

A spatiotemporal model for predicting grain aphid population dynamics and optimizing insecticide sprays at the scale of continental France

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Abstract We expose here a detailed spatially explicit model of aphid population dynamics at the scale of a whole country (Metropolitan France). It is based on convection–diffusion–reaction equations, driven by abiotic and biotic factors. The target species is the grain aphid, *Sitobion avenae* F., considering both its winged and apterous morphs. In this preliminary work, simulations for year 2004 (an outbreak case) produced realistic aphid densities, and showed that both spatial and temporal *S. avenae* population dynamics can be represented as an irregular wave of population peak densities from southwest to northeast of the country, driven by gradients or differences in temperature, wheat phenology, and wheat surfaces. This wave pattern fits well to our knowledge of *S. avenae* phenology. The effects of three insecticide spray regimes were simulated in five different sites and showed that insecticide sprays were ineffective in terms of yield increase after wheat flowering. After suitable validation, which will require some further years of observations, the model will be used to

forecast aphid densities in real time at any date or growth stage of the crop anywhere in the country. It will be the backbone of a decision support system, forecasting yield losses at the level of a field. The model intends then to complete the punctual forecasting provided by older models by a comprehensive spatial view on a large area and leads to the diminution of insecticide sprayings in wheat crops.

Keywords *Sitobion avenae* · Wheat · Convection–diffusion–reaction equations · Aphid outbreaks · Chemical control

Introduction

Widely used for human and animal feeding, wheat is the second agricultural crop in the world in volume of production. In France, wheat is the first crop for acreage and for annual production (around 40,000,000 t; (FAO 2010)). However, wheat yields are frequently lowered by weeds, fungal diseases, and insect pests. Chemical use is the most common way to prevent these losses.

In French cereal crops, the agrochemical pressure is moderate during the growing season, e.g., four full-dose treatments in bread wheat (two herbicides and two other) on average (Butault et al. 2010). However, due to their very large surface (6.5 million hectares), cereals account for around 45 % of the total amount of pesticides used yearly in French crops. Consequently, sparing even a single treatment should contribute significantly to the decrease of agrochemicals use in the country. While weeds and fungal diseases inoculum exert a constant and very strong pressure in French cereal growing areas, the main insect pests build up much more sporadically and do not require systematic treatments. Sparing insecticides in cereals is thereby possible, provided that valuable information on the risk of loss is given to farmers.

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Aphids are in many areas the most important insect pests in wheat fields. They cause direct damages by sap feeding and indirect ones by transmitting plant viruses (Dixon 1998; Dedryver et al. 2010; Al Hassan et al. 2012), which induce up to 50 % yield losses. Aphids reproduce parthenogenetically and viviparously from spring to autumn, which confers them a high potential of increase. During this period, they produce alternatively apterous and winged adult morphs. Apterous ones are mainly adapted to the exploitation of host plants in situ, while winged ones are adapted to dispersion of the species. Transition from apterous to winged morphs is due to damaging environmental conditions like resource decrease and/or overcrowding (Dixon 1987). Aphids can disperse either over short or medium distances (several meters to several kilometers) by active flight (diffusion) (Loxdale et al. 1993; Llewellyn and Loxdale 2003) or over long distances by passive flight, lifted by wind streams (convection) (Loxdale et al. 1985; Hardie 1993; Simon et al. 1999). Aphid populations are subject to large outbreaks governed by the conjunction of favorable climatic and/or biotic conditions (Kindlmann et al. 2007) because, firstly, of their high reproductive rate due to parthenogenesis and viviparity and, secondly, of their high dispersive potentialities due to winged morphs production.

Here, we focused on the grain aphid, *Sitobion avenae*, which is the most noxious aphid species on cereals in spring in Europe (Pierre and Dedryver 1984; Dixon 1987; Fiévet et al. 2007). This aphid feeds mainly on cultivated cereals (wheat, barley, oat) and causes important damage in spring on wheat (Vereijken 1979). Because of the scarcity of decision tools, insecticide treatments are most often done at the wrong time or systematically, even when unnecessary.

Since the late 70s, several forecasting models of *S. avenae* outbreaks on cereals were set up, mainly in Europe. Some of them were statistic models (Pierre and Dedryver 1984; Latteur and Oger 1987) and others were deterministic (Rabbinge et al. 1979; Carter et al. 1982; Rossberg et al. 1986; Plantegenest and Kindlmann 1999; Hansen 2006). Their common characteristic was (1) to run at field scale (only the so called reaction term in the language of partial differential equations, i.e., the apterous population dynamics of aphid on plants was simulated) and (2) the need of field observations of aphid population levels at an early stage of the crop (e.g., heading) in order to initiate the calculations. The initial field contamination, however, was impossible to assess because neither the immigration of winged aphids nor their take-off and landing processes were modeled. Modeling the whole process of crop invasion by aphids and especially winged aphid flows needs the use of different mathematical or simulation tools of spatially explicit type (Parry et al. 2006).

At large scale, the aerial spread of flying insects is well described by mathematically explicit convection–diffusion–reaction equations. The reaction–diffusion equations were introduced in ecology by Fisher (1937) and Kolmogorov

et al. (1937) with homogenous coefficients and are now commonly employed to describe spatially explicit biological invasions (Okubo 1980; Andow et al. 1990; Smoller 1994; Shigesada and Kawasaki 1997; Turchin 1998; Cantrell and Cosner 2003; Murray 2003; Berestycki and Rossi 2008; Roques et al. 2008). Diffusion is suitable to describe the free flight of small insects in a weak or null wind. Convection is convenient when the wind is stronger and trails the insects in its direction. The reaction term represents the local population dynamics which is strongly influenced by emigration and immigration resulting from take-off and landing of the aerial stock of insects. However, some parameters have, in some cases, to be defined at a lower scale (e.g., the landing rate) using a microscale system as described in Ciss et al. (2013).

In order to describe the process of invasion of a large area, we developed a two-dimensional convection–diffusion–reaction system of equations, including parameterization and coupled them to a geographic information system (GIS) (Richter et al. 2012). The model runs at the French scale, considering biotic (wheat surface and growth stage) and abiotic (temperature) factors in the landscape. The model is now at the stage of tuning, running on historical databases. After field validation, it will give farmers useful information as where and when to spray their crops.

In this paper, we give an example of the outputs of this model only considering the reaction–diffusion part, and of its possibilities of use for a better management and sparing of insecticide sprays in wheat crops.

Material and methods

Biological description of the model

The model involves the following equations and parameters allowing simulating successively the different phases of aphid population dynamics, as represented on Fig. 1: aerial dispersion of winged adults by diffusion and/or convection, landing

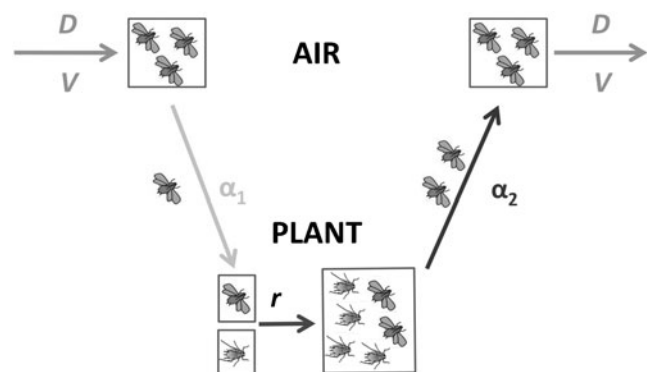


Fig. 1 Description of the model: D diffusion coefficient, V convection coefficient, r growth rate, α_2 take-off rate, and α_1 landing rate

on crops, multiplication of apterous individuals on crops (reaction), and take-off of winged individuals produced on crops. It consists in the coupling of a mobile (for winged aphids) and of a sedentary (for apterous aphids) compartment. A similar model description was also used for modeling the population dynamics in river drift and benthos (Haderler and Lewis 2002; Lutscher et al. 2005; Pachepsky et al. 2005; Haderler et al. 2009), suggesting a generic approach to model the biological systems involving the alternating between a migratory and a sedentary phase.

Initial conditions

The initial conditions consist in aphid infestation of the crops at the end of winter. Their assessment is tricky, as no direct sampling method is available to do that. Till the early spring, aphids are present at such a low level that they are essentially undetectable, while present. A density of two aphids per square meter, although sufficient to build up a noxious population, results in four aphids per thousand tillers. Aerial captures are also useless, as *S. avenae* flies very few and is almost never trapped in winter. We were then obliged to devise an approximate procedure based on our knowledge of the species biology.

Aphid initial populations depend on minimum temperatures during winter that control survival of parthenogenetic individuals in previously infected fields (Dedryver and Gelle 1982). We must distinguish oceanic and continental areas; the number of overwintering aphids located in the oceanic zone is known to be higher than the continental one because overwintering is more likely in the former. Then, initial conditions from the literature were set as follows: (1) in areas where the cumulated minimum temperatures of January were greater than 0 °C (west and southwest), a mean infestation of 20 overwintering aphids per square meter of wheat was affected; (2) in other areas, a mean of 2.5 overwintering aphids per square meter of wheat was fixed (Dedryver and Gelle 1982; Dedryver and Tanguy 1984). Absence or scarcity of overwintering aphids in eastern and southern parts of the country was then explained by conjunction of low wheat surfaces and the occurrence of negative temperatures in January.

For the proportion of wheat fields and their spatial arrangement at the French scale, we used field data from the European Common Agricultural Policy Register retrieved from a GIS.

Aerial dispersion

When the wind speed is higher than 2 km/h, aphids cannot control their flight (Loxdale et al. 1993). They are carried by the direction and the speed of the wind. This process was named “convection.”

When the wind speed is null or weak, aphids fly actively at the speed v , with a maximum speed of $v_{max} \approx 3$ km/h

(Compton 2002). This process of controlled flight has no common direction among aphids and leads to individual random walks which converge at a medium scale (10–100 m) to diffusion. We applied the formula given by Shigesada and Kawasaki (1997), which is generally used for approximation of the diffusion coefficient D (for example by Roques (2004) and Robinet (2006)), as follows:

$$D = \frac{d^2}{\pi h} = \frac{v^2 h}{\pi}$$

Where d is the mean displacement by an individual's “random walk” during time h . The spatial movement was assumed to be isotropic and only depending on diffusion.

Landing on crops

Aphid landing is known to be governed by two mechanisms as follows: a phototactism (Moericke 1955) and/or an optomotor reflex (Kennedy and Booth 1963). Aphids are primarily attracted by areas reflecting a large proportion of long wave energy (e.g., green or yellowing fields), and secondarily by color contrasts in the landscape due to field edges and alternation of different crops and/or plants and bare soil. In our model, the landing rate, named α_1 , depends on the proportion of wheat fields and of their spatial disposition (see supplementary materials 1 and Ciss et al. 2013), and winged aphids having landed on crops are then considered as apterous aphids (Fig. 1).

Multiplication on crops

In the fields, aphid growth rate depends on environmental factors, among which temperature (Pierre and Dedryver 1984; Vialatte et al. 2005), host plant phenology (Watt 1979; Carter et al. 1982; Dixon 1987; Loxdale and Lushai 1999), and the action of natural enemies (Vereijken 1979; Plantegenest et al. 2001) have a key effect.

In our model, aphid growth rate, named r , is derived from field counts and varies with mean temperature and wheat growth stage according to the numeric scale of Zadoks (Zadoks et al. 1977) (see supplementary materials 1). As this growth rate function is estimated through observed growth rate in the field, it is assumed to be lowered at any plant stage and temperature by the effect of natural enemies.

Take-off

Aphids have the ability to generate both apterous and winged adult individuals. Indeed, when apterous aphids reproduce in wheat fields, limiting environmental conditions (decreasing food, increasing number of aphids at the same place...) involve a production of winged individuals at the next

generation, hence overcrowding (Beament and Treherne 1966) and host plant phenology (Akli 1984) are important facts for aphid take-off rate.

In our model, take-off rate, named α_2 , depends on temperature (*S. avenae* does not take-off below 14 °C, (Dry and Taylor 1970; Compton 2002)) and on the quantity of winged aphids produced in the fields in function of aphid population levels and of wheat growth stage. (see supplementary materials 1).

Mathematical description of the model

In a short and synthetic form, the whole model, in our spatial domain named Ω corresponding to France, can be written as follows:

$$\begin{cases} \frac{\partial C}{\partial t} = \lambda_v \nabla_x (D \nabla_x C) - (1 - \lambda_v) V \nabla_x C - a_1 C + a_2 A \\ \frac{\partial A}{\partial t} = rA + a_1 C - a_2 A \end{cases} \quad (1)$$

Where

- $A=A(t,x)$ and $C=C(t,x)$ represent the population density of apterous and winged aphids at time t and at position $x=(x_1, x_2)$
- $\alpha_1=\alpha_1(t,x)$ is the aphids landing rate with $0 \leq \alpha_1 \leq 1$ and its unit is day
- $\alpha_2=\alpha_2(A(t,x))$ is the aphids take-off rate with $0 \leq \alpha_2 \leq 1$ and its unit is day
- $r=r(t,x)$ is the observed growth rate and its unit is aphids/aphid/day
- $\lambda_v=\lambda_v(t,x)$ is a switch coefficient between the diffusion and the convection
- $D=D(t,x)$ is the two-dimensions diffusion coefficient; its unit is square kilometer per day and $\nabla_x^2 = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2}$
- $V=V(t,x)$ is the two-dimensions convection coefficient; its unit is kilometer per day and $\nabla_x = \frac{\partial}{\partial x_1} + \frac{\partial}{\partial x_2}$

For initial and boundary conditions, Eq. 2 is shown as follows:

$$\begin{cases} C(0,x) = C_0(x) \\ A(0,x) = A_0(x) \\ C(t,x) = 0 \quad \forall (t,x) \in \Gamma_1 \\ A(t,x) = 0 \quad \forall (t,x) \in \Gamma_1 \\ D \nabla C(t,x) \cdot v = 0 \quad \forall (t,x) \in \Gamma_2 \\ \nabla A(t,x) \cdot v = 0 \quad \forall (t,x) \in \Gamma_2 \end{cases} \quad (2)$$

Where

- $C_0(x)$ and $A_0(x)$ are initial conditions of $C(t,x)$ and $A(t,x)$ with $C_0(x) \geq 0$ and $A_0(x) \geq 0$ on $\overline{\Omega}$ (adherence of the spatial domain Ω).

- Γ_1 represents marine borders and hostile mountains: homogeneous Dirichlet conditions
- Γ_2 represents land frontiers and uncrossable (but not hostile) mountains: homogeneous Neumann conditions
- $\Gamma_1 \cup \Gamma_2 = \Gamma$, $\Gamma_1 \cap \Gamma_2 = \emptyset$, where Γ is the boundary domain
- v is the unit outward normal to Γ_2 on Ω

The daily mean temperatures of 2004 (an aphid outbreak year) were used for calculating all temperature-dependant coefficients, as well as wheat growth stage (Saiyed et al. 2009). A simulation was run from March 31 to July 9 at the scale of France discretized into pixels of 25 km².

For this present work, no convection was considered in the model. Wind speed was considered as null, and aphids were supposed to fly actively at their maximum speed (≈ 3 km/h), as soon as the temperature is convenient, and the diffusion coefficient D was kept constant ($D=141.18$ km²/day) and isotropic (Eq. 3). Numerical simulations were carried out with finite differences approach (space step=5 km), with a splitting operator method (see supplementary materials 2) and the time step size is 1/125.

$$\begin{cases} \frac{\partial C}{\partial t} = D \nabla_x^2 C - a_1 C + a_2 A \\ \frac{\partial A}{\partial t} = rA + a_1 C - a_2 A \end{cases} \quad (3)$$

All the calculations were carried out using R free software (R Development Core Team 2012). We coded the numerical scheme ourselves and used specialized packages to fulfill our functional specifications (sparse matrices linear algebra: *bandspase* package, handling spatial data: *maptools* package, point pattern handling: *spatstat* package).

Simulation of insecticide treatments and effects

The effects of a pyrethroid insecticide treatment at field scale (Deltamethrin, Décis® at recommended concentration of 6.25 g/ha (Couteux and Lejeune 2013)) on aphid density and then wheat yield were simulated. The model outputs, in the conditions of 2004, were used as initial data for the software “Colibri®” (Plantegenest et al. 1999; Plantegenest et al. 2001; Pierre 2007) in order to evaluate yield gain in case of treatment (for more details about the mathematical modeling of the treatment see (Plantegenest 1995; Plantegenest et al. 2001)). Three different treatments were simulated as follows:

- Treatment at heading
- Treatment at flowering
- Treatment at doughy stage

We focused on the following five locations: Le Mans (48°0'27.72"N, 0°11'54.24"E), Orléans (47°54'9"N, 1°54'32.4"E), Boigneville (48°20'6.36"N, 2°22'14.52"E),

Reims (49°15'46.08"N, 4°2'4.92"E), and Nancy (48°41'36.96"N, 6°11'4.56"E).

Results

Aphid dynamics at country scale

Figure 2a shows the initial conditions of wheat infestation by overwintering *S. avenae* populations on March 31, 2004.

Figure 2b shows the situation on May 22; aphids largely diffused in the Southern half of the country, from the large overwintering site of the Garonne valley in the southwest. In the northern part of France, there was a large spread of aphid populations, especially in the main cereal growing areas in the north and around Paris. On June 9 (Fig. 2c), aphid populations increase slightly in the west and very strongly in the areas of Paris and in the north. On July 9 (Fig. 2d), aphids populations have decreased in most regions of France, especially in the western half, and the most infested areas are restricted to the east (Champagne and Lorraine) and to small particularly cold areas of Normandie.

Local dynamics and treatment simulation

Figure 3 gives a focus on the simulated dynamics of *S. avenae* in 2004 (in number of aphids per 25 km² pixel), on five

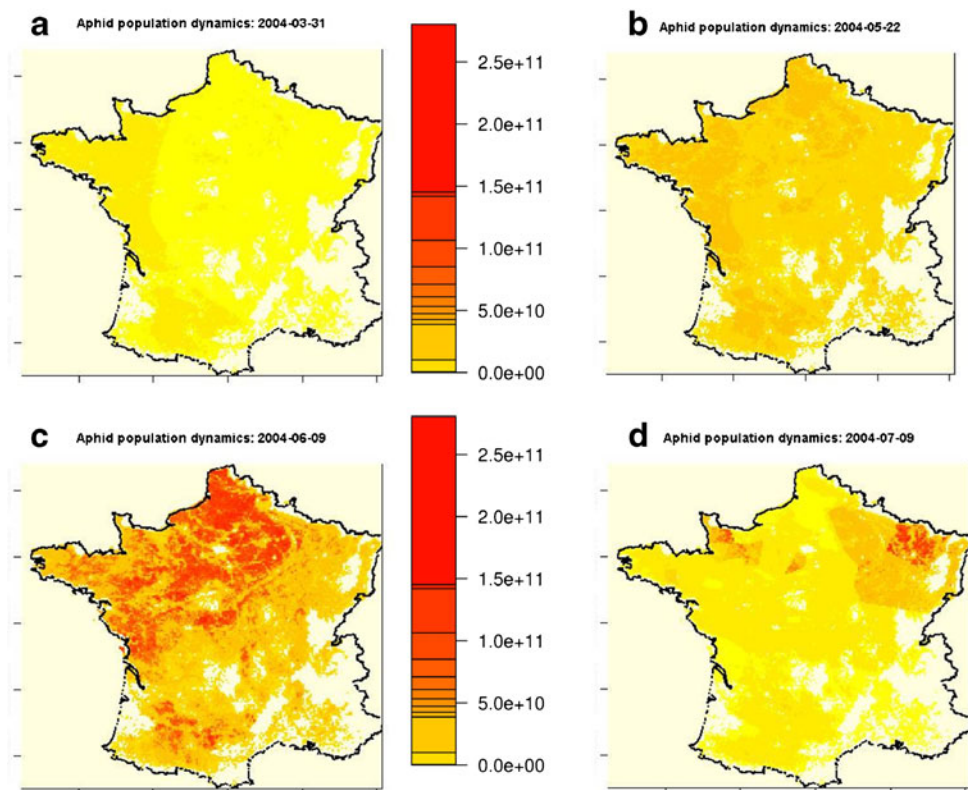
selected sites on a west–east transect along France; they show clearly a wave of population peaks from west to east (Le Mans; Boigneville; Orléans; Reims; Nancy) for both aphids on plants (apterous) and in the air (winged).

Table 1 shows the outputs of the model at heading and at population culmination, in numbers of aphids per wheat tiller in the five sites, and a further simulation by the model “Colibri®” of yield gain due to an insecticide (pyrethroid) spray at different growth stage of the wheat. This shows that, from the population dynamics results of our model and in the climatic conditions of 2004, insecticide spray increases yield in all our five cases and that spraying after wheat flowering (a frequent situation when an outbreak occurs) was ineffective in terms of yield increase.

Discussion and conclusion

In this work, we used a model based on partial differential equations, via convection–diffusion–reaction equations. These models are well adapted to describe biological phenomena at large scale, particularly in heterogeneous environments and when it is impossible to follow the movement of each individual independently (Richter et al. 2012). This is indeed the case of aphids that develop populations of billions of small short-living organisms.

Fig. 2 Aphid population dynamics at four different times: **a** 31st March, **b** 22th May, **c** 9th June, and **d** 9th July 2004 (in aphid numbers/25 km² pixel)



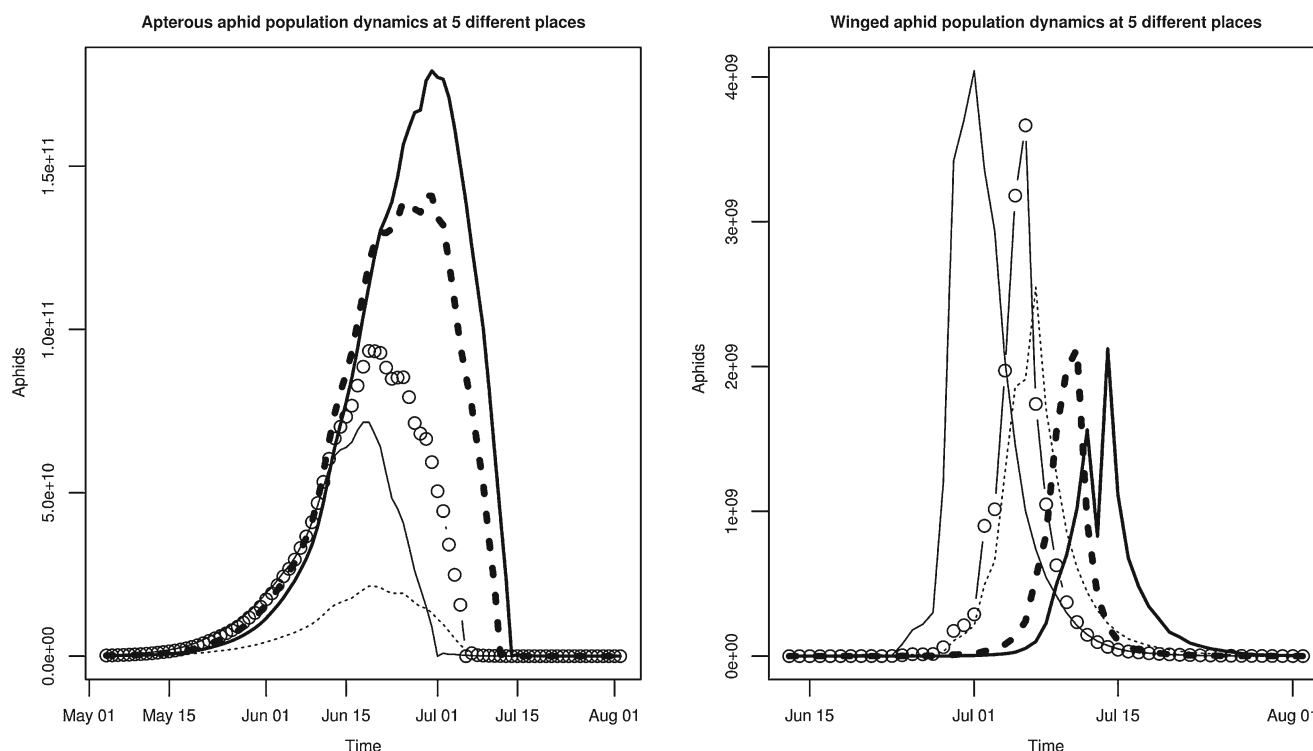


Fig. 3 Apterous (*left*) and winged (*right*) aphid population dynamics at five different locations: Le Mans (—), Orléans (o-o-o), Boigneville (- - -), Reims (- · - ·), and Nancy (—) in aphid numbers/25 km² pixel

The values of several coefficients calculated by the model are in the range of magnitude of those derived from previous field works; that is the case for r (Dean 1974; Salman 2006), for $C.\alpha_1$ (Vialatte et al. 2007), and for the function of alate production in fields (Watt and Dixon 1981). For the values of these ranges, see Supplementary materials 1. Temperature-dependant functions for take-off and initial conditions estimation were taken directly from the literature (Walters and Dixon 1984; Dedryver and Gelle 1982).

Other parts were more difficult to evaluate. The diffusion coefficient, indeed, is taken from literature (Shigesada and Kawasaki 1997; Compton 2002), and does not vary with

temperature which may be problematic. The effect of rainfall was not considered, and we did not introduce convection in this preliminary work. The introduction of these factors (rainfall and wind) in the model is straightforward, however, providing the availability of the weather data.

Despite these limitations, the outputs of our model reflect realistic aphid densities. In fact, the maximal simulated populations for 2004 were comprised between 2 and 15 aphids per wheat tiller (see Table 1), (1) which is close from populations levels (3 aphids/tiller) observed punctually in the same year (Fiévet et al. 2007) and (2) which is in the range of the aphid population peaks observed during a 30-year survey of *S.*

Table 1 Effect of pesticide spray at heading, flowering, and doughy stage on wheat yield at five locations: Le Mans, Orléans, Boigneville, Reims and Nancy. Aphid populations are simulated by our model, yield gains are calculated by the software “Colibri®”

	Population at heading per wheat tiller	Maximal population per wheat tiller	Wheat yield gain with treatment at heading	Wheat yield gain with treatment at flowering	Wheat yield gain with treatment at doughy stage
Orléans	0.067	7.5	0.16 t/ha (May, 27th)	0.16 t/ha (June, 6th)	0.01 t/ha (June, 18th)
Boigneville	0.081	1.7	0.2 t/ha (May, 26th)	0.19 t/ha (June, 6th)	0.01 t/ha (June, 18th)
Reims	0.043	11.3	0.11 t/ha (May, 28th)	0.10 t/ha (June, 8th)	0.01 t/ha (June, 22th)
Nancy	0.092	14.3	0.22 t/ha (June, 4th)	0.21 t/ha (June, 14th)	0.01 t/ha (June, 26th)
Le Mans	0.053	5.7	0.13 t/ha (May, 22th)	0.12 t/ha (June, 1st)	0.01 t/ha (June, 13th)

avenae in France (1–60 aphids/wheat tiller; see Dedryver et al. (2009)). Our model outputs also reflect real population trends corresponding to a sigmoidal increase of aphid populations from stem extension to doughy ripeness and a sharp decrease up to the maturity stage (Carter et al. 1982).

Moreover, simulation results at France scale also show that both spatial and temporal *S. avenae* migration can be represented as a southwest to northeast irregular wave, even without considering the effect of dominant winds. By irregular wave, we want to talk about population dynamics strongly affected by spatial irregularities of biotic and abiotic factors. In this paper, we did not intend to explore the traveling waves derived from our reaction–diffusion system; but as our system does not include capacity limit for the growth rates (i.e., reaction function), the wave speed should be near that obtained in Skellam's model (Skellam 1951). In further works, we plan on assessing the traveling waves derived from our system following methods recently published in this field (Lutscher et al. 2005; Pachepsky et al. 2005). This irregular wave effect is in concordance with our knowledge of *S. avenae* phenology (Dedryver et al. 1987). The southwest dominant winds observed, in June and July, in the northern half of France (Arléry 1979) would certainly accentuate the speed of that wave.

The model needs to be finely tuned and validated now during several consecutive years in different French regions by Arvalis-Institut du Végétal in order to be used as a decision tool by extension services. The tuning process involves of course a sensitivity analysis which is now under study (Saltelli et al. 2009).

Chemicals are applied in fields to control pests and increase crop yields. This mode of pest control, however, is recognized as a major threat to ecosystem integrity and the realization of low-carbon agriculture (Needelman et al. 2007; Rask et al. 2010; Wohlfahrt et al. 2010; Mozner et al. 2012; Pärn et al. 2012). In a preliminary step to use this model for sparing insecticides, we simulated the effects of three types of insecticide regimes in order to compare their efficiency in term of potential economic losses for farmers (Tatchell 1989). We show that, when validated, the model could be used firstly to forecast aphid densities in real time at any date or growth stage of the crop, at any pixel (25 km²) of France, and secondly to initiate a decision tool estimating yield losses (e.g., Colibri®) at field level in any cereal-growing area (Plantegenest et al. 1999; Plantegenest et al. 2001; Pierre 2007). The preliminary results mentioned before show that even in an outbreak situation as in 2004, a chemical treatment after flowering wheat stage is useless and time and money consuming. They illustrate also the interest of such a tool in the general framework of a drastic reduction of pesticide use in Europe for identifying optimal crop protection policies both spatially explicit and episodic.

The range of application of this kind of model, moreover, when calibrated is much wider than described above.

For scientific purpose as well as for pest management, it will be possible to test as many scenarios as wanted, both on spatial and temporal population dynamics of an aphid species at country scale or larger. This includes climatic scenarios, modifications of wheat surfaces, or of their localization or other landscape changes, but also effects of regional insecticide treatments (e.g., in the West) on the further dynamics of the species in other regions, and of the timing of pesticide applications in relation to aphid immigration waves.

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