSS software (SPSS, 2004).

2.4. Model selection

To evaluate the models statistically, adjusted coefficient of determination (R^2_{adj}) and Akaike's and Bayes-Schwarz information criteria (AIC and BIC) were used (Burnham and Anderson, 2002). R^2_{adj} was calculated as follows:

$$R^2_{adj} = 1 - \left(\frac{RSS/([n-(p+1)])}{SS/(n-1)}\right) \tag{2}$$

where *RSS* is the residual sum of squares, *SS* is the total sum of squares, *n* is the number of observations, and *p* is the number of parameters estimated. Higher values of R^2_{adj} indicate better fit of the model.

AIC and BIC both express the degree of fit of the model, based on

Table 1
Description of sites for monitoring of cumulative emergence of the cabbage aphid in canola fields, Isfahan province, Iran, 2011–2014.

Site			Planting date	Accumulated degree-days[b]	Total population density[c]
Code[a]	Place	Year			
1	Alavije	2011–12	29 September	30449.4	145245.7
2	Alavije	2011–12	30 September	30449.4	143448.9
3	Alavije	2012–13	1 October	28373.1	32523.9
4	Alavije	2012–13	29 September	28373.1	32107.5
5	Isfahan	2011–12	26 September	30558.3	233258.2
6	Isfahan	2011–12	24 September	30558.3	241482.6
7	Isfahan	2012–13	25 September	24893.5	95481.3
8	Isfahan	2012–13	27 September	24893.5	95812.1

[a] Sites 1, 2, 5 and 6 were used for model calibration and sites 4, 7 and 8 were used for model validation.
[b] Accumulated degree-days with a lower developmental threshold of 5 °C and the biofix as plant emergence (mid-October), using half-day sin wave.
[c] Total population density (sum of apterous and alates) of the cabbage aphid per 20 plants in a 32-week sampling period, from mid-October to late May.

Table 2
The distribution models tested for the interaction of accumulated degree-days and the cumulative emergence of the cabbage aphid.

Nonlinear equation	Model	Reference
$F(x) = a/(1 + \exp(-(x - b)/c))$	Eq. (1), Sigmoid 1	Drapper and Smith (1998)
$F(x) = a + b/(x/c)^d))$	Eq. (2), Logistic 1	Sokal and Rohlf (1995)
$F(x) = \exp(-\exp(-ax + b))$	Eq. (3), Exponential	Brown and Mayer (1988)
$F(x) = a\exp(b\exp(cx))$	Eq. (4), Gompertz	Schirone et al. (1990)
$F(x) = a\exp(-\exp(b - c(x - d)))$	Eq. (5), Modified Gompertz	Stevenson et al. (2008)
$F(x) = \exp(a + bx)/(1 + \exp(a + bx))$	Eq. (6), Logistic 2	Knight (2007)
$F(x) = a/(1 + (x/b)^c)$	Eq. (7), Sigmoid 2	Brown and Mayer (1988)
$F(x) = 1 - \exp(-((x - a)/b)^c)$	Eq. (8), Weibull	Wagner et al. (1984)

F(x) is the cumulative proportion and *x* is the accumulated degree-days based on 5 °C from plant emergence (mid-October) in all equations. Eq. (1): *a* and *c* are upper and lower asymptotes and set the vertical limits of the curve, and *b* implies the time (degree-day) of 50% emergence; Eq. (2): *b* is the upper asymptote, and *c* describes the time (degree-day) of 50% emergence; Eq. (3): *a* and *b* are empirically derived constants. *a* is the rate of increase of this curve and *b* is related to the lag; Eq. (4): *a* is the upper asymptote, *b* is the negative number and sets the *x* displacement, and *c* is the also negative number and sets the increasing rate of the curve; Eq. (5): *a* modifies the shape of curve along the y-axis and is the upper asymptote, *b* controls the shape of curve along the x-axis, *c* is the shape parameter and indicates the short early tail of the curve and d controls starting point of prediction on the x-axis; Eq. (6): *a* and *b* are constant parameters; Eq. (7): *a* is the upper asymptote, *b* is the time (degree day) of 50% emergence, and *c* is a shape parameter of the curve; Eq. (8): *a* represents the lag in the onset of emergence, *b* is an emergence rate constant and describes the time (degree-day) of 50% emergence, and *c* is a shape parameter.

the log-likelihood goodness of fit and the number of parameters estimated. The models with lower AIC and BIC values were preferred, which are the models with the fewest parameters and with a higher fit. Statistical criteria were calculated using the following formula.

$$AIC = n[\ln(RSS)] - [n - 2(p + 1)] - n\ln(n) \quad (3)$$

$$BIC = n[\ln(RSS)] + (p + 1)\ln(n) - n\ln(n) \quad (4)$$

2.5. Model validation

Selected models were validated with a separate data set collected from three canola experimental fields in Isfahan province during 2013–2014. Conditions of these fields and sampling procedure for estimating the population density of the cabbage aphid were similar to the fields used to build the models. The selected models were evaluated based on linear regressions, through placing the observed values in the *y*-axis and the predicted values in the *x*-axis. Model evaluation based on the opposite regression leads to incorrect estimates of both the slope and the *y*-intercept (Pineiro et al., 2008).

3. Results

3.1. Distribution model

The distribution of proportional emergence for total population of the cabbage aphid was highly skewed with the right end much longer than the left from the time of the population peak (Fig. 1). Despite running regression programs, each time with a new set of starting values, some equations could not provide a good convergence to the data (modified Gompertz, logistic equation, and Weibull equation) (Table 3). The exponential equation (3) had the highest R^2_{adj} and the lowest values of AIC and BIC and was therefore selected as the preferred model, followed by the Gompertz equation and the sigmoid 2 equation (Table 3).

3.2. Model validation

When the three selected models were applied to the separate data sets, the values of the parameter representing 50% cumulative emergence were compared between predicted and observed values. Difference between predicted and observed values for 50% cumulative aphid emergence differed among models. However, in the sigmoid 2 equation (7), mean of predicted values was close to the mean of observed value (Table 4). Parameters of linear regression between observed and predicted patterns of cumulative emergence (Table 5) and comparison between curves of observed and estimated cumulative emergence (Fig. 2) for the validation dataset showed that the pattern of cumulative emergence for the cabbage aphid population was well described by the three selected models.

4. Discussion

Predicting insect phenology based on chronological time can be

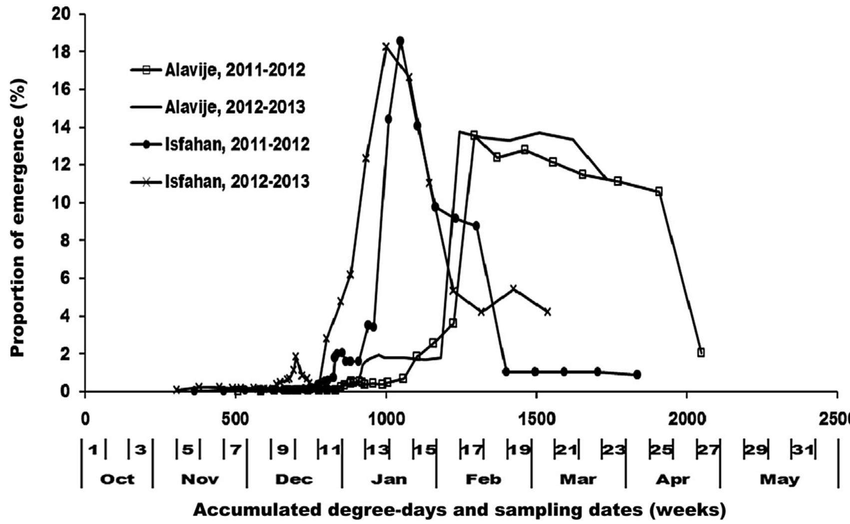

Fig. 1. The distribution of proportional emergence for total population (sum of apterous and alates) of the cabbage aphid at four representative sites (i.e., the first canola fields in each site-year combination listed in Table 1, Isfahan province, Iran, 2011–2013.

Table 3
Parameter estimates (±SE), coefficient of determination and values of statistical selection criteria of distribution models for describing cumulative emergence of the cabbage aphid population.

Equation[a]	Parameters	Estimated value ± SE	df	F[b]	R^2	R^2_{adj} [c]	AIC[d]	BIC[e]
Eq. (1)	a	94.527 ± 2.430	3,255	129156.39**	0.090	0.9992	952.254	1226.435
	b	1129.004 ± 13.036						
	c	124.88 ± 7.889						
Eq. (2)	a	−0.332 ± 1.237	4,255	97015.4**	0.902	0.9988	947.841	1226.568
	b	99.567 ± 3.936						
	c	1136.9 ± 16.172						
	d	−7.887 ± 0.647						
Eq. (3)	a	0.005 ± 0.001	2,255	194056.4**	0.902	0.9996	945.355	1214.991
	b	4.813 ± 0.0224						
Eq. (4)	a	1.024 ± 0.036	3,255	129387.8**	0.902	0.9992	945.981	1220.067
	b	−105.044 ± 32.081						
	c	−0.004 ± 0.001						
Eq. (7)	a	98.933 ± 3.123	3,255	129350.7**	0.902	0.9992	946.918	1221.099
	b	1137.011 ± 15.92						
	c	−8.001 ± 0.532						

[a] Eq. (1), Eq. (2) Eq. (3), Eq. (4) and Eq. (7) were sigmoid 1, logistic 1, exponential, Gompertz and sigmoid 2 equations, respectively (see Table 2).
[b] Significant at $P < 0.01$.
[c] Adjusted coefficient of determination.
[d] Akaike information criterion.
[e] Bayes–Schwartz information criterion.

Table 4
Comparison between observed and estimated accumulated degree-days[a] for 50% emergence of the cabbage aphid population.

Site	Observed	Predicted[b]		
		Eq. (3)[c]	Eq. (4)[c]	Eq. (7)[c]
Alavije	1335.24	1036.24 (299)	1247.26 (87.98)	1139.03 (196.21)
Isfahan-I	1041.66	1036.17 (5.49)	1245.36 (−203.7)	1140.43 (−98.77)
Isfahan-II	1041.36	1036.17 (5.49)	1245.36 (−204)	1140.43 (−99.07)
Mean ± SE	1139.42 ± 97.91	1036.19 ± 0.023	1245.99 ± 0.633	1139.96 ± 0.466

[a] Accumulated degree-days with a lower developmental threshold of 5 °C and the biofix as plant emergence (mid-October), using half-day sin wave.
[b] Values in parentheses indicate difference between estimated and observed values (DD unit) for 50% emergence.
[c] Eq. (3), Eq. (4) and Eq. (7) were exponential, Gompertz and sigmoid 2 equations, respectively (see Table 2).

unreliable because of variation in weather patterns from year to year (Higley et al., 1986; Ro et al., 1998; Welch et al., 1978). The present study showed that required degree-days for 50% cumulative aphid emergence differed among the studied sites. Some sources of error in the present study may account for the observed differences. First, daily developmental events of the aphid could not be discerned because the sampling was conducted weekly. Second, microclimate factors, such as humidity, rainfall and wind may alter development of the aphids on plants.

Estimation of required degree-days for peak population or 50% cumulative aphid emergence is of special interest for controlling this aphid. In the present study, three out of five models with good

Table 5
Parameters of linear regression between observed and predicted patterns of cumulative emergence of the cabbage aphid, in 2013–2014.

Site	Eq. (3)[a]			Eq. (4)[a]			Eq. (7)[a]		
	df	F	r^2	df	F	r^2	df	F	r^2
Alavije	1,30	143.65**	0.821	1,30	11152.21**	0.972	1,30	323.23**	0.912
Isfahan-I	1,30	1199.92**	0.974	1,30	321.29**	0.912	1,30	1005.29**	0.970
Isfahan-II	1,30	2716.84**	0.988	1,30	310.24**	0.908	1,30	935.69**	0.967

** Significant at P < 0.01.
[a] Eq. (3), Eq. (4) and Eq. (7) were exponential, Gompertz and sigmoid 2 equations, respectively (see Table 2).

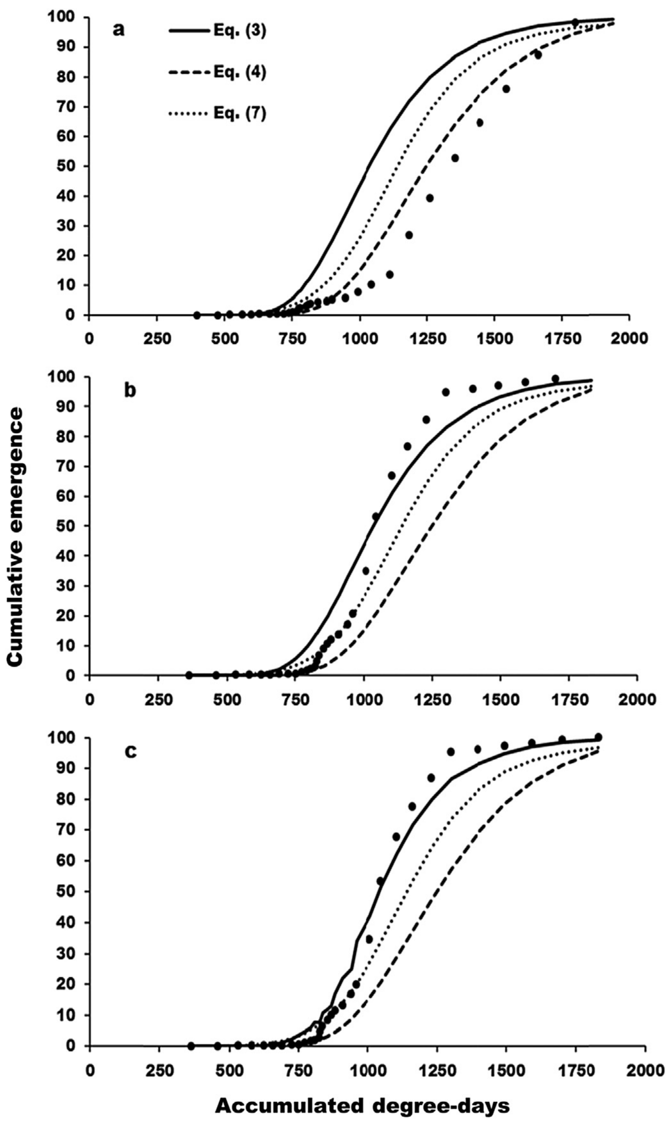

Fig. 2. Comparison between observed and estimated cumulative emergence of the cabbage aphid at three canola sites used to validate models: (a) Alavije, 2013–2014, (b) Isfahan-I, 2013–2014, and (c) Isfahan-II, 2013–2014. Eq. (3), Eq. (4) and Eq. (7) were exponential, Gompertz and sigmoid 2 equations, respectively (see Table 2).

fit had parameters that had biological interpretation since they represent the mean of the distribution (i.e., 50% cumulative emergence). Values of these parameters (Table 3) were similar in equation (1) ($b = 1129.004$ DD), equation (2) ($c = 1136.9$ DD), and equation (7) ($b = 1137.011$ DD). While the information could be determined using simple linear regression, this would assume a symmetrical normal distribution, whereas the tested distribution models were mostly based on an asymmetrical skewed distribution. Thus, without knowing the proper distribution pattern model linear regression may overestimate the values for the aphid population, as reported for *Grapholita molesta* (Busck) (Ahn et al., 2012).

Important differences were found among different nonlinear regression equations in their sensitivity to choice of starting values. According to Brown and Mayer (1988) some equations, such as Weibull, Gompertz and logistic, are insensitive and can converge from starting values markedly different from their final values (i.e., the estimated parameters). Moreover, in our study starting values for these equations seemed to have no effect on convergence or on goodness of fit of the models. Non-convergence of some studied models may be due to their intrinsic characteristics. For example, it was hard to fit the logistic equation having a symmetrical distribution to our data having an asymmetrical distribution (see Fig. 1). On the other hand, Weibull function provides useful descriptions of populations consisting of two groups of individuals (i.e., active and inactive states) with a rapid transition between the two states (Brown and Mayer, 1988). Distribution pattern of the cabbage aphid did not have characteristics similar to a Weibull function and this likely was a cause of its frequent non-convergence.

AIC and BIC determine the preferred model based on goodness of fit and the simplicity of the model parameters (Damos and Savopoulou-Soultani, 2010). Selected models had high R^2_{adj} and low AIC and BIC values. Thus, to choose the best model, ease of use and meaningfulness were also considered to improve model selection criteria. Although the nonlinear pattern of cumulative emergence of the cabbage aphid population was described best by the power model (3), proposed by Brown and Mayer (1988), none of the parameters of this model have a biological meaning. Thus, sigmoid model (7) proposed by Brown and Mayer (1988), is recommended to describe 50% cumulative emergence of the cabbage aphid, because the model is simple and the parameter b denotes the accumulated degree-days at 50% emergence of the aphid.

In the present study the estimated cumulative emergence pattern of the aphid population was validated with the patterns observed in the field, and the values of 50% cumulative aphid emergence predicted by the selected model (sigmoid model) is very close, within nearly 100DD, to the observed values. The accumulation of degree-days is commonly used to forecast seasonal emergence of insect pests (e.g., Ahn et al., 2012; Borchert et al., 2004; Damos and Savopoulou-Soultani, 2010; Kim et al., 2000; Knight, 2007; Milonas et al., 2001; Stevenson et al., 2008; Thöming and Saucke, 2011) and also to control some major pests (e.g., Knight, 2007; Stevenson et al., 2008).

5. Conclusion

It is expected that by using the selected model (sigmoid model), canola farmers in Isfahan province (central Iran) could predict 50% cumulative emergence of the cabbage aphid in unsprayed fields ahead of time, without knowing the total or peak population of the aphid. Findings of the present study could be used for preparing an efficient and successful forecasting system to manage this pest on canola. The selected model would not replace common monitoring programs or using economic thresholds before deciding to apply insecticides. In practice, this model specifies the time to start careful crop monitoring, from which growers can then make better control decisions in a timely manner. This model is presented for Isfahan province (central Iran), its use in other canola producing areas, will require field evaluation and possible reevaluation of the model parameters. It is expected that degree-day computation will remain essentially intact, but optimum starting dates or the biofix will vary with local climate, landscapes attributes, planting dates, canola varieties, and cultural practices.

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