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Assessment of the relative impact of different natural enemies on population dynamics of the grain aphid *Sitobion avenae* in the field

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Abstract. 1. A detailed population dynamics model was devised to provide a tool for integrated pest management against the cereal aphid *Sitobion avenae* on winter wheat.

2. This model allowed investigation of the relative impact of different natural enemies on aphid population dynamics.

3. The output of the model was compared with a set of data collected in the western part of France from 1976 to 1986.

4. Fungal diseases accounted for 75% of the reduction in peak aphid density and were the key factor acting on aphid dynamics in this region.

5. This study highlights the importance of detailed population dynamics modelling of keystone species, like aphids, for elucidation of the relations between the keystone species and other species associated in the ecosystem.

Key words. Cereal aphids, entomophthorales, modelling, parasitoid Hymenoptera, Von Foerster's equations, winter wheat.

Introduction

Cereal aphids have become serious pests in western Europe since the 1970s (Carter *et al*., 1980) and occasionally cause significant yield losses. The three commonest species are the grain aphid *Sitobion avenae* F., the rose grain aphid *Metopolophium dirhodum* Wlk., and the bird-cherry oat aphid *Rhopalosiphum padi* Wlk., with *S. avenae* being the most damaging pest. Outbreaks of these species are, however, too sporadic to justify prophylactic control. The low frequency of outbreaks is generally attributed to the effect of natural enemies or to density-independent factors such as weather. The main natural enemies of grain aphids in the field are fungus diseases (Entomophthorales) and parasitoids (Hymenoptera), while predators like Coccinellidae, Chrysopidae, Syrphidae, ground beetles, and spiders are much less important (Dedryver, 1987; Dixon *et al*., 1995; Kindlmann & Dixon, 1999a,b). The size of the effect of the main natural enemies in reducing aphid population densities is not clear and may vary geographically with climate and cereal phenology. The work reported here was designed to develop a method for the assessment of the relative importance of the natural enemies. This was achieved in two steps: a detailed population dynamics model for aphids in the absence of natural enemies was developed, and differences between predicted and observed densities were related to the presence of natural enemies.

The main characteristics of aphid population dynamics (overlapping generations, short generation time, large population size, continuous reproduction) are easily incorporated into a deterministic age-structured simulation model based on Von Foerster's (1959) partial differential equations, similar to that used by Rodolphe *et al*. (1977) to describe whitefly *Trialeurodes vaporariorum* population dynamics. This model, continuous both in age and time, is a generalisation of Lotka's (1925) continuous model and Leslie's (1945) age-structured discrete model. It allows differentiation between the relative influence of density-independent factors such as temperature and host plant characteristics, the effects of which are fairly well known, and the relative influence of density-dependent factors (morphogenesis, immigration, natural enemies), which are too numerous to be taken into account exhaustively in a model. Von Foerster's model incorporates each life-history

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trait explicitly in a modular way. Identification of the fundamental functions included in the basic model (reproduction, death rate, ageing rate, etc.) was achieved via laboratory experiments and by using data published elsewhere (mainly by Dean, 1974; Carter *et al.*, 1982; Kieckhefer *et al.*, 1989).

Materials and methods

Wheat phenological stage is expressed in terms of the Zadoks' scale (Zadoks *et al.*, 1977).

Modelling the population dynamics of the aphid

Theoretical foundations. The model makes the following assumptions: (1) a stage-specific physiological age scale is used, as the age of a poikilotherm depends on the temperature experienced during its life; (2) future morph is determined at the moment of birth (Carter *et al.*, 1982); (3) winged adults leave the crop on moulting to the adult stage. The population density of each developmental stage of *Sitobion avenae* (four larval instars, pre-reproductive and reproductive adults) is described by a function with two variables: $a_i^{\mathrm{P}}(x_i,t)$ for *i*th-instar larvae that become apterous adults, $a_i^{\mathrm{w}}(x_i,t)$ for *i*th-instar larvae that become winged adults, $a_{\mathrm{p}}(x_{\mathrm{p}},t)$ for pre-reproductive adults, and $a_{\mathrm{A}}(x_{\mathrm{A}},t)$ for reproductive adults, where t is time and x_i is the physiological age in stage i, $x_i = 0$ at the beginning of each developmental stage. The number of aphids at time t, in stage i, of age between $x_{i,1}$ and $x_{i,2}$ is then

$$A_{\mathrm{i}}(t) = \int_{x_{i,1}}^{x_{i,2}} a_{\mathrm{i}}(x_{\mathrm{i}},t)\mathrm{d}x_{\mathrm{i}} \tag{1}$$

Let $\theta(t)$ = temperature at time t, x_i = age of *i*th-instar larvae on *i*th-instar physiological age scale, x_{A} = adult age on adult physiological age scale, $R_i(.)$ = temperature-dependent *i*th-instar larva ageing rate, $R_{\mathrm{A}}(.)$ = temperature-dependent adult ageing rate, $d_i(.,.)$ = *i*th-instar larval age- and time-dependent intrinsic mortality rate, $ri_i(.)$ = *i*th-instar larval age-dependent moult rate, $m(.)$ = adult age-dependent fecundity, and $T(t)$ = the proportion of larvae born on date t that become winged adults. The population development is then described by a set of 10 partial differential equations added to eight moult functions and two birth functions (for details see Curry & Feldman, 1989; Rodolphe *et al.*, 1977). For the first instar (apterous):

$$\left\{\begin{array}{l}
\text{continuity equation:}\\
\dfrac{\partial a_1^{\mathrm{P}}}{\partial t} + R_1[\theta(t)]\cdot\dfrac{\partial a_1^{\mathrm{P}}}{\partial x_1} = \\
\qquad -\{[d_1(x_1,t) + ri_1(x_1)]\cdot R_1[\theta(t)]\}.a_1^{\mathrm{P}}(x_1,t)\\
\text{birth equation:} \qquad\qquad\qquad\qquad\qquad\qquad (2\mathrm{a})\\
a_1^{\mathrm{P}}(0,t) = [1-T(t)]\cdot\displaystyle\int_0^{\infty} m(x_{\mathrm{A}})\cdot a_{\mathrm{A}}(x_{\mathrm{A}},t)\mathrm{d}x_{\mathrm{A}}
\end{array}\right.$$

For first-instar larvae that become winged adults, equations are identical except that the coefficient $[1-T(t)]$ in the birth equation is replaced by $T(t)$.

For the other stages (second instar to pre-reproductive adults), the equations are similar except that the birth equation is replaced by a moult equation:

$$\left\{\begin{array}{l}
\text{continuity equation:}\\
\dfrac{\partial a_i^j}{\partial t} + R_i[\theta(t)]\cdot\dfrac{\partial a_i^j}{\partial x_i} = \\
\qquad -\{[d_i(x_i,t) + ri_i(x_i)]\cdot R_i[\theta(t)]\}.a_i^j(x_i,t)\\
\text{moult equation:} \qquad\qquad\qquad\qquad\qquad\qquad (2\mathrm{b})\\
a_i^j(0,t) = \displaystyle\int_0^{\infty} ri_{i-1}(x_{i-1})\cdot a_{i-1}^j(x_{i-1},t)\mathrm{d}x_{i-1}
\end{array}\right.$$

where $i = 2, 3, 4$ or p (second instar to pre-reproductive adult), $j = p$ or w (future apterous or winged adults).

Finally, for adults, there is no moult rate in the continuity equation:

$$\left\{\begin{array}{l}
\text{continuity equation:}\\
\dfrac{\partial a_{\mathrm{A}}}{\partial t} + R_{\mathrm{A}}[\theta(t)]\cdot\dfrac{\partial a_{\mathrm{A}}}{\partial x_{\mathrm{A}}} = \\
\qquad -\{d_{\mathrm{A}}(x_{\mathrm{A}},t)\cdot R_{\mathrm{A}}[\theta(t)]\}.a_{\mathrm{A}}(x_{\mathrm{A}},t)\\
\text{moult equation:} \qquad\qquad\qquad\qquad\qquad\qquad (2\mathrm{c})\\
a_{\mathrm{A}}(0,t) = \displaystyle\int_0^{\infty} ri_{\mathrm{p}}(x_{\mathrm{p}})\cdot a_{\mathrm{p}}(x_{\mathrm{p}},t)\mathrm{d}x_{\mathrm{p}}
\end{array}\right.$$

Ageing rate, $R_i[\theta(t)]$. Ageing rates are assumed to be temperature-dependent. For the four larval instars and the pre-reproductive adult stage, the model chosen was very similar to that proposed by Dean (1974):

$$R_i[\theta(t)] = \frac{a}{1 + c\cdot\theta + d\cdot\theta^2} \tag{3}$$

Parameter values provided by Dean (1974) could not be used because they imply the existence of two values for θ (22.4 and 44.6 °C) when the denominator becomes zero (ageing rate becomes infinite). In the original model, the numerator is not constant but equal to $a + b\cdot\theta$, however a repeated parameter fitting of eqn 3 to Dean's (1974) data showed that b is not significantly different from zero and that its inclusion did not improve the accuracy of the model significantly. The parameters a, c, and d were estimated by the Gauss–Marquardt least-square method using mixed data collected at constant temperatures by Dean (1974) (eight temperatures) and Kieckhefer *et al.* (1989) (six temperatures), for the first to fourth instars. Following Kramer *et al.* (1991), the function $1/R(.)$ was fitted to stage duration values instead of $R(.)$ to ageing rate. For pre-reproductive adults, only Dean's (1974) data were used. No distinction was made in the ageing rates of future winged and apterous adults except for the fourth instar, whose duration is about 1.5 times longer in alatoid morphs (Carter *et al.*, 1982). In this case, data from Kieckhefer *et al.* (1989) were used to fit the model. Results of parameter fitting are presented in Table 1 and Fig. 1.

Table 1. Results of fitting the ageing model to data from the literature. *n* = number of observations. Sources: D = Dean (1974), K = Kieckhefer *et al.* (1989). p = future apterous adults, w = future winged adults, Pre = pre-reproductive adults.

Instar	Source	*n*	a	c	d	R^2
1	D + K	14	0.00396	–0.0700	0.00147	0.86
2	D + K	14	0.00481	–0.0680	0.00145	0.87
3	D + K	14	0.00388	–0.0762	0.00173	0.82
4 (p)	D + K	14	0.00389	–0.0709	0.00155	0.78
4 (w)	K	6	0.00170	–0.0818	0.00187	0.97
Pre	D	8	0.00882	–0.1020	0.00296	0.95

For reproductive adults, a linear day-degrees model was used:

$$R_{\mathrm{A}}(\theta) = \frac{1}{K_{\mathrm{T}}} \cdot \sup(\theta - \theta_0, 0) \tag{4}$$

Physiological age was fixed arbitrarily at 1 when 50% of total reproduction was achieved. The model was fitted to data obtained from laboratory experiments carried out at constant temperatures (four temperatures, $R^2 = 0.95$). In this case, $\theta_0 = -0.68$ °C (development threshold temperature) and $K = 243.9$ day-degrees (thermal constant) (Plantegenest, 1995; Plantegenest *et al.*, 1996).

Rate of moulting, $ri_i(x)$. The moulting rates were assumed to be dependent on physiological age. The probability of an individual completing stage *i* at age *x* was assumed to have a normal distribution $N(\mu_i, \sigma_i)$. From the definition of ageing rate μ_i, the mean duration of stage *i*, expressed on physiological scale, is equal to 1. The parameters σ_i were estimated from data of Dean (1974) and Kieckhefer *et al.* (1989). Finally, the instantaneous moult rate is

$$ri_i(x_i) = \frac{1}{1 - G_i(x_i)} \left(\frac{dG_i}{dx_i}\right)(x_i)$$

where $G_i(.)$ is a cumulative probability function corresponding to $N(\mu_i, \sigma_i)$ (Curry & Feldman, 1989).

Intrinsic death rates, $d_i(x)$. In cereal aphids, larval intrinsic death rate is known to be very low (Dean, 1974; Watt, 1979; Kieckhefer *et al.*, 1989) and was assumed to be constant throughout the larval development. Therefore, the instantaneous death rate $d_i(x)$ was set equal to $-1/4 \cdot \ln(L)$ in all stages, where L is the proportion of larvae completing their development. According to Watt (1979), L was set at 0.95 before wheat phenological stage 73 (favourable conditions) and at 0.4 after that stage. For adults, age at death was assumed to be distributed normally. This is not strictly true for arthropods but the results of simulations were not sensitive to the precise shape of the adult survival curve and the choice of a Gaussian distribution had the advantage of involving only two parameters. The mean and variance ($\mu = 3.13$, $\sigma = 0.79$) of the distribution were estimated from experiments carried out at four constant temperatures (Plantegenest, 1995; Plantegenest *et al.*, 1996). Data were pooled after conversion to a physiological time scale (Fig. 2). In order to take into account the decrease in life duration as wheat matures, adult mortality rate was multiplied by a coefficient K_{m}, which increased exponentially from 1 to 10 000 (arbitrarily chosen value) between stages 73 and 90. No external causes of mortality were incorporated in this model.

Morph determination. Morph determination was described by the linear regression model proposed by Carter *et al.* (1982):

$$100T(t) = 2.603N(t) + 0.847S(t) - 27.189 \tag{5}$$

where $T(t)$ is the proportion of larvae born at date t that will become alate, $N(t)$ is the aphid density at time t (all stages and morphs), and $S(t)$ is the wheat phenological stage at time t.

Fecundity, $m(x)$. Fecundity was considered to be dependent on physiological age, x (Plantegenest, 1995; Plantegenest *et al.*, 1996):

$$m(x) = K_{\mathrm{s}} \cdot 95.81 \cdot \ln(1.46x) \cdot e^{-1.10x} \tag{6}$$

where K_{s} is a coefficient dependent on the wheat phenological stage. Watt (1979) and Carter *et al.* (1982) indicated that the reproductive rate of *Sitobion avenae* increased by about 1.5 after earing (stage 55) then decreased during the milky-ripe stage (stage 70–80). K_{s} was therefore set at 1 before stage 55, at 1.5 between stages 55 and 70, and was reduced linearly to 0 between stages 70 and 78.

Wheat phenological stage development model. The date on which the crop reached each particular growth stage was estimated using a stepwise linear regression model adapted from Meynard (1985), which is based on daily temperatures and sowing date.

Field data

Data collection. Grain aphid population densities were measured on winter wheat from 1976 to 1986 at the I.N.R.A. station at Rennes (Brittany, France; 1°47′73″ W, 48°6′21″N) by Dedryver (1987). Fifty to 100 tillers were observed each week from the beginning of May to harvesting and densities per tiller of the three most common aphid species (*Sitobion avenae*, *Rhopalosiphum padi*, *Metopolophium dirhodum*) and of their natural enemies were recorded. This set of data contains 50 complete time series of aphid density on different wheat cultivars and under varied weather conditions.

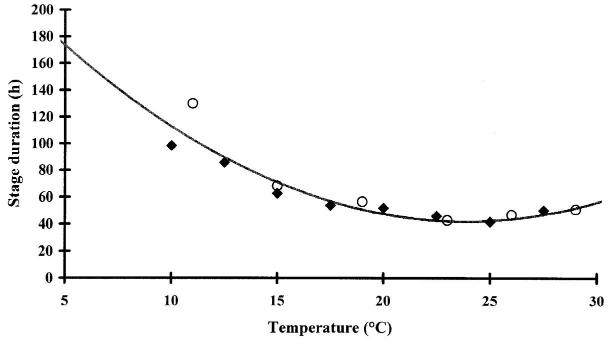

Fig. 1. Dependence of stage duration of the first-instar larvae of *Sitobion avenae* on temperature: points are data taken from the literature (◆ = data from Dean, 1974; ○ = data from Kieckhefer *et al.*, 1989). Line is prediction of the model – eqn 3.

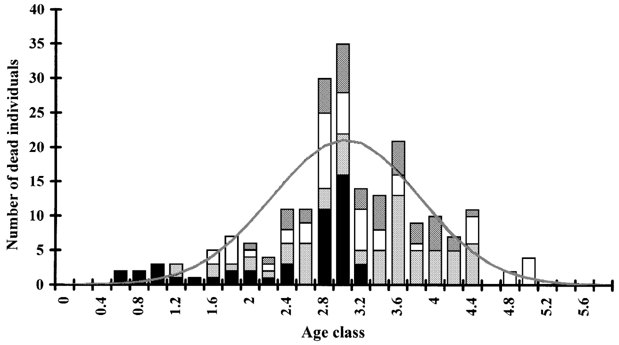

Fig. 2. Bars indicate numbers of individuals that died at the physiological age indicated by the age class at four constant temperatures ($n = 211$, data of Plantegenest, 1995; Plantegenest *et al.*, 1996). Line is approximation of age distribution at death used in the model here.

Measurement of the abundance of natural enemies. The abundance of natural enemies was estimated using the percentage of mummies (parasitoids, I_p) and cadavers of aphids killed by fungus diseases (Entomophthorales, I_m) for all observation dates before stage 75:

$$I_p = 100\left(\frac{\sum_{i=1}^{N_d} N_{p,i}}{\sum_{i=1}^{N_d} N_{a,i} + N_{m,i} + N_{p,i})}\right)$$

$$I_m = 100\left(\frac{\sum_{i=1}^{N_d} N_{m,i}}{\sum_{i=1}^{N_d} N_{a,i} + N_{m,i} + N_{p,i})}\right)$$

where N_d is the number of observation dates before stage 75, $N_{p,i}$ is the number of mummies, $N_{m,i}$ is the number of cadavers of aphids killed by fungus disease, and $N_{a,i}$ is the number of living aphids at day i. The estimates were based on five to 10 sampling dates, depending on the year. In 15 field experiments carried out in Le Rheu in 1980, differing in cultivar and sowing date, the average estimates were: $I_m = 4.54\%$ (coefficient of variation, CV = 49%) and $I_p = 5.96\%$ (CV = 39%). As these values include the effect of cultivar and sowing date, the true sampling error is lower than the coefficient of variation observed here.

Comparison of the observed and simulated dynamics. Typically, the population dynamics of grain aphids are characterised by a phase of roughly exponential increase until a peak density is reached at about stage 75. This is followed by a more or less speedy decline in abundance as food quality deteriorates with grain maturation.

The index of reliability of simulation was defined as $I_s = \ln(D_{ps}/D_{po})$, where D_{ps} and D_{po} are the simulated and observed peak densities respectively.

Let T_s and T_o be the simulated and observed dates of reaching peak density ($T_s > T_o$) and r_s and r_o be the simulated and observed average intrinsic rates of increase of the population ($r_s > r_o$). Then $D_{ps} \approx N_0 \cdot e^{r_s \cdot T_s}$ and $D_{po} \approx N_0 \cdot e^{r_o \cdot T_o}$ where N_0 is initial density of aphids and $I_s = \ln(D_{ps}/D_{po}) \approx r_s \cdot T_s - r_o \cdot T_o$.

Now, let $\Delta r = r_s - r_o$ and $\Delta T = T_s - T_o$, then $I_s \approx \Delta r \cdot T_s + \Delta T \cdot r_s - \Delta r \cdot \Delta T$. Assuming that the relations between Δr and ΔT and I_m and I_p are linear, and that T_s and r_s can be assumed to be constant (i.e. climate is not too variable), this leads to

$$I_s \approx k_p \cdot I_p + k_m \cdot I_m - k_{pp} \cdot (I_p)^2 - k_{mm} \cdot (I_m)^2 - k_{pm} \cdot I_p \cdot I_m \qquad (7)$$

(see Appendix) where the k_i are positive regression coefficients to be determined.

Regressions and statistical analysis were carried out using SAS Software (SAS Institute Inc., 1988).

Temperature. Temperature data were collected *in situ* in standard conditions (2 m high under a shelter) at a distance between 20 and 500 m according to where the culture in the I.N.R.A. station of Le Rheu was situated. The daily maximum and minimum were recorded, and the instantaneous value estimated by extrapolation using a sine function.

Results

Typological analysis

The cases studied were classified into four types with respect to the value of the ratio D_{ps}/D_{po} and related to the level of natural enemy activity (Table 2). The first type ($0 < D_{ps}/D_{po} < 2$) corresponds to situations in which one of the two enemies studied was present at a low level and the second at a low to medium level (16 out of 50 cases). The simulated dynamics were then in good agreement with the corresponding observations: an example of the model output when there was low activity of natural enemies is shown in Fig. 3 ($D_{ps}/D_{po} = 1.05$). Although D_{ps}/D_{po} should always be > 1, the empirical value was slightly < 1 in five out of 50 cases due to measurement errors. These were also considered as type 1. Types 2–4 ($2 < D_{ps}/D_{po} < 5$, $5 < D_{ps}/D_{po} < 10$, $D_{ps}/D_{po} > 10$

Table 2. Relationship between the ratio D_{ps}/D_{po}, number of cases and the percentage [$\pm(\sigma/\sqrt{n})$] of fungus disease (I_m) and of parasitoids (I_p).

	Type 1	Type 2	Type 3	Type 4
Ratio D_{ps}/D_{po}	0–2	2–5	5–10	$10-\infty$
Number of cases	16	17	7	10
Average I_p (%)	2.6 ± 0.59	4.6 ± 0.70	4.1 ± 0.40	6.1 ± 1.79
Average I_m (%)	3.7 ± 1.12	5.3 ± 0.94	7.6 ± 0.99	15.7 ± 3.44

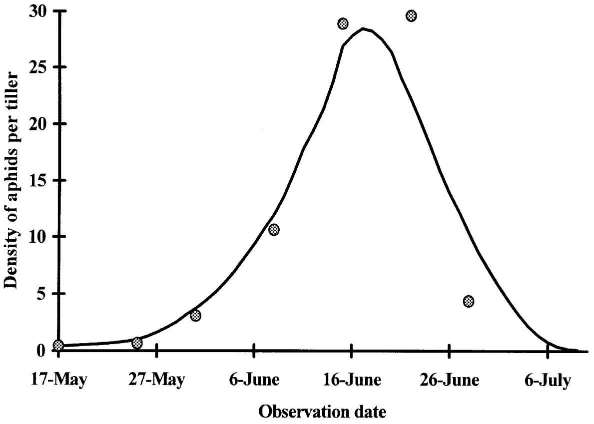

Fig. 3. Dependence of the density of grain aphids per tiller on observation date. Dots are empirical data (year 1977), line is simulation of the model presented here under the assumption of low activity of natural enemies (the ratio of the simulated and observed peak densities, $D_{ps}/D_{po} = 1.05$).

Table 3. Values of the Mallow's C_p statistic, adjusted R^2, and R^2 associated with each set of variables in the regression (sorted in decreasing order with respect to the C_p values).

C_p	Adjusted R^2	R^2	Number	Identity
−0.396	0.731	0.742	2	I_m, $(I_m)^2$
1.10	0.729	0.745	3	I_m, I_p, $(I_m)^2$
1.28	0.727	0.744	3	I_m, $(I_m)^2$, $(I_p)^2$
1.51	0.726	0.742	3	I_m, $(I_m)^2$, $I_m \times I_p$
1.72	0.725	0.741	3	I_m, I_p, $I_m \times I_p$
2.10	0.722	0.739	3	I_m, $(I_p)^2$, $I_m \times I_p$
3.01	0.723	0.745	4	I_m, I_p, $(I_m)^2$, $I_m \times I_p$
3.07	0.723	0.745	4	I_m, I_p, $(I_m)^2$, $(I_p)^2$
3.14	0.722	0.745	4	I_m, $(I_m)^2$, $(I_p)^2$, $I_m \times I_p$
3.55	0.708	0.720	2	I_m, $I_m \times I_p$
3.68	0.719	0.742	4	I_m, I_p, $(I_p)^2$, $I_m \times I_p$
3.74	0.713	0.730	3	I_m, I_p, $(I_p)^2$
5.00	0.717	0.745	5	I_m, I_p, $(I_m)^2$, $(I_p)^2$, $I_m \times I_p$
13.0	0.652	0.666	2	I_m, $(I_p)^2$
15.4	0.645	0.666	3	I_p, $(I_m)^2$, $(I_p)^2$
15.7	0.634	0.641	1	I_m
16.8	0.636	0.651	2	I_m, I_p
17.0	0.634	0.656	3	I_p, $(I_p)^2$, $I_m \times I_p$
20.9	0.637	0.666	4	I_p, $(I_m)^2$, $(I_p)^2$, $I_m \times I_p$
26.4	0.610	0.633	3	I_p, $(I_m)^2$, $I_m \times I_p$
32.2	0.573	0.590	2	I_p, $(I_p)^2$
33.5	0.537	0.546	1	I_p
34.1	0.532	0.550	2	I_p, $I_m \times I_p$
63.3	0.528	0.547	2	I_p, $(I_m)^2$
73.3	0.354	0.393	3	$(I_m)^2$, $(I_p)^2$, $I_m \times I_p$
73.9	0.297	0.325	2	$(I_m)^2$, $(I_p)^2$
75.8	0.296	0.310	1	$(I_p)^2$
75.8	0.285	0.299	1	$(I_m)^2$
75.8	0.282	0.311	2	$(I_p)^2$, $I_m \times I_p$
77.8	0.270	0.299	2	$(I_m)^2$, $I_m \times I_p$
78.2	0.271	0.286	1	$I_m \times I_p$

respectively) were characterised by a medium to high level of parasitism and a low (type 2), medium (type 3), or high (type 4) level of fungus disease. This typology suggests that entomophthoralean fungi were the most important factor responsible for the reduction of population growth rate in the field conditions studied. Indeed, belonging to one or other of the classes of typology seems to be related more strongly to the abundance of Entomophthorales than of parasitoids.

Regression analysis

In order to find the relationship between I_s, I_m, and I_p, linear regression analysis was carried out using eqn 7. In the absence of natural enemies, $I_m = 0$ and $I_p = 0$, which implies that $I_s = 0$, so the intercept value was assumed to be zero. This assumption was supported by the complete statistical analysis, which showed that the intercept was not significantly different from zero. The factors in the regression were I_m and I_p, their squares $(I_m)^2$ and $(I_p)^2$, and their product $I_m \times I_p$. The relationship obtained was highly significant ($F = 26.3$, $P < 0.001$) and the percentage of the variance explained was high $\{I_s = 0.0447(I_p) + 0.215(I_m) + 0.00115\,(I_p)^2 - 0.00311(I_m)^2 - 0.00296(I_m \times I_p),\ R^2 = 0.745\}$. The coefficient associated with $(I_p)^2$ was not of the expected sign and its value was not significantly different from zero ($T = 0.072$, $P =$ NS). The only factor with a significant effect was I_m. This is consistent with the typological analysis and suggests that the influence of parasitoids was negligible compared with that of Entomophthorales. In order to determine which variables were important, stepwise regression analysis was carried out and the adjusted R^2 and Mallow's C_p statistics were computed. For both the criterion based on the C_p value and that based on the adjusted R^2, the most relevant model was that containing solely the index of Entomophthorales abundance, I_m (Table 3). It is therefore relevant to reduce the number of variables introduced into the regression to two: I_m and $(I_m)^2$. In this case, both variables had a highly significant effect ($P < 0.001$) and R^2 was reduced very weakly (from 0.745 to 0.742). Moreover, both parameters were of the expected sign: $I_s = 0.240(I_m) - 0.00436(I_m)^2$. Observed values of D_{ps}/D_{po} against those calculated from this regression equation are shown in Fig. 4.

The estimates of both I_m and I_p might have been subject to sampling errors (and I_p might have been underestimated due to

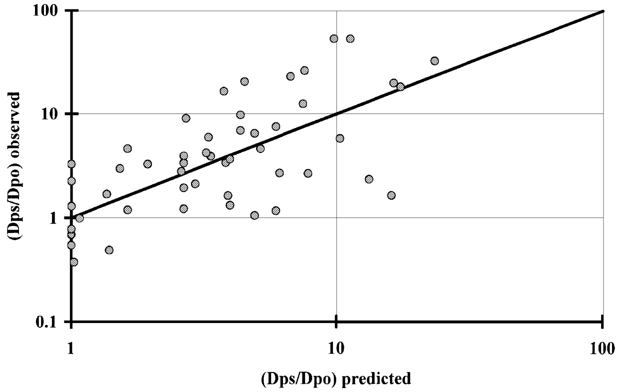

Fig. 4. Comparison of the ratio of the simulated and observed peak densities, D_{ps}/D_{po}, predicted by the regression analysis (abscissa) with observed values (ordinate).

the indirect measurement of the percentage of parasitism). These values were therefore subjected to sensitivity analysis, in which they were varied by 50%, which exceeds both observed coefficients of variation in Le Rheu in 1980. One hundred new data sets were created by replacing each observed I_p value by a random number taken from a normal distribution with the mean I_p and variance equal to $0.25 \cdot I^2_p$ – formally: from $N(I_p, 0.25 \cdot I^2_p)$, and by replacing each observed I_m value by a random number taken from $N(I_m, 0.25 \cdot I^2_m)$. Performing new regression analyses with each of the 100 data sets resulted in only a slight reduction of the average R^2. In the complete model (containing I_m, I_p, I^2_m, I^2_p and $I_p \times I_m$), the average R^2 was 0.70 (range 0.57–0.81) and in the reduced model (containing only I_m, I^2_m) the average R^2 was 0.64 (range 0.50–0.77). Thus the model predictions are not sensitive to variation in I_m and I_p.

Discussion

The work presented here shows a very strong relationship between the extent to which a simulation model that does not include natural enemies overestimates the peak number of grain aphids and the level of activity of two natural enemies: entomophthoralean fungi and parasitoid Hymenoptera. The presence of a high proportion of disease-killed aphids implies a significant reduction in population growth. The correlation between I_s and I_m was highly significant and the addition of I_p resulted in only a slight increase in R^2 when compared with the regression based purely on the abundance of Entomophthorales. This does not mean that parasitoid Hymenoptera have no effect on grain aphid population dynamics but that this effect was hidden by the stronger effect of entomophthoralean fungi. This shows that the method can be used to determine and order the key factors that influence the population dynamics of a given species in a given environment by estimating what form the population trend would take in the absence of natural enemies. Such an analysis does not, however, establish a causal relationship but only the existence of a correlation. It was demonstrated that the presence of both parasitoids and entomophthoralean fungi was associated strongly with a reduction in aphid population growth but only the latter seemed to be responsible for that reduction. To assess whether it is actually due to fungi, it would be necessary to account for the effect of Entomophthorales diseases in the simulation model and assess by simulation whether it increases the reliability of the prediction. This will be subject of further studies. A high increase in reliability is expected as it was shown that nearly 75% of the present discrepancy was attributable to the abundance of entomophthoralean fungi in the data. The methodology can be applied iteratively until the desired precision of the model according to the purpose for which it was built is reached. It would also be very interesting to extend the analysis to cases where other natural enemies are suspected to have an important role in the reduction of aphid densities.

The method described here can be applied to a wide range of problems, such as the quantification of the effects of a large number of factors that are likely to influence aphid dynamics (change in climate, chemical or biological control, agricultural practices, etc.). Of course, in each particular case the population dynamics model would have to be adapted (for example, the Leslie matrix model would be more appropriate) for homeothermic organisms with overlapping generations; in the case of multiple peak dynamics, it would be better to consider each peak separately, etc.

The method requires three steps: (1) identification of the intrinsic biological parameters (fecundity, spontaneous mortality, ageing, etc.) in controlled or semi-controlled conditions, (2) comparison of simulated dynamics with observed dynamics accompanied by a measurement of uncontrolled factors, not taken into account in the model and suspected to be of importance, and (3) quantification of the influence of those factors on the dynamics according to their known characteristics (do they affect fecundity, mortality, etc.). The method is very powerful and of great interest for two main reasons: it allows distinction between causal and correlated factors, and it allows identification of the key factors and an accurate quantification of their effect.

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Appendix

It was shown that $I_s \approx \Delta r \cdot T_s + \Delta T \cdot r_s - \Delta r \cdot \Delta T$.

Assuming that Δr and Δt are linearly dependent on I_p and I_m, this can be written

$$\begin{cases} \Delta r = a_p \cdot I_p + a_m \cdot I_m \\ \Delta T = b_p \cdot I_p + b_m \cdot I_m \end{cases}$$

Then,

$$I_s \approx (a_p \cdot I_p + a_m \cdot I_m) \cdot T_s + (b_p \cdot I_p + b_m \cdot I_m) \cdot r_s - (a_p \cdot I_p + a_m \cdot I_m) \cdot (b_p \cdot I_p + b_m \cdot I_m)$$

or

$$I_s \approx (a_p \cdot T_s + b_p \cdot r_s) \cdot I_p (a_m \cdot T_s + b_m \cdot r_s) \cdot I_m - a_p \cdot b_p \cdot (I_p)^2 - a_m \cdot b_m \cdot (I_m)^2 - (a_p \cdot b_m + a_m \cdot b_p) \cdot I_p \cdot I_m$$

If T_s and r_s are assumed to be constant,

$$I_s \approx k_p \cdot I_p + k_m \cdot I_m - k_{pp} \cdot (I_p)^2 - k_{mm} \cdot (I_m)^2 - k_{pm} \cdot I_p \cdot I_m$$

$$\text{where} \begin{cases} k_p = a_p \cdot T_s + b_p \cdot r_s \\ k_m = a_m \cdot T_s + b_m \cdot r_s \\ k_{pp} = a_p \cdot b_p \\ k_{mm} = a_m \cdot b_m \\ k_{pm} = a_p \cdot b_m + a_m \cdot b_p \end{cases}$$

The presence of natural enemies tends to reduce the values of both T and r, so coefficients a_p, a_m, b_p, and b_m are expected to be positive and so are the coefficients k_i.