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Modelling the spatio-temporal expansion of an exotic seed chalcid, *Megastigmus schimitscheki*, recently introduced in southeastern France

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Abstract

An exotic, specialist seed chalcid, *Megastigmus schimitscheki*, has been introduced along with its cedar host seeds from Turkey to southeastern France during the early 1990s. It is now expanding in plantations of Atlas Cedar (*Cedrus atlantica*). We tested the efficiency of a reaction-diffusion-advection model to survey the spatio-temporal expansion of the insect populations. The model was also used to study the influence of some biological and spatial criteria on the species dispersal.

Keywords: Insect dispersal; Reaction-diffusion model; *Megastigmus*; Cedar;

1 Introduction

As a result of technological advances and of globalization trade, forest products are moved around the globe with an ever-increasing speed and frequency. This movement has precipitated a substantial increase in biological invasions by allowing organisms to pass the natural barriers that limit their dispersal (Liebhold *et al.* 1995). This is especially true for the insects infesting tree seeds, whose cryptic way of life does not usually allow a detection easier than using X-rays, the more as phytosanitary regulations are limited or non existent in many countries. In the West Palearctic, 8 of the 21 species recorded in the seed chalcid genus

Megastigmus Dalman (Hymenoptera: Torymidae) are exotic invasive species introduced through seed trade (Roques, A. and Skrzypczynska 2003). Fabre *et al.* (2003) just noticed a newly invasive seed chalcid, *Megastigmus schimitscheki* Novitzky (Hymenoptera: Torymidae) in southeastern France. The insect has probably been introduced from Asia Minor (Turkey) along with seeds of Cedar-of-Lebanon (*Cedrus libani* A. Rich.).

The major objectives of Fabre *et al.* (2003) were to define the impact of *M. schimitscheki* on the potential of natural regeneration of the cedar plantations planted in southern France, and to compare the biological patterns exhibited by the chalcid populations in the area invaded in France with these observed in the native range of Asia Minor (Çanakçıoğlu, 1990; Özkazanç, 1979). Therefore, this study provides us with many useful data in order to build a model. Although little was known about the factors underlying the establishment process in the invaded area, the biological characteristics of *M. schimitscheki* in both native and invaded area appeared rather similar to these of other *Megastigmus* seed chalcids which have been extensively studied in Europe, North America and Japan (e.g. Hedlin *et al.*, 1980; Kamijo, 1962; Roques, A., 1983; Roques, A. and Skrzypczynska, 2003). Thus, the chalcid is considered as specifically related to seeds of cedars (*Cedrus* spp.) but capable of developing in the seeds of all cedar species, like Atlas Cedar (*Cedrus atlantica* (Endl.) G. Manetti ex. Carr.) onto which it shifted in France. The host recognition is likely mediated by olfactory and visual cues emitted by the cones (Luik *et al.*, 1999; Roques, A., 1998).

Previous studies developed in southeastern France also suggested that *M. schimitscheki* has been introduced during the period 1990-1994 (Fabre, 1986, 1989; Fabre *et al.*, 1994; Fabre *et al.*, 2003). Hence, the invasion has occurred recently, and the spreading is still limited. Because of this recent introduction, *M. schimitscheki* did not recruit any predators in France yet. In addition, the insect is facing little competition for the exploitation of seed resources because the new host, *Cedrus atlantica*, is also introduced (but from North Africa) and its cones and seeds are still not colonized by the indigenous entomofauna. There is only one competitor, *Megastigmus pinsapinis* Hoffmeyer, an other *Megastigmus* seed chalcid which has been introduced half a century ago from North Africa (Roques, A. and Skrzypczynska, 2003). However, *M. pinsapinis* seems dominated by *M. schimitscheki* (Fabre *et al.*, 2003). These patterns make the study of the spatio-temporal dispersal processes from the source point easier than in the case of a species introduced since a longer time, distributed on a wider area, and facing a large cortege of natural enemies and competitors.

Moreover, several biological traits facilitate the establishment of *Megastigmus* seed chalcids in exotic countries: (i) an ability to extend larval diapause in seeds for up to 4 years in most species, allowing them to bridge periods where seeds are unavailable because of masting phenomenon (Turgeon *et al.*, 1994); (ii) parthenogenesis (the females can reproduce without males; Roques, A., 1983); (iii) an ability of some species to develop within unfertilized seeds, thus there is no need for the seed cones to be pollinated for the insect to survive (Rouault *et al.*, 2004). These patterns contribute to the interest of modelling

the spatio-temporal expansion.

Although seed chalcids constitute good models for the study of the expansion processes in newly invaded areas, there are few papers attempting at modelling such a process. Only Jarry *et al.* (1997) proposed a reaction-diffusion model to survey the colonization of Douglas-fir seed orchards by surrounding populations of a related seed chalcid introduced from North America, *Megastigmus spermotrophus* Wachtl. However, reaction-diffusion models are widely used in population dynamics, especially when one cannot follow the movement of each organism independently (for review see Shigesada and Kawasaki, 1997 or Turchin, 1998).

The aim of our work was to build a model of the spatio-temporal dispersion of *M. schimitscheki*, and to study, through this model, the influence of some biological and spatial criteria on the species dispersal.

2 Study site and data collections

The location of the cedar plantations in Southeastern France was obtained from the French National Forestry Office as well as an estimation of the annual cone crop in each plantation. Then, standardized cone samplings were carried out annually by the Avignon Laboratory of the French National Institute of Agriculture (INRA) from 1994 to 2004. The number of cones collected per plantation varied between 8 to 139 according to the size of the annual cone crop.

Immediately after being collected the cones were brought back to the laboratory where they were individually disarticulated and all their seeds were X-rayed in order to calculate the proportion of filled, empty and chalcid-infested seeds. However, *M. schimitscheki* cannot be separated from *M. pinsapinis* through observations of larvae on X-ray plates. Therefore, the infested seeds were placed in emergence boxes until adult emergence in order to know the proportion of each species, and to estimate the specific damage that can be attributed to *M. schimitscheki*.

The percentage of seed damage was calculated using the following formula:

$$\%infestation = \frac{\text{number of seeds infested by } M. \textit{schimitscheki}}{\text{total number of seeds} - \text{unfertilized seeds}} \times 100, \quad (2.1)$$

assuming tentatively that larvae of *M. schimitscheki* cannot develop in unfertilized seeds unlike other *Megastigmus* spp.

Wind direction and speed was obtained from Météo-France stations, which are distributed throughout the studied area.

3 The model

3.1 Simplifying hypothesis and life cycle

The data obtained by Fabre *et al.* (2003) revealed a quite constant sex-ratio at emergence, with about the same proportion (50:50) of females and males. Moreover, fecundation is not necessary to produce an offspring because of a possible arrhenotokous parthenogenesis (Roques, A. and Skrzypczynska, 2003). Therefore, we did not include the fecundation process and the interaction between males and females in our model. Moreover, we only studied the females dispersal. In addition, even if the variations of the emergence dates in function of the altitude could be included, we did not take them into account, for the sake of simplicity.

Each female lays the eggs in the seeds by inserting its long ovipositor through cone scales during the first year of cone development, and then the whole larval development occurs within the same seed. Adult emergence may occur two years later but emergence may also be delayed for one to four additional years (Roques, A. and Skrzypczynska, 2003). A simplified life cycle of *M. schimitscheki* used for building the model is shown in Figure 1.

3.2 Behaviour

The female emergence occurs over a 6-11-day period, with a quite constant rate (Fabre *et al.*, 2003). The individual flight period was assumed to last 10 days as for *Megastigmus spermotrophus* (Jarry *et al.* 1997); moreover, because *Megastigmus* are essentially day-active insects (Roques, A., 1981), the effective flight period was assumed to be reduced to 7 days.

Experimentally, a large amount of insects could be found far (e.g. 50 km) from the front observed the year before (A. Chalon, unpublished data). Hence, a passive dispersal by wind can be ruled out. Indeed, in the case of a totally passive dispersal of tree seeds by wind, the recorded dispersal distance are in most cases less than 200 meters (Nathan *et al.*, 2002). That is why we were brought to assume that the insects can modify their flying altitude. Moreover, in the seeds'case (dandelion seeds), Tackenberg *et al.* (2003) have shown that for long-range dispersal, the main factor was not the horizontal wind speed but the vertical turbulence, and especially convective updrafts. It could explain why the insects can cover rather long distances by increasing their flying altitude.

Thus made the following assumption: inside a forest the insects move by diffusion, and when the diffusion processes bring them to a boundary of the forest, they fly to move upwards and therefore be subject to stronger winds. When they are again close to a forest, say at a distance d_a , they may reduce their flying altitude in order to be subject to weaker winds and to approach the forest by diffusion (visual and olfactory attractiveness of cones; Luik *et al.*, 1999; Roques, A., 1998).

During this flying period, we assumed that the mortality rate was constant.

We used two coupled models. One simulated the laying of eggs and the larval

stage whereas the other simulated the movements of the adults. The former was a reaction-diffusion-advection model.

3.3 Model for the flying period

In order to model the adult dispersal, we used the following reaction-diffusion-advection equation:

$$\frac{\partial u}{\partial t}(\mathbf{x}, t) = D\Delta u(\mathbf{x}, t) - v_* V(\mathbf{x}, t) \cdot \nabla u(\mathbf{x}, t) + f(\mathbf{x}, t) - X(\mathbf{x}, t)u, \quad (3.2)$$

for $t \in [0, N_d]$ (N_d is the total period where one can find living adults, expressed in days), where the unknown $u(\mathbf{x}, t)$ is the female adult population density at time t and spatial coordinate $\mathbf{x} = (x, y) \in \Omega$, where Ω is a sufficiently big open set of \mathbb{R}^2 , and

$$u \equiv 0 \text{ on } \partial\Omega.$$

Let us explain each term of (3.2) and give its value.

The function $f(\mathbf{x}, t)$ is a source term that models the progressive emergence of the adults. The results of Fabre *et al.* (2003) (Fig. 2) showed a female emergence that was quite constant over a period N_{em} . Let $m(\mathbf{x})$ be the total density of female adults that are going to emerge during the period $[0, N_{em}]$, at the position $\mathbf{x} \in \mathbb{R}^2$. Then,

$$f(\mathbf{x}, t) = \frac{m(\mathbf{x})}{N_{em}} \text{ for } t \in [0, N_{em}], \text{ and } f(\mathbf{x}, t) = 0 \text{ for } t > N_{em}. \quad (3.3)$$

The term $X(\mathbf{x}, t)$ corresponds to the daily mortality rate during the flight period. Assuming that this rate is constant, we have

$$X(\mathbf{x}, t) = \frac{1}{\text{mean flight period}} \text{ for } \mathbf{x} \text{ outside a cedar plantation}, \quad (3.4)$$

moreover, we assume that $X(\mathbf{x}, t) = 0$ when \mathbf{x} is inside a cedar plantation.

Let us now turn to the diffusion term. It is difficult to estimate the value of the diffusion coefficient D since the insects are too small to be marked and recaptured, therefore, it did not appear useful to take a space-varying or time-varying diffusion coefficient. Moreover, similar models for other insect species turned out to be efficient with constant diffusion coefficient and time and space-varying advection coefficients (Banks *et al.*, 1988).

We chose a space-varying and time-varying advection term. The time variations correspond to the daily changes of the winds. For the space variations, in addition to the sampled wind speed and direction, we took into account the ‘‘distance to a forest’’ criterion. Indeed, we assumed the following: the insect cannot ‘‘decide’’ to exit from a forest when the later is saturated with insects, and it only exits from it by random diffusion, and then, as described in Section 3.2, it raises in order to be subject to higher winds, depending on its distance to the closest cedar plantation. We assumed that the flight altitude was proportional to the distance to the forest, up to a maximal distance d_a . Nathan *et al.*

(2002), analyzing the mean horizontal windspeed at different heights, showed that in open landscapes, over a low vegetation, this wind profile was typically logarithmic. In our case, the flying altitude being quite high, the environment is rather a low vegetation than a dense forest. Therefore, we used the following formula for V :

$$V(\mathbf{x}, t) = V_r(\mathbf{x}, t) \min\{\ln[d(\mathbf{x}, forest)(e - 1)/d_a + 1], 1\}, \quad (3.5)$$

where V_r is the recorded wind, and $d(\mathbf{x}, forest)$ is the distance to the closest cedar forest. However, even if the dispersal range of the insects is much higher than the passive “long distance dispersal” of seeds (Tackenberg *et al.*, 2003), it remains smaller than the total distance covered by the wind. Therefore, we added another coefficient v_* . This coefficient is estimated in Section 4.

3.3.1 Numerical methods

The solution $u(\mathbf{x}, t)$ of equation (3.2) was calculated through an “alternate directions” method: the fractional steps method, with an implicit Euler’s scheme. This method was proposed by Godunov (1957) and Yanenko (1991) for the heat equation.

Such a scheme, with only second order terms is proved to be unconditionally stable in the Fourier sense. A computation with the first order terms would be more fastidious, however the numerical experiments conducted in this work suggested that the method was stable.

3.4 Model for the larval stage

Let $u_f(\mathbf{x})$ be the (female) adult population density at the end of the flying period of the year n . Each insect that has managed to get into a cedar plantation lays ε eggs, depending on the amount of available resources. Thus,

$$o(\mathbf{x}) = \min\{g(\mathbf{x}), \varepsilon u_f(\mathbf{x})\},$$

where $o(\mathbf{x})$ is the density of new-laid eggs and $g(\mathbf{x})$ is density of available seeds. Let $d_1(n)$ be the 1 year larval prolonged diapause rate of and $d_2(n)$ be the rate of insects that emerge after a 2-year prolonged diapause (we assumed in this work that the duration of the prolonged diapause period was at most of 2 years). Namely, from the eggs which were laid during year n , a proportion $1 - d_1(n) - d_2(n)$ of adults will emerge in May of year $n + 2$, whereas $d_1(n)$ will emerge during year $n + 3$ and $d_2(n)$ during year $n + 4$.

Thus, the total density of (female) adults that are going to emerge in May of year $n + 2$ is

$$m(x) = [o(\mathbf{x})(1 - d_1(n) - d_2(n)) + o_{-1}(\mathbf{x})d_1(n - 1) + o_{-2}(\mathbf{x})d_2(n - 2)] / 2,$$

where o_{-1} and o_{-2} are the number of eggs that have been laid respectively during year $n - 1$ and $n - 2$ (with a sex-ratio of 50:50 at emergence, see Section 3.1).

During the larval stage, we assumed that the mortality rate was 0, as it has been proved for a closely-related species (Jarry *et al.*, 1997). Indeed, at present, the larvae do not have parasite nor predators in the invasion zone.

4 Parameters estimates

Some parameters could be directly estimated whereas others needed to be numerically computed.

Jarry *et al.* (1997) have shown that $D = 1 \text{ km}^2/\text{day}$ for *M. spermotrophus*. Shigesada and Kawasaki (1997) estimated the value for gypsy moth, which is a better flyer, to $D = 0.08 - 0.46 \text{ km}^2/\text{day}$. In order to compute the value of D that best corresponds to our experimental data, we used a formula of Shigesada and Kawasaki (1997), which is valid when D is the only parameter that has an influence on insects dispersal (in our model the advection term vanishes inside the forests):

$$D = \frac{\langle r \rangle^2}{\pi T}, \quad (4.6)$$

where $\langle r \rangle$ is the mean distance from the source point, during the period T . Using data from the Luberon's forest, between the plantations of Oppede and Menerbes (see Figure 2), the mean displacement of the insects was estimated: $\langle r \rangle = 1 \text{ km/day}$. Similar values were obtained in the other cedar plantations. Thus, the formula (4.6) gives $D = 0.32 \text{ km}^2/\text{day}$.

The mortality rate, $X(\mathbf{x}, t)$, was directly computed with the formula (3.4), using a mean flight period of 10 days (Jarry *et al.*, 1997). The value of N_{em} was also known to be between 6 and 11 days (Fabre *et al.*, 2003). Actually, the computations were made with the 2/3 of the mean flight period and the 2/3 of the emergence period, in order to take into account that the insect's activity is only diurnal (Roques, A., 1981). The fecundity rate ε was assumed to be close to the one observed in *M. spermotrophus* by Jarry *et al.* (1997), 10 eggs/female. Experiments still under way tends to confirm this value (A. Chalon, unpublished results). In a first approximation based on the data provided by Fabre *et al.* (2003), we fixed the rates of prolonged diapause as $d_1 = 15\%$ and $d_2 = 5\%$. Indeed, these rates seemed much more variable both among plantations and years, depending on yearly cone abundance, and could be higher (see Section 6.2.2). Concerning the advection term 3.5, the value of V_r and the direction of V were given by Meteo-France stations. The parameter d_a corresponds to the distance from which the forests have no more influence on the insects flying altitude. Basing ourselves on the observations of Jarry *et al.* (1997), we set $d_a = 10 \text{ km}$.

In order to estimate the parameter v_* , we used a method summarized in Turchin (1998) (after a series of papers of Banks *et al.* 1987, 1988). We first had to make an initial guess on the numerical value of the parameter v_* . For that, we computed the quotient between the maximal recorded distance crossed by the invasion front during one year and the maximal distance covered by the wind, in the same direction during a 15-day period (effective flight period of 6.5% of the insects, from formula (3.4), which supposedly correspond to those who could cross the longest distance). We obtained $v_* = 0.012$. We then numerically computed the results of the model (using Matlab®), and compared them to the data, in order to adjust the value of v_* . We finally obtained the following range: $v_* = 0.04 - 0.08$.

5 Numerical simulations

In this section, we studied the influence of some biological characteristics of *M. schimitscheki* on its expansion, under several hypothesis on winds and cedar plantations. Hence, we were concerned with (i) the influence of the length of the emergence period, (ii) the role of prolonged diapause, and (iii) the effects of the presence of isolated trees between the forests. With the help of numerical tests, we have discussed the above questions. These tests also allowed us to appraise the realism of the model.

In each of the following numerical experiments, the real configuration of the winds and cedar plantations was replaced by some “laboratory cases”, which allowed an easier interpretation of the tests. Besides, we allowed some biological characteristics to vary (such as diffusion coefficient and diapause rate).

The initial infestation rate was always supposed to be 0 everywhere, except on one plantation, which was marked on the figures with an arrow, and corresponded to the place of introduction.

5.1 Test 1: length of the emergence period

We were concerned here with the role of the emergence period’s length on the insects spreading, as predicted by our model.

Test 1.1 The winds are assumed to be constant (their direction is given by Figure 3 (1.a)) over the emergence period. The cedar plantations are distributed as in Figure 3 (1.b), and the fructification is homogeneous and positive. Figure 3 (1.c), (1.d), illustrates the dispersal of the insects in function of the length of the emergence period, over a 6-year total duration. Conclusion: the emergence period’s length does not have a significative influence on the insects spreading under constant winds.

Test 1.2 The wind’s strength is assumed to be constant but its direction varies. Namely, it is oriented to the north during the first 7 days of emergence and then to the south. The plantations are similar to that of Figure 3 (1.b), and the winds are described on Figure 3 (2.a), (2.b). The results of the simulation, over a 6-year period are presented on Figure 3 (2.c), (2.d). In the case of an emergence over 10 days, 7 plantations become attacked, whereas in the case of a 5-day emergence period, only 4 plantations are colonized.

Test 1.3 The wind direction is constant (Figure 3 (3.a)), but its strength is variable. During the first week of emergence $v_* \|V\| = 3$ km/day whereas $v_* \|V\| = 6$ km/day after (see Figure 3 (3.b) for plantations distribution). Simulations results are given on Figure 3 (3.c), (3.d). The insects with a 5-day emergence period do not manage to reach the northern plantations whereas those who emerge over 10 days colonize two additional plantations on the northern part of the map.

5.2 Test 2: Role of the prolonged diapause

We focused here on the influence of the prolonged diapause period on the spreading of the insects over 6 years.

Test 2.1 The fructification is assumed to be constant in time and homogeneous in space. Even if this hypothesis is highly improbable it allows us to estimate the influence of the prolonged diapause on spreading speed, independently of the forests fructification. The winds and the plantations are distributed as in Figure 3 (1.a), (1.b). The numerical results of Figure 3 (4.a), (4.b) show that the invasion zone is slightly more important when there is no prolonged diapause.

Test 2.2 The fructification is initially positive and uniform, and then vanishes on every plantations for one or two years. The prolonged diapause rates are supposed to be $d_1 = 5\%$ and $d_2 = 15\%$. The winds and the plantations are again distributed as in Figure 3 (1.a), (1.b), with an homogeneous positive fructification during the first year. The fructification is set to 0 during years 2 and 3. The results are shown on Figure 3 (4.c), (4.d). Conclusion: the two years without fructification have a small influence on the spreading of the population.

Test 2.3 In this test, the fructification may vary with time for some plantations. The winds and the plantations are distributed as in Figure 3 (1.a), (1.b). The fructification is assumed to be homogeneous and positive the first year, and then vanishes on some plantations the next years (Figure 3 (5.a), (5.b)) (this hypothesis is experimentally relevant: see remark 5.1 below). The numerical results are presented on Figure 3 (5.c), (5.d), showing a wider spreading in the case of the species with prolonged diapause.

Remark 5.1 *Figure 5 shows some fructification data of two studied forest plantations. The fructification can vanish some years, even on large plantations like the Ventoux forest (800 ha). It illustrates the interest of the preceding tests.*

5.3 Test 3: Influence of the presence of isolated trees

Two different distributions of cedar plantations were analyzed (see Figure 4 (6.a), (6.b)). We studied the question of the influence of the presence of isolated trees between two forest zones. The wind profile is as in Figure 3 (1.a). The numerical tests are made over a 6-year period.

Test 3.1 The advection term is assumed to have a norm $v_* \|V\| = 5$ km/day, and the diffusion coefficient is $D = 0.25$ km²/day. The obtained results are presented on Figure 4 (6.c), (6.d). The spreading is wider in the case without isolated trees.

Test 3.2 This time, the advection term norm is $v_* \|V\| = 2$ km/day, whereas the diffusion is $D = 3$ km²/day. The results are presented on Figure 4 (6.e), (6.f). Here, the spreading is improved in the case with isolated trees, where the insects manage to reach the northern plantations, whereas they could not in the case without isolated trees.

6 Model verification and validation

6.1 Interpretation of the tests results

All the numerical results of Section 5 can be associated to a logical biological interpretation. Moreover, these results were in accordance with our expectations. That made us think that the qualitative behavior given by the model was not unreasonable. In the next section, the experimental data were compared with the model's forecasts.

6.2 Comparison with experimental data

The available data allowed us to check the predictions of the model between the years 2001 and 2003.

From the samplings of years 2000 (without prolonged diapause) and 1999 (prolonged diapause of 1 year), we knew the proportion of seeds from which adults of *M. schimitscheki* emerged in may 2001. The female emergence began between the 5th and 7th of may 2001; it took place within a period of 11 days. Using the fructification and infestation rates, we were able to estimate the total number of emerging adults. These parameters, and the wind data, allowed us to compute the theoretical infestation rates of the harvest 2002. The experimental results were obtained in may 2003, during the adult emergence, which was measured in laboratory.

6.2.1 Position of the invasion front line

See Figure 6 for the comparison with experimental data.

The model predicted that the plantations of Sisteron and Lure were going to be infested. Indeed, the analysis of seed samples confirmed that Sisteron was the only plantation newly colonized by chalcids in 2001. In addition, a few chalcid-infested seeds were also collected at Lure during autumn 2002; i.e. corresponding to chalcid egg-laying having occurred in 2001. From the predictions of the model, the Gap, Saou, Barjac, Moulin and Saumon plantations were not supposed to become invaded. These results agreed with the experimental data. Moreover, the Ventoux, Aurel and Luberon plantations which were already infested before 2001 remained infested in both cases.

Thus, from the point of view of spreading, the model's results seemed to be coherent.

6.2.2 Attack rates

The only available data for the size of the cone crop were these of the plantations which were already colonized by *M. schimitscheki* in 1999 and 2001. Using the value of the size of the cone crop of 1999 and the infestation rates of 2001, we estimated the number of adults which were going to emerge in 2001. Implementing these data in the model, as well as the size of the cone crop of 2001, we computed the predicted infestation rates of the crop 2003. Figure 2

illustrates the numerical map which was used for the computations. The results of the model (**M**), the infestation rates of the seeds by adults of *M. schimitscheki* in 2003 (measured at emergence) (**S**), and the total rate of infested seed (**R**) (measured with X-rays) are plotted in Figure 7.

The curves corresponding respectively to the model’s predictions **M** and to the infestation rates **S** of *M. schimitscheki* have a very similar behaviour. **M** corresponds to the total rate of infested seeds, including the insects in prolonged diapause. This could partly justify the inequality $\mathbf{M} > \mathbf{S}$. Moreover, **R** remain very large compared to **S**, and even if the gap can partly be caused by the presence of *M. pinsapinis*, that may also be the consequence of a large amount of *M. schimitscheki* which remain in prolonged diapause. The curve **D** show the predicted infestation rates of the seeds by adults of *M. schimitscheki* in 2003, assuming that the prolonged diapause of the eggs of 2001 was $d_1 + d_2 = 60\%$. In that case, there is narrow relationship with the measured data.

7 Conclusions

Even if the results of Section 6 seemed encouraging, our model has some limits, especially in terms of forecasting. Indeed, the computation of the number of emerging insects on year n requires to know (i) the size of the cone crop of the years $\leq n - 2$ and (ii) the weather data of May of year $n - 2$. Thus, the forecasts can only be done over two years. However, as in Section 5, the dispersion of the insects under various conditions of wind and fructification can be studied, and some deductions on the role of some biological characteristics of *M. schimitscheki* can be made.

Test 1 suggested that the duration of the emergence period had no influence on the insects dispersal independently of the winds; however, in the case of variable winds, it could have a great incidence. Thus, in a real situation, where the winds direction and strength are time-dependent, a longer emergence period can result in a wider dispersal.

Next, Test 2 suggested that the presence of a prolonged diapause period could be an advantage in terms of propagation and survival, in the case of a “non-constant” environment. However, in the highly unlikely case of a constant fructification the position of the insects front line could be slightly delayed by the prolonged diapause. Note that the mortality rate was assumed to be 0 during the larval stage. In the case of a positive mortality rate, a prolonged diapause period could also be detrimental for the species.

Furthermore, Test 3 showed that the presence of some isolated trees between two plantations was not always an advantage in terms of species dispersal. It depends on the strength of the wind and on the insect’s characteristics (diffusion).

In addition to these theoretical results, we have carried out a new estimate of the diffusion coefficient.

Such reaction-diffusion models, but without advection term, have been successfully used in various situations of biological invasions (Kareiva 1983; Okubo 1980).

In the case of species which orient themselves toward external stimuli, or are carried by wind, the results obtained with models based on a reaction-diffusion-advection equation have given more mitigated results (Banks *et al.* 1987). However, in some situations, satisfactory results have been obtained in particular for the study of local dispersion phenomena. Banks *et al.* (1988) have successfully fitted some data of Hawkes (1972) on a cabbage root fly with such a model. This model included an advection vector, which was in opposition to the wind, giving the expected pattern if cabbage root flies travelled upwind when presented with host odors.

In the case of a species closely related to *M. schimitscheki*, which was also showing “passive” downwind flights, Jarry *et al.* (1997), have also obtained good results on a wider area, when forecasting the importance of annual seed orchard infestation by immigrating populations, coming from a limited number of surrounding populations.

In our work, we show that interesting results can also be carried out by reaction-diffusion-advection models at a larger scale and for an entire invasive population. Moreover, our study emphasizes that such an approach, where each specific biological process is considered separately, can provide a good tool to study the role of each characteristic of the modelled species.

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8 Figures

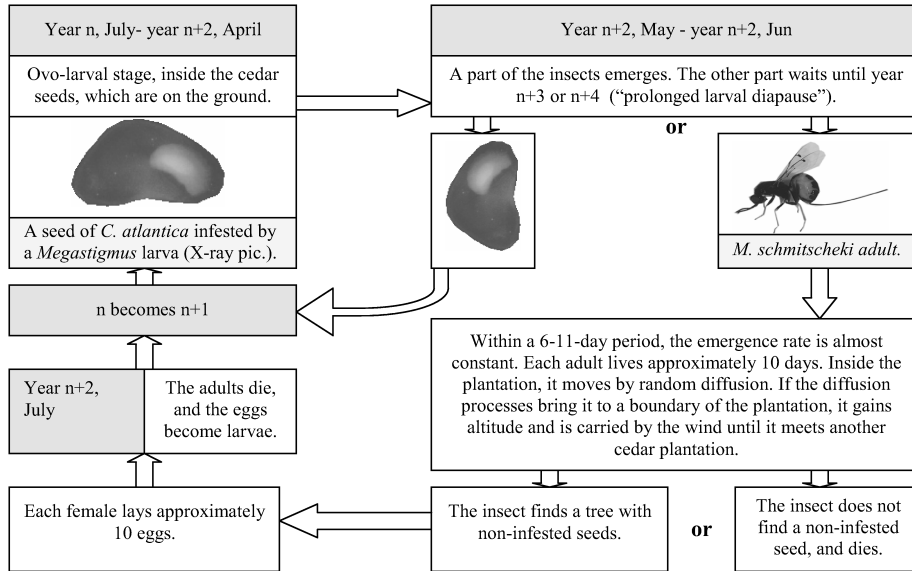


Figure 1: Simplified life cycle of *M. schimitscheki*

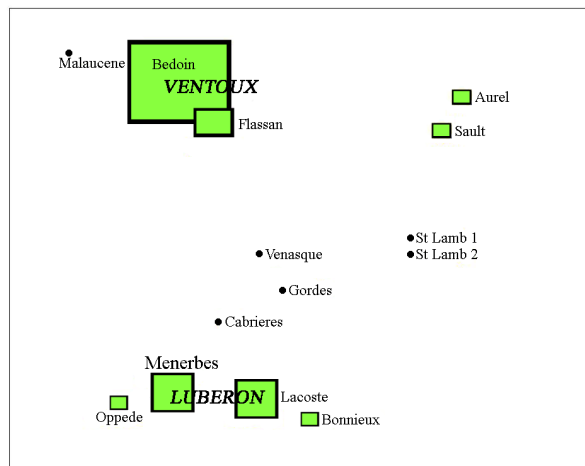


Figure 2: Numerical map which was used for the computations of the infestation rates.

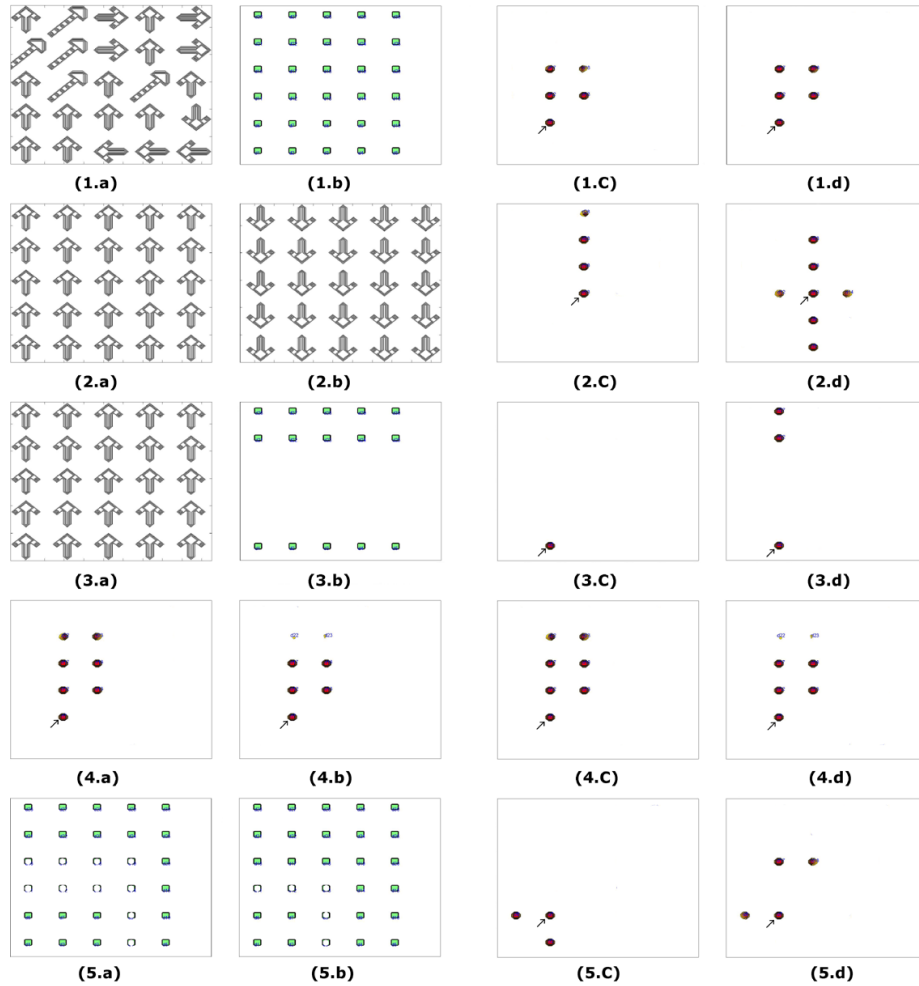


Figure 3: Numerical simulations. (1.a): wind profile of tests 1.1, 2.1, 2.2, 2.3, 3.1, 3.2; (1.b): distribution of the cedar plantations of tests 1.1, 1.2, 2.1, 2.2, 2.3; (1.c): result of test 1.1 for a 2-day emergence period; (1.d): result of test 1.1 for a 10-day emergence period; (2.a): wind profile during first 7 days of test 1.2; (2.b): wind profile of test 1.2 from day 8; (2.c): result of test 1.2 for a 5-day emergence period; (2.d): result of test 1.2 for a 10-day emergence period; (3.a): wind profile of test 1.3; (3.b): plantations distribution of test 1.3; (3.c): result of test 1.3 for a 5-day emergence period; (3.d): result of test 1.3 for a 10-day emergence period; (4.a): result of test 2.1 for an insect without prolonged diapause; (4.b): result of test 2.1 for an insect with prolonged diapause; (4.c): result of test 2.2 for an insect without prolonged diapause; (4.d): result of test 2.2 for an insect with prolonged diapause; (5.a): test 2.3, fructification of years 2 and 3; (5.b): test 2.3, fructification of years ≥ 4 ; (5.c): result of test 2.3 for an insect without prolonged diapause; (5.d): result of test 2.3 for an insect with prolonged diapause.

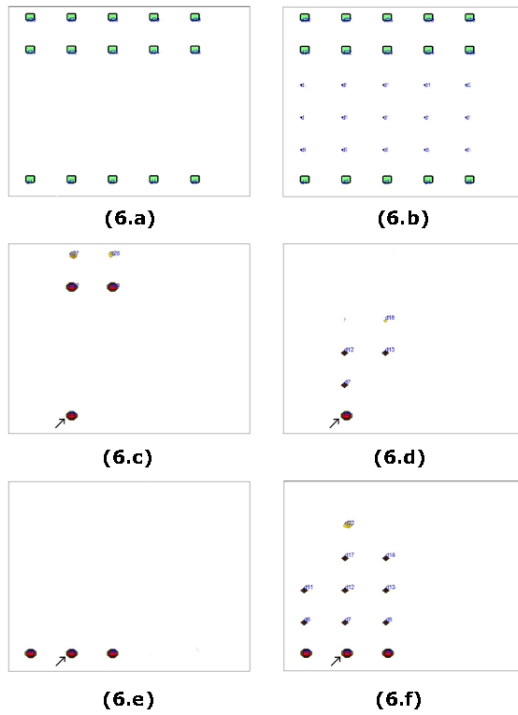


Figure 4: Numerical simulations. (6.a): distribution of the cedar plantations of tests 3.1, 3.2, case without isolated trees; (6.b): distribution of the cedar plantations of tests 3.1, 3.2, case with isolated trees; (6.c): result of test 3.1, case without isolated trees; (6.d): result of test 3.2, case with isolated trees; (6.e): result of test 3.2, case without isolated trees; (6.f): result of test 3.3, case with isolated trees;

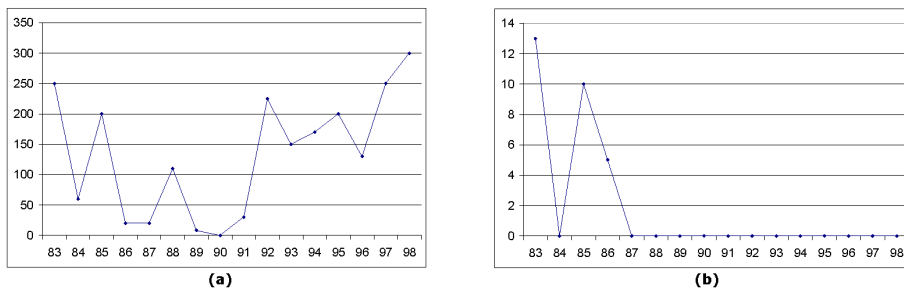


Figure 5: Variation in annual size of the cone crop (in hl) from 1983 to 1998 at the forests of (a) Mount Ventoux, and (b) Oppede.

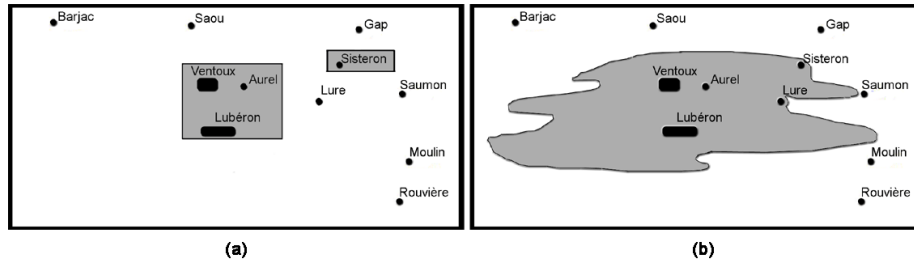


Figure 6: (a): Experimental estimation of the insect dispersal in Mai 2001, (b): Result of the model for the same period. The plantations that are inside the shaded zones are infested by *M. schimitscheki*.

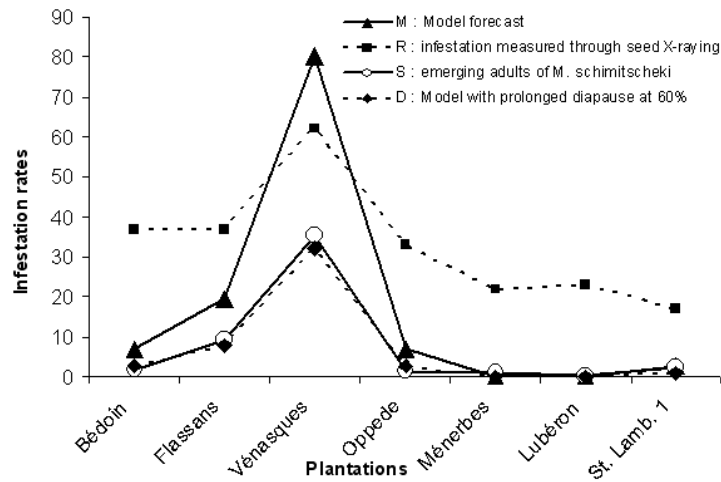


Figure 7: Comparison between the infestation rates forecasted by the model, the results of the X-ray analysis, the emergence rate of *M. schimitscheki*, and the results of the model for a total prolonged diapause rate of 60%.

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