

An exponential growth model with decreasing r captures bottom-up effects on the population growth of *Aphis glycines* Matsumura (Hemiptera: Aphididae)

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- Abstract**
- 1 There is ample evidence that the life history and population dynamics of aphids are closely linked to plant phenology. Based on life table studies, it has been proposed that the growth of aphid populations could be modeled with an exponential growth model, with r decreasing linearly with time. This model has never been tested under field conditions.
 - 2 The soybean aphid *Aphis glycines* is a new invasive pest to soybean production in the U.S.A. In the present study, we present five datasets on the growth of colonies of *A. glycines*, monitored during population growth and decline under predator-free conditions in three soybean fields, from 2003 to 2006.
 - 3 We demonstrate that an exponential growth model, with r decreasing linearly with time, gives a much better description of *A. glycines* dynamics for all datasets ($R^2 = 0.94\text{--}0.99$) than the exponential ($R^2 = 0.42\text{--}0.98$) or logistic growth models ($R^2 = 0.77\text{--}0.99$). Furthermore, it is shown by cross-validation that the exponential model with decreasing r can be used to make population predictions, as shown by the coefficient of prediction, R^2_{pred} ranging from 0.55 to 0.97. An improved fit of the model was obtained using both aphid ($R^2_{\text{pred}} > 0.79$) and soybean ($R^2_{\text{pred}} > 0.86$) degree-days scales, indicating temperature effects on the phenological time scale for the decrease in r .
 - 4 Our model suggests important bottom-up control of *A. glycines* population growth, which may interact with other mortality factors. The generality and potential applications of these results are discussed.

Keywords Bottom-up control, degree-days, host plant quality, intrinsic rate of increase, population dynamics, population growth model, plant phenology, soybean aphid.

Introduction

Aphids constitute one of the most important groups of agricultural pests. One of the key features that allow aphids to reach outbreak populations on crops is their capacity towards

rapid exponential population growth. Despite this immense biotic potential, aphid populations can also remain at low levels, and it is still debatable whether this is the result of bottom-up factors affecting host plant quality, top-down control by natural enemies, and/or abiotic factors (Dixon, 1987, 1998, 2000; Dixon *et al.*, 1997). An understanding of the separate and combined effect of these factors on aphid population growth is crucial to the design of appropriate and sustainable pest management.

Late season decline of aphid field populations has been commonly attributed to lower host plant quality of older plants, even in the presence of other confounding factors, such as weather and natural enemies (Way, 1967; Rossing *et al.*, 1994; Van den Berg *et al.*, 1997; Dixon, 1998; Williams

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et al., 1999; Honek & Martinkova, 2004). Life-history studies showed that the aphids *Myzus persicae* and *Aphis fabae* reared on sugar beet had significantly lower survivorship, reproduction, and intrinsic rate of increase when reared on older plants and leaves (Williams, 1995; Kift et al., 1996, 1998; Williams et al., 1999). Based on these results, Williams et al. (1999) proposed an exponential model of aphid population growth assuming a linear decrease of the intrinsic rate of increase (r) with time. However, to our knowledge, this model has not been tested under field conditions.

We use soybean and the soybean aphid *Aphis glycines* Matsumura (Hemiptera: Aphididae) as a model system. *Aphis glycines* is native to Asia and has become an important invasive pest in North America. It was observed for the first time in North America in 2000 (Ragsdale et al., 2004; Venette & Ragsdale, 2004) and has expanded its distribution throughout the soybean producing region, including both the U.S.A. and Canada, becoming the most important insect pest of this crop (Venette & Ragsdale, 2004; Mignault et al., 2006). Yield losses due to *A. glycines* in the range 50–70% have been reported in Asia (Wu et al., 2004) and up to 40% in the U.S.A. (DiFonzo & Hines, 2002). Manipulation of bottom-up factors resulting from different regimes of tillage, fertilization, and weed control did not affect population growth of *A. glycines* in field experiments conducted in Michigan, U.S.A. (Costamagna & Landis, 2006). By contrast, deficiencies in soil potassium have been shown to increase *A. glycines* populations in Wisconsin and Michigan, U.S.A. (Myers et al., 2005; Walter & DiFonzo, 2007). Finally, life table studies conducted by Van den Berg et al. (1997) in Indonesia showed that the intrinsic rate of increase of *A. glycines* is affected by plant phenology.

Natural enemies have been reported to significantly reduce *A. glycines* populations in Asia (Van den Berg et al., 1997; Liu et al., 2004; Wu et al., 2004) and North America (Fox & Landis, 2003; Fox et al., 2004, 2005; Nielsen & Hajek, 2005; Costamagna & Landis, 2006). The most important natural enemies recorded in North America include 12 groups of generalist predators, of which the most important species are *Harmonia axyridis* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) and *Orius insidiosus* (Heteroptera: Anthracoridae) (Fox et al., 2004; Rutledge et al., 2004; Costamagna, 2006; Costamagna & Landis, 2006). However, despite substantial suppression by natural enemies early in the growing season, outbreak populations of *A. glycines* have been reported during 2003 and 2005, and the causes remain unclear (Costamagna, 2006; Costamagna & Landis, 2006).

To fully understand *A. glycines* population dynamics, it is necessary to develop a predictive model. In the absence of elaborate life table data on *A. glycines* under the influence of relevant abiotic factors, at the same time as having access to several field data sets on the population growth of this species under predator exclusion, we propose the development of a parameter-sparse and structurally simple model. Such a model has the advantages of transparency and parsimony, and can be very easily be built into computer models for decision support. It can also be used as a component in more complex models in which the impacts of natural enemies and

different management practices on *A. glycines* population dynamics are investigated.

The objective of the present study was to develop a simple and robust analytical model for *A. glycines* population growth under field conditions. We focused on endogenous aphid population dynamics under the influence of bottom-up factors, such as host plant quality, and excluding the effects of natural enemies, which vary in composition, abundance, and impact at different localities and seasons (Entwistle & Dixon, 1986). To determine *A. glycines* parameters of population growth, we utilized data from five field experiments in which aphids were reared in predator exclusion conditions. Aphid population growth was modeled with the traditional exponential and logistic growth models (Dixon, 1987; Honek et al., 2006). In addition, because previous evidence on *A. glycines* suggest that the intrinsic rate of increase (r) might decline with time due to host plant quality (Van den Berg et al., 1997), in accordance with Williams et al. (1999), we incorporated a linearly decreasing r into an exponential growth model (i.e. the 'decreasing r model'), and tested this model for the first time using data from aphid field populations. Contrasting these different models of population growth is particularly relevant for *A. glycines* because the only available forecasting system for this aphid in the U.S.A. (i.e. the SAGE model) is based on aphid exponential growth at intrinsic rates of increase affected only by temperature (Venette et al., 2004). We compared the fit of the decreasing r model with the traditional exponential and logistic growth models in the five datasets available. Next, we combined all experiments to create models that account for temperature effects (i.e. scaling to aphid degree-days after initial infestation) and plant phenology effects (i.e. scaling to soybean degree-days after sowing). Finally, using cross-validation, we demonstrate that the latter models give robust predictions of the growth of populations of *A. glycines* in the absence of predation and under the variable range of temperature, locality, and host plant conditions of our field data.

Materials and methods

Study sites and field experiments

We conducted five field experiments in which 56 *A. glycines* colonies were reared in predator exclusion cages (Table 1). The first four experiments were conducted at two locations in Michigan (U.S.A.): the Michigan State University (MSU) Entomology Farm and the biodiversity study site of the MSU Kellogg Biological Station Long Term Ecological Research site in row crop agriculture (KBS-LTER), between 2003 and 2005. The last experiment was conducted at the University of Minnesota Research, Outreach and Education Park (Umore Park), during 2006. The experiments were conducted by caging aphids on naturally-infested plants (field source), or by gently placing controlled numbers of aphids reared in the laboratory on soybean plants using a camel-hair brush (colony source; Table 1). A mixture of apterous adult and near adult aphids was used to seed the field cages at various rates (Table 1). Aphids from a colony maintained in Michigan

Table 1 Characteristic features of five experiments studying *Aphis glycines* population dynamics under field conditions in predator exclusion cages (for a detailed description, see the Materials and Methods)

Experiment	Year	Cage	n^a	Location ^b	Planting date	<i>Aphis glycines</i> inoculation				Mean temperature ^d
						Source	Date	Rate ^c	Plant phenology	
1	2003	Sleeve	18	Ent. Farm MSU	22 May	Field	3 July	4.6	V3–V4	22.4 ± 0.3 a
2	2004	1 m ²	6	Ent. Farm MSU	7 May	Colony	16 June	3.4	V3	18.8 ± 0.6 c
3	2004	Sleeve	12	KBS-LTER	7 June	Colony	1 July	5	V2	20.6 ± 0.5 b
4	2005	Sleeve	12	KBS-LTER	25 May	Colony	23 June	5	V3–V4	23.1 ± 0.6 a
5	2006	Sleeve	8	Agric. St. UMN	2 June	Colony	30 June	10	V3	23.4 ± 0.4 a

^aNumber of cages per experiment, in experiment 1 reduced to six cages for the last two sampling dates.

^bEnt. Farm MSU, Entomology Farm; KBS-LTER, Kellogg Biological Station – Long Term Ecological Research site in row crop agriculture, at Michigan State University, Michigan; Agric. St. UMN, Minnesota Agricultural Research Station of the University of Minnesota at Rosemount, Minnesota.

^cInitial number of *A. glycines*/plant.

^dMean ± SE temperature for the first 28 days after infestation, different letters indicate significant differences among experiments.

State University were used in experiments 2–4, whereas aphids from a separate colony maintained at the University of Minnesota were used for the last experiment. Planting date varied among experiments, resulting in different plant phenology at equivalent dates. All aphid inoculations were performed between the V2–V4 stage of plant phenology (Ritchie *et al.*, 1994).

Two cage designs were utilized: sleeve cages that enclosed aphids on one to three plants, and field cages that enclosed a 1-m² area (29.1 ± 2.0 plants/m², mean ± SD). Sleeve cages consisted of a cylindrical frame of wire (diameter 0.4 m, height 1.0 m) that was completely covered by fine-mesh white no-see-um netting (Kaplan Simon, Braintree, Massachusetts), which was buried 15 cm below the surface of the soil. The field cages consisted of a PVC frame (1 × 1 × 1 m) covered by the same material on the upper portion and with a basal plastic barrier (10 cm buried in the soil, 20 cm above soil surface), connected to the netting by velcro. Two bands of mesh with coarse openings (2 mm) were included all around the sides of the field cages, one located at the top (10 cm wide) and the other at the canopy level (30 cm wide). These bands of coarse mesh were permeable to the movement of alate aphids and small predators, and thus the cage design provides a potentially conservative measure of aphid increase. Sampling was performed weekly by counting the total number of aphids on all the enclosed plants in the sleeve cages, and on four to ten random plants, diminishing the sampling size as the population increased, in the larger cages (Costamagna & Landis, 2006). All counts are expressed as number of *A. glycines* per plant.

Models of *A. glycines* growth

The *A. glycines* population growth curves obtained in the five experiments were modeled using exponential, logistic and decreasing r models of population growth. Exponential growth was modeled using the equation:

$$N_t = N_0 e^{r \cdot t} \quad (1)$$

where t is time (days), N_t is the aphid population size at time t (aphids/plant), N_0 is the initial aphid population (aphids/plant), and r is the intrinsic rate of increase (aphids/aphid/day).

Logistic growth was modeled using:

$$N_t = \frac{K}{1 + \frac{K - N_0}{N_0} e^{-rt}} \quad (2)$$

where K is the carrying capacity (aphids/plant). Finally, we modeled *A. glycines* growth assuming a linear decrease of r with time:

$$\frac{dN}{Ndt} = r_{\max}(1 - at) \quad (3)$$

where r_{\max} is the value of the intrinsic rate of increase at time $t = 0$, and a is the slope of the linear relationship between r and t . Thus, a can be biologically interpreted as the decrease of r per unit of time as the host plant advances in phenological stage. The solution for N_t is:

$$N_t = N_0 \cdot e^{r_{\max}t(1 - (1/2)at)} \quad (4)$$

This equation describes a symmetrical bell-shaped population curve (similar in shape to the normal distribution model, although there is no underlying similarity in derivation) with the peak at $t = 1/a$. The relative rate of increase is largest at $t = 0$, and decreases linearly in time. It becomes zero at $t = 1/a$, which is the time of the population peak, and becomes more and more negative as time passes. The population returns to a value of N_0 at $t = 2/a$, at which time the relative rate of change is $-r_{\max}$. We emphasize that this model, unrealistic as it may seem, is on firm empirical ground of life table data of the aphids *M. persicae* and *A. fabae* reared on sugar beet (Williams *et al.*, 1999). In the present study, we test for the first time the performance of this model in describing and predicting the growth of predation-free aphid populations in the field.

Statistical analysis

Nonlinear regression (PROC NLIN; SAS Institute, 2001) on log-transformed data was used to fit the three population

growth models and estimate mean \pm SE parameter values and assess goodness of fit, using R^2 :

$$R^2 = 1 - \frac{SS_{\text{error}}}{SS_{\text{corrected total}}}$$

To contrast the three population growth models, we fitted them separately for each of the five experiments and evaluated their explanatory power graphically and using R^2 values. Within each experiment, we further assessed the goodness of fit of the decreasing r model by fitting it to the individual aphid colonies of each experiment (i.e. for each cage of the experiment).

We obtained a generalized model of *A. glycines* population growth by fitting the decreasing r model to the combined data of all experiments, and tested whether inclusion of aphid physiological (i.e. *A. glycines* degree-days) or plant phenological (i.e. soybean degree-days) scales resulted in improved explanatory power. We expect that, when population dynamics of *A. glycines* are sensitive to changes in temperature, a better fit will be obtained using a degree-day scale based on aphid growth (basal temperature = 8.6°C; McCormack *et al.*, 2004) rather than time after infestation (calendar time). Similarly, if plant phenology were the most important factor driving the population dynamics of *A. glycines*, the model is likely to provide the best fit when scaled to soybean degree-days after sowing (basal temperature = 10°C; Zhang *et al.*, 2001). Differences in mean temperature among experiments were assessed for the first 28 days after infestation, which was the duration of the shortest experiment, using analysis of variance with day as a blocking factor (PROC MIXED; SAS Institute, 2001).

To test the model assumption that r decreases linearly with time, we performed linear regressions between r and calendar time, *A. glycines* degree-days and soybean degree-days (PROC REG; SAS Institute, 2001). The intrinsic rate of increase was calculated between sampling intervals using:

$$r = \frac{\ln(N_{t+\Delta t}) - \ln(N_{t-\Delta t})}{2\Delta t}$$

Finally, the decreasing r model, as well as the exponential and logistic models, were evaluated through cross-validation, each time leaving out one of the five experiments and comparing the observations of that experiment with the predictions of the model fitted using the remaining four experiments (Turchin, 2003). To assess the accuracy of the prediction for each experiment, we calculated the coefficient of prediction (Turchin, 2003):

$$R^2_{\text{pred}} = 1 - \frac{\sum_{i=1}^n (Y_i^* - Y_i)^2}{\sum_{i=1}^n (\bar{Y} - Y_i)^2}$$

where Y_i^* is the prediction of the model based on four experiments, and Y_i is the corresponding observation of the experiment excluded from the model. This procedure resulted in 15 sets of predicted values (i.e. five experiments \times three timescales), where the observed value was not used in determining the parameters of the predictive model. The closer that R^2_{pred} is to 1, the better is the prediction for the experiment excluded from the model. For models that predict worse than the mean of the predicted dataset, R^2_{pred} is less than 0 (Turchin, 2003).

Results

The decreasing r model was the only one accurately representing population dynamics of *A. glycines* in all five experiments ($R^2 > 0.94$; Fig. 1, Table 2). Exponential and logistic models produced very good fits for experiments 1 and 2 ($R^2 > 0.98$; Fig. 1A, B, Table 2), in which the observations were discontinued before aphids reached their peak and crashed. There was, however, a clear lack of fit of the exponential and logistic models for the data of experiments 3, 4 and 5, in which the number of aphids increased, levelled off, and decreased ($R^2 = 0.42\text{--}0.91$; Fig. 1C–E; Table 2). In experiments 3, 4, and 5, exponential and logistic models underestimated r to account for the latter decrease in aphid population, resulting in low to intermediate r values in comparison with values of r_{max} estimated by the decreasing r model (Table 2). Thus, the decreasing r model provided a complete description of *A. glycines* population dynamics on soybeans over the whole season and can be fitted accurately accounting for the full range of available data during aphid population growth. By contrast, the exponential and logistic models can only be fitted accurately during the exponential phase of aphid population growth and result in a lack of fit when the aphid population collapses.

To test the robustness of the decreasing r model against variability within experiments, we fitted separate models for each aphid colony within each of the five experiments. All the models fitted to individual cages were significant ($P < 0.01$) and the values of the parameters r_{max} , $\ln(N_0)$, and a had overlapping 95% confidence intervals. The R^2 values indicate a very good fit of individual aphid colonies to the model [experiment 1: all $R^2 > 0.99$ ($n = 6$); experiment 2: all $R^2 > 0.97$ ($n = 6$); experiment 3: $R^2 > 0.79$ ($n = 7$) and $R^2 > 0.90$ ($n = 5$); experiment 4: $R^2 > 0.69$ ($n = 1$), $R^2 > 0.79$ ($n = 5$), and $R^2 > 0.90$ ($n = 6$); and experiment 5: $R^2 > 0.88$ ($n = 8$)]. These results show that the decreasing r model accurately describes the population growth of *A. glycines* at the level of individual colonies.

A generalized model of *A. glycines* population growth in the absence of predation was obtained by fitting the decreasing r model using the data of all experiments combined. The fit of the model to the observed data expressed at the scale of days after infestation had high explanatory power ($R^2 = 0.87$; Fig. 2A, Table 3). Mean temperatures recorded during the first 28 days after infestation differed significantly among experiments, with lower mean temperatures observed in 2004 ($F_{4,112} = 19.59$; $P < 0.0001$; Table 1). Thus, to account for the effect of temperature on the population dynamics of *A. glycines*, we tested the model using *A. glycines* degree-days instead of days after infestation, obtaining substantially higher explanatory power on this scale ($R^2 = 0.94$; Fig. 2B, Table 3). Using soybean degree-days as a time scale improved the model explanatory power in a similar fashion ($R^2 = 0.94$; Fig. 2C, Table 3). In all cases, the assumption of a linear decrease of r in time was met, as shown by highly significant negative linear regressions between r and the time scale of each model (Table 3).

Finally, generalized models fitted using calendar days, *A. glycines* degree-days, and soybean degree-days were validated through cross-validation, resulting in 15 models contrasted to those observations that were excluded from the

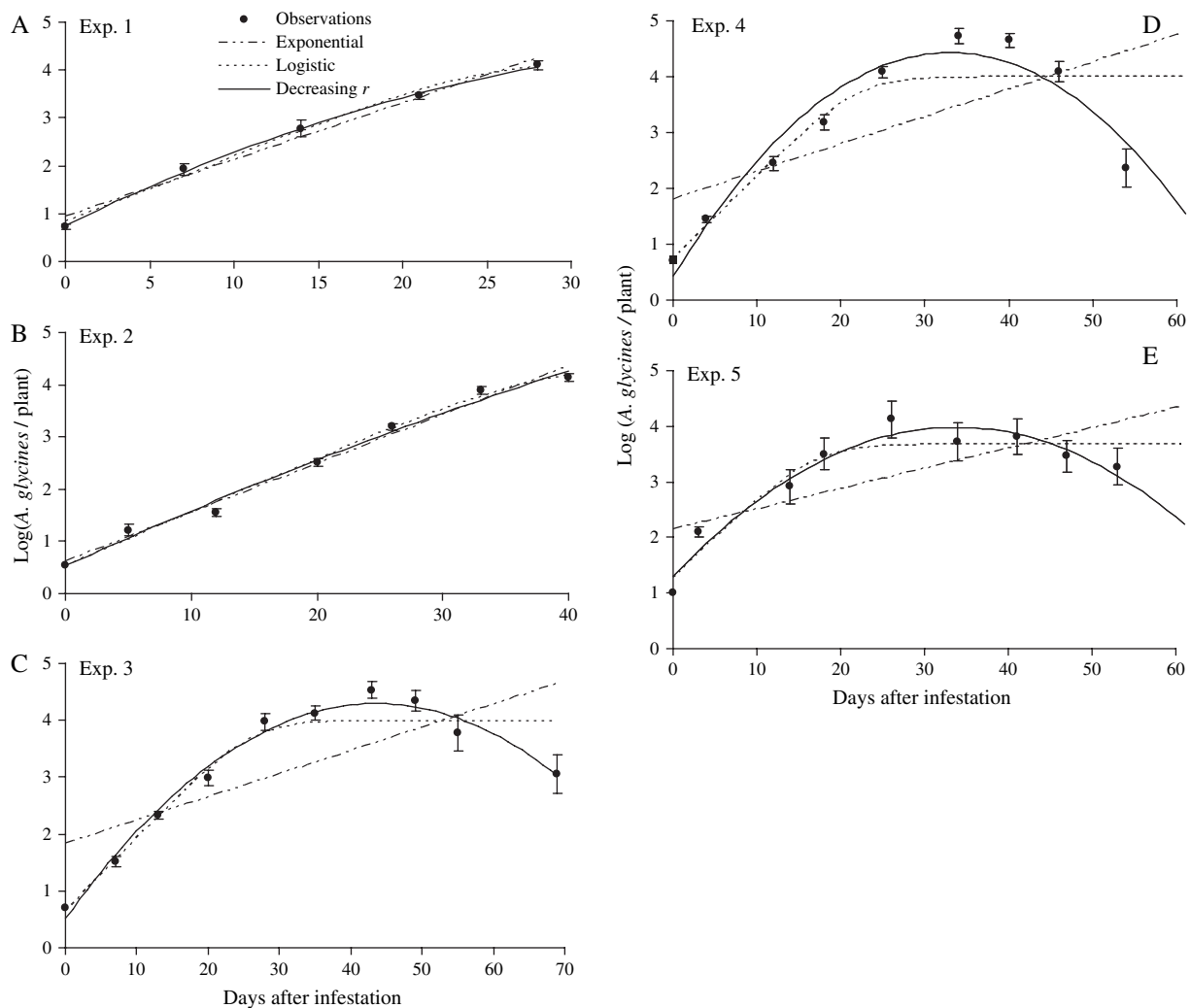


Figure 1 Observed population dynamics of *Aphis glycines* in five field experiments using predator exclusion cages and the fit of three competing models, for experiments 1 (A), 2 (B), 3 (C), 4 (D) and 5 (E). Observations (mean \pm SE) are indicated by points and the exponential, logistic, and decreasing r models by dashed, dotted and solid lines, respectively. Parameter values and statistics for these models are given in Table 2.

fitting procedure. There was very good agreement between models fitted excluding individual experiments and the observed values of the excluded experiments (Table 3). In all cases, the model showed a higher predictability for each experiment when fitted to *A. glycines* ($R^2_{\text{pred}} > 0.79$) or soybean ($R^2_{\text{pred}} > 0.86$) degree-days than when it was scaled to calendar days after infestation ($R^2_{\text{pred}} > 0.55$, Table 3). Fitting the model to either degree-day scale resulted in minor differences, and only in experiment 5 was there a substantially higher R^2_{pred} using soybean degree-days (Table 3).

Discussion

The present study provides novel insights into the modeling of the population dynamics of *A. glycines* in particular and aphids in general. Previous work on different aphid species showed a trend of decreasing host plant quality with plant age (Williams, 1995; Kift *et al.*, 1996, 1998; Van den Berg

et al., 1997; Williams *et al.*, 1999) and several models including a decreasing r with time to account for the effect of plant phenology were proposed (Rossing *et al.*, 1994; Williams *et al.*, 1999; Bianchi & van der Werf, 2004). However, to our knowledge, this is the first time that a model with a linearly decreasing r has been validated using data from aphid field colonies in the absence of predator impacts, thus revealing strong and significant bottom-up control of aphid dynamics. Furthermore, we demonstrated that this model provides a more complete and accurate description of aphid population growth than the traditionally used exponential and logistic models, and without the complications of more elaborate, mechanistic simulation models.

The decreasing r model developed for *A. glycines* was robust against variability among five experiments conducted at three separate locations over 4 years. The model showed high explanatory power, both when fitted to the individual colonies followed in the experiments or to the average of each experiment. Furthermore, cross-validation showed a high

Table 2 Parameters (mean \pm SE) obtained by fitting three population growth models to mean population abundances of *Aphis glycines* in five field experiments in Michigan and Minnesota (for details on the parameters, see the Materials and Methods)

	Experiments				
	1	2	3	4	5
Exponential					
r	0.273 \pm 0.022	0.215 \pm 0.012	0.094 \pm 0.033	0.113 \pm 0.050	0.084 \pm 0.032
$\log(N_0)$	0.939 \pm 0.162	0.614 \pm 0.123	1.832 \pm 0.546	1.806 \pm 0.687	2.145 \pm 0.442
R^2	0.981	0.985	0.505	0.418	0.494
	$F_{1,3} = 157.46$	$F_{1,5} = 325.10$	$F_{1,8} = 8.18$	$F_{1,7} = 5.03$	$F_{1,7} = 6.83$
	$P = 0.001$	$P < 0.001$	$P = 0.021$	$P = 0.06$	$P = 0.035$
Logistic					
r	0.315 \pm 0.030	0.236 \pm 0.016	0.294 \pm 0.069	0.341 \pm 0.138	0.327 \pm 0.084
$\log(N_0)$	0.828 \pm 0.138	0.531 \pm 0.114	0.650 \pm 0.375	0.737 \pm 0.620	1.281 \pm 0.276
$\log(K)$	4.189 \pm 0.248	4.368 \pm 0.284	3.990 \pm 0.203	3.992 \pm 0.379	3.671 \pm 0.158
R^2	0.993	0.991	0.902	0.774	0.905
	$F_{2,2} = 136.46$	$F_{2,4} = 233.27$	$F_{2,7} = 32.47$	$F_{2,6} = 10.28$	$F_{2,6} = 28.59$
	$P = 0.007$	$P < 0.001$	$P < 0.001$	$P = 0.012$	$P < 0.001$
Decreasing r					
r_{\max}	0.395 \pm 0.026	0.252 \pm 0.045	0.398 \pm 0.023	0.560 \pm 0.063	0.366 \pm 0.042
$\log(N_0)$	0.753 \pm 0.067	0.532 \pm 0.159	0.518 \pm 0.148	0.421 \pm 0.298	1.301 \pm 0.201
a	0.022 \pm 0.003	0.007 \pm 0.007	0.023 \pm 0.001	0.030 \pm 0.001	0.030 \pm 0.001
R^2	0.999	0.987	0.982	0.943	0.944
	$F_{2,2} = 683.66$	$F_{2,4} = 154.03$	$F_{2,7} = 190.42$	$F_{2,6} = 49.60$	$F_{2,6} = 50.24$
	$P = 0.002$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

predictability for the five available datasets. Despite the particularities of each experiment, we observed a good fit of the model using days after infestation as the time scale. This was most likely due to the relatively narrow range of phenological stages of the plants initially infested with aphids (V_2 – V_4) and temperatures that generally fell within the optimum range for *A. glycines* development in all experiments (McCornack *et al.*, 2004). Notably, *A. glycines* populations in experiments 2 and 3, which experienced lower mean temperatures during the first weeks of study, were below the curve predicted by the model, whereas populations in experiments 1, 4 and 5, which experienced higher temperatures, were above the fitted curve (Fig. 2A). However, when the model was fitted using physiological scales for aphids and soybeans, these differences disappeared, indicating an effect of temperature on *A. glycines* population growth (Fig. 2B, C). The cross-validation results also support the importance of temperature affecting the dynamics of the system, with higher coefficients of prediction for all experiments when the model was fitted in degree-day scales. The very similar results obtained using aphid and soybean degree-days may be due to two factors. First, the basal temperatures for *A. glycines* and soybeans are very close, resulting in a relatively small difference in scale (8.6 vs. 10°C, respectively, Zhang *et al.*, 2001; McCornack *et al.*, 2004). Second, our experiments were conducted under a narrow range of plant phenology; greater effects could be expected on populations reared on more separated soybean phenological stages (Van den Berg *et al.*, 1997).

We found only one study on aphid population dynamics that included an analytical model with r decreasing in func-

tion of time. Williams *et al.* (1999) studied the population dynamics of *M. persicae* and *A. fabae* (Hemiptera: Aphididae) on sugar beet *Beta vulgaris* and found, in greenhouse trials with clip-caged reared cohorts, that r decreased with plant phenology. Based on this effect of plant quality on r , the authors proposed a model with r decreasing linearly with time and used this to explore the different population dynamics of the two aphid species on sugar beet. However, they did not develop a general analytical model and the predictions of their model were not validated with field data. Two additional simulation studies on the population dynamics of *Sitobion avenae* (F.) (Hemiptera: Aphididae) in wheat assumed a linear decrease in r (Rossing *et al.*, 1994; Bianchi & van der Werf, 2004). The data used to support this approach were obtained from aphid field populations under ambient levels of predation, and thus predator impacts cannot be separated from effects of plant quality. Likewise, Van den Berg *et al.* (1997) used a similar approach to model *A. glycines* population growth under field conditions in Indonesia, but no validation was performed in the absence of predation. Finally, similar dynamics were shown modeling the populations of the pecan aphid *Monellia caryella* (Fitch) (Homoptera: Aphididae) but, again, natural enemy effects were not accounted for because the studies were performed in open field conditions (Matis *et al.*, 2006). It is also interesting to note that similar field population dynamics as those predicted by our model have been observed in a variety of aphid species, including *A. fabae* (Way, 1967), *S. avenae* (Carter *et al.*, 1982), *Metopolophium dirhodum* (Honek & Martinkova, 2004), *Ericaphis fimbriata* (Raworth, 2004), and several other

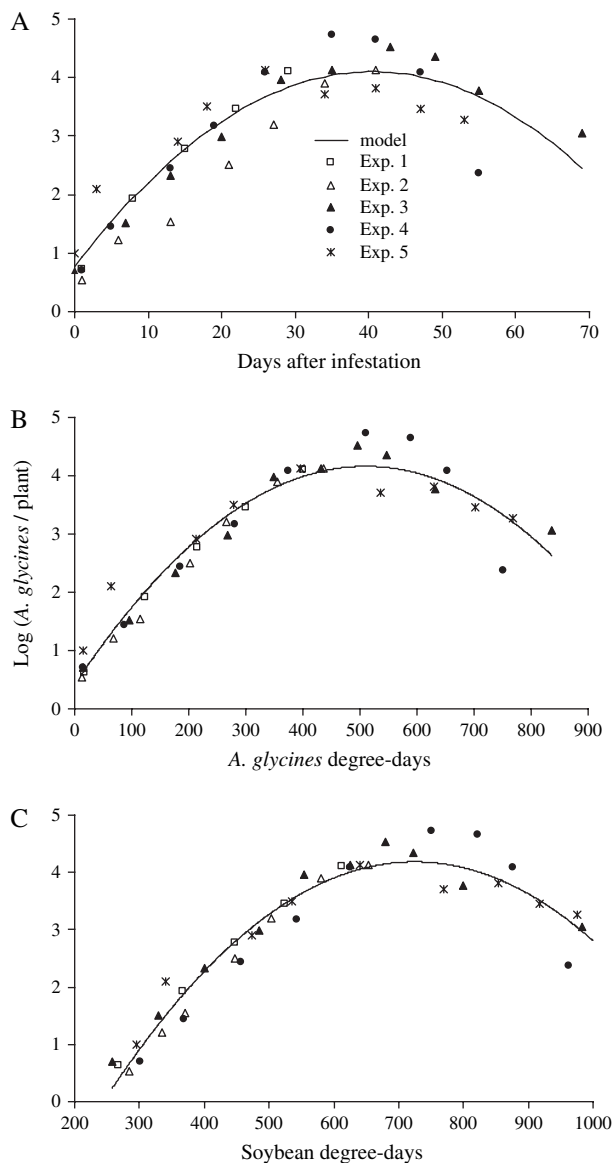


Figure 2 Fit of the decreasing r model (solid line) when fitted to observations of the five field experiments combined, scaled to days after infestation (A), *Aphis glycines* degree-days (B), and soybean degree-days (C). Different symbols represent different experiments (1–5). Parameter values for these models are given in Table 3.

aphid species cited by Dixon (1998). Although most of these studies were performed under ambient levels of natural enemies, evidence that predation was not an important mortality factor lead some of these authors to attribute the decline in aphid population growth to lower host plant quality. Thus, the pattern of aphid population growth represented by our model could represent a widespread dynamic in aphid populations.

The evidence available in the *A. glycines* system suggests that the observed reduction of r in time may be a result of a lower nutritional quality of older soybean plants.

The previously mentioned study by Van den Berg *et al.* (1997) found a linear decrease of r in cohorts of aphids reared on plants at three different phenological stages. In addition, recent studies conducted in Minnesota showed significant and consistent reductions in *A. glycines* population growth due to plant phenology (B. P. McCornack, personal communication). Further evidence of the effect of plant phenology on *A. glycines* population growth comes indirectly from field observations that late-planted soybeans are more susceptible to develop aphid outbreak populations (O'Neal & Johnson, 2005). By contrast, a recent study found no effects of plant phenology on *A. glycines* reared on clip-cages (Rutledge & O'Neil, 2006). However, in that study, aphids were reared on the youngest developing trifoliolate, and it has been shown that the youngest leaves on an ageing plant may retain their suitability to aphids for a longer time than the plant as a whole (Williams, 1995; Kift *et al.*, 1998; B. P. McCornack, personal communication), therefore being less likely to reveal differences in aphid growth.

Because our experiments were not specifically designed to manipulate the effect of plant phenology, the observed decrease of r in time could be due to other factors as well. Rapidly increasing aphid populations may deteriorate host plant quality, as documented for several aphid species (Dixon, 1998; Williams *et al.*, 1999). Significant reductions in soybean biomass and yield due to *A. glycines* feeding have been demonstrated (Costamagna *et al.*, 2007) but whether this results in lower quality for aphid reproduction remains to be investigated. In addition, programmed reductions in aphid fecundity in response to seasonal changes in habitat quality have also been demonstrated. Wellings *et al.* (1980) showed that six aphid species of the subfamilies Aphidinae and Callaphidinae had a lower number of ovarioles in the generations at the end of the summer season, which resulted in significantly lower reproduction. Finally, late season epizootics have been suggested as potential causes of population crashes in *A. glycines* (Nielsen & Hajek, 2005) as well as other aphids (Dixon, 1998; Honek & Martinkova, 2004). However, we did not observe typical symptoms of fungal infections in any of our studies, and therefore we can exclude this factor from our experiments. The elucidation of the potential role of these factors in the population growth of *A. glycines* and other aphids showing similar dynamics needs further investigation.

In summary, we demonstrate for the first time that a generalized mathematical model incorporating a linearly decreasing r provides accurate and robust predictions of aphid field population dynamics in the absence of predators. The model suggests that bottom-up effects can have strong impacts on aphid population growth, possibly mediated by plant phenology. Thus, the decreasing r exponential growth model can be a useful building block in simulation models and decision support systems for aphids that take account of additional extrinsic factors affecting population dynamics. It is also a concise and elegant summary model that can capture bottom-up effects all on its own. Similar effects of host plant phenology and field population dynamics of other aphid species suggest that this model could provide a good description of systems

Table 3 Parameters (mean \pm SE) obtained by fitting the decreasing r model to observations scaled to days after infestation, *Aphis glycines* degree-days and soybean degree-days as time scales

	Days after infestation	A glycines degree-days	Soybeans degree-days
Decreasing r model			
r_{\max}	0.3792 \pm 0.0287	0.0338 \pm 0.0017	0.0606 \pm 0.0033
$\log(N_0)$	0.7659 \pm 0.1549	0.4165 \pm 0.1187	-5.3492 \pm 0.4010
a	0.0247 \pm 0.00971	0.00196 \pm 0.00004	0.00138 \pm 0.00001
R^2	0.872	0.938	0.939
$F_{2,37}$	125.39	277.15	282.89
P	<0.0001	<0.0001	<0.0001
Linear regression r			
β_0	0.4461 \pm 0.0426	0.03475 \pm 0.00298	0.06221 \pm 0.00555
β_1	-0.0120 \pm 0.00144	-0.00007 \pm 0.00001	-0.00009 \pm 0.00001
R^2	0.685	0.734	0.736
$F_{1,32}$	69.70	88.07	89.03
P	<0.0001	<0.0001	<0.0001
Coefficient of prediction			
Experiment 1	0.973	0.994	0.986
Experiment 2	0.857	0.968	0.960
Experiment 3	0.547	0.939	0.947
Experiment 4	0.787	0.876	0.858
Experiment 5	0.629	0.792	0.893

In the middle, results of the statistical analyses testing the assumption of linear decrease of r in time are presented for each model. At the bottom, coefficients of prediction for each experiment obtained through cross-validation.

in which the quality of the resources decrease significantly with time, and this change is directly translated into reduced reproduction of the herbivore.

Acknowledgements

We are indebted to all the Landis and Ragsdale laboratory personnel for their help during the field studies, in particular to C. Sebolt, and to all the KBS-LTER staff. Statistical advice was generously provided by Albert Otten, Biometrics Group, Plant Sciences, Wageningen University. We thank J. Vos for his comments on a previous version of this manuscript. Funding for this research was provided by USDA-CSREES grant 2004-35302-14811, the Michigan Agricultural Experiment Station, the NSF Long Term Ecological Research Program at KBS (NSF DEB 0423627), the North Central Soybean Research Program, the Minnesota Soybean Research and Promotion Council, a C.S. Mott Fellowship in Sustainable Agriculture (A.C.C.), and a Travel Fellowship (MSU Graduate School, OISS, Dept. of Entomology, and Insect Ecology and Biological Control Laboratory), to support a 3-month visit to Wageningen University by A.C.C. The C.T. de Wit Graduate School for Production Ecology and Resource Conservation of Wageningen University provided travel grants to A.C.C., F.J.J.A.B. and W.W. to stimulate international collaborative research.

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Accepted 10 April 2007