

COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields

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ABSTRACT

A stochastic individual-based model called COSMOS was developed to simulate the epidemiology of banana weevil *Cosmopolites sordidus*, a major pest of banana fields. The model is based on simple rules of local movement of adults, egg laying of females, development and mortality, and infestation of larvae inside the banana plants. The biological parameters were estimated from the literature, and the model was validated at the small-plot scale. Simulated and observed distributions of attacks were similar except for five plots out of 18, using a Kolmogorov–Smirnov test. These exceptions may be explained by variation in predation of eggs and measurement error. An exhaustive sensitivity analysis using the Morris method showed that predation rate of eggs, demographic parameters of adults and mortality rate of larvae were the most influential parameters. COSMOS was therefore used to test different spatial arrangements of banana plants on the epidemiology of *C. sordidus*. Planting bananas in groups increased the time required to colonise plots but also the percentage of banana plants with severe attacks. Spatial heterogeneity of banana stages had no effect on time required to colonise plots but increased the mean level of attacks. Our model helps explain key factors of population dynamics and the epidemiology of this tropical pest.

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1. Introduction

Understanding the epidemiology of pests is of special importance for better management (Zadoks and Schein, 1979; Madden, 2006). The spatial component of epidemiology is a crucial element in the spread of damages from a localised inoculum or when pest dispersal is limited (Winkler and Heinken, 2007). Fecundity, mortality, and dispersal are the driving forces of insect epidemiology (Schowalter, 2006, p. 137). Pests can disperse heterogeneously (Lopes et al., 2007). The dispersal behaviour of mobile stages between each host plant contributes greatly to explaining variations of local densities of the species (Coombs and Rodriguez, 2007). In tropical and subtropical regions, where populations of plants and pests are not synchronised by severe winters, all stages of most insects are present simultaneously (Godfray and Hassell, 1987). In these conditions, all stages should be considered simultaneously to understand the distribution and abundance of organisms in the field. This approach is different from the ones in temperate regions, which focus on a particular part of the life cycle of

insects that is considered as a key point of spatial patterning and demography, such as attacks or dispersal behaviour of adults (e.g. Cain, 1985; Brewster et al., 1997), egg laying of females (Zu Dohna, 2006), or post-embryonic stages (egg or larva) (e.g. Johnson et al., 2007).

In this work, we took as case study the banana weevil *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Germar, 1825), a major pest of banana cropping systems. Larvae bore into the corm of banana plants and damage the points of insertion of primary roots, leading to plant snapping and toppling (Montellano, 1954; Gold et al., 2001). *C. sordidus* can contaminate new banana plantations through infested planting material or by means of adults that have survived since the last banana planting, because it has a long development time and life span, a low mortality rate, and is able to survive without food for extended periods (2–6 months) in moist environments (Gold et al., 2001). Adult weevils, which have limited dispersal abilities, can also invade new plantations from nearby plantations or from fallows when heavily infested banana plots are transformed into fallows (Gold et al., 2001). Banana plant stages may be heterogeneous in a plot, because plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner, 1994). This spatial heterogeneity of banana plant stages is likely to

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influence weevil population dynamics because of the influence of banana stage on female egg laying (Cuillé, 1950; Vilardebo, 1973). Based on these characteristics, we chose (i) a spatially explicit approach to understand how local movements influence the spatial distribution and damages of this pest in relation to its habitat and (ii) an individual-based modeling (IBM) approach to help explain observed population patterns (Winkler and Heinken, 2007), considering that different behaviours at the individual level can lead to the emergence of population-level properties (Grimm and Railsback, 2005). Modeling was considered as a good means to implement these approaches and an IBM was chosen as the modeling framework.

In this paper, we present the COSMOS model, aimed at simulating the spatial epidemiology of *C. sordidus* in the long-term by describing its population dynamics and the resulting infestation of host plants. The model considers all insect stages simultaneously and assumes there are individual variations in behaviour according to each developmental stage. We hypothesised that the distribution of *C. sordidus* populations and attacks in banana fields can be modelled according to epidemiological rules identified at an individual level and calibrated from the literature, with a model that is less parameter-demanding than most IBMs. The COSMOS model, like many IBMs, aims at bridging the gap between individual behavioural ecology and population dynamics (De Angelis and Gross, 1992). We validated COSMOS by comparing model outputs with field data, which is rarely done with most IBMs (Alderman and Hinsley, 2007; Charnell, 2008). Then, because sensitivity analyses are key steps of the modelling processes (Parry et al., 2006; Arrignon et al., 2007), we first conducted an exhaustive sensitivity analysis using the Morris method (Morris, 1991) to identify the most influential parameters in our model. In a second step, these parameters were studied in detail on an extended range of variation, including extreme values. Finally, we used COSMOS to test how planting patterns and the spatial heterogeneity of plant stages, resulting from the variability of sucker appearance over cropping cycles, could modify the time necessary to colonise the whole plot and the level of damage during three cropping cycles, when the initial weevil population was distributed along one side of the plantation.

2. Model description and parameterisation

2.1. General features of the COSMOS model

The COSMOS model is a stochastic IBM that runs on a daily time step. It simulates the local movement and egg laying of females in the field, infestation of larvae in banana plants, and the main features of insect and host plant development (Fig. 1). According to the model, individual *C. sordidus* disperse in a field that is represented by a grid with one banana plant per cell (grid area ranged between 144 and 441 m²). Plants pass through three distinct stages until harvest: maiden sucker, preflowering, post-flowering. Just before flowering, a new sucker of the mother plant is selected that grows simultaneously in the same cell. The time lag between two consecutive harvests, corresponding to a cropping cycle, is about 200 days (see Tixier et al. (2004) for details on banana cropping cycles).

C. sordidus females lay eggs on banana plants, and larvae issued from these eggs bore into the corm of the plants. The stage duration of juveniles and the phenologic stages of banana plants are temperature-dependent. In the COSMOS model, each *C. sordidus* is an autonomous individual that has a set of rules for egg laying and movement behaviour, depending on the plant stage at the insect's current position. Males do not cause damage, and no data are available on the influence of mating on egg laying. Therefore, males were excluded from the model.

A rule is an algorithm specified by the modeller to define a behaviour of individuals (Grimm and Railsback, 2005). The platform used to develop the model was the CORMAS (Common-pool Resource and Multi-Agents System) software (Bousquet et al. (1998); see <http://cormas.cirad.fr>), which is based on the Smalltalk object-oriented language (Visual Works 7.5, Cincom Softwares). The architecture of the model was developed in accordance with Ginot et al. (2002). Table 1 presents all the model parameters described below and their estimated values.

2.2. Dispersion

Eggs, larvae, and pupae cannot disperse between banana plants, and adults disperse slowly by crawling (Gold et al., 2001). Although the banana weevil has functional wings, most observers have reported that the weevil seldom, if ever, flies (Gold et al., 2001). In banana fields planted in monoculture (1500–2200 plants/ha, with standard planting distances of 2.4 m × 2.4 m), individuals do not search for food in a large area; their behaviour rather corresponds to an area-restricted search response type (Morris and Kareiva, 1991). The proportion of individuals that disperse to a given banana plant can be estimated as a negative exponential function of the distance to the plant (Schowalter, 2006). Adjusting the data of Delattre (1980) and Gold et al. (2001) to such a function, the probability (P) each time step of an adult moving to a given banana plant at distance d (in m) is the following (Eq. (1)):

$$P = 0.06 e^{-0.62 d} \quad (1)$$

2.3. Egg laying and longevity of adults

Once inseminated, *C. sordidus* females can stay gravid for 15 months without renewed mating (Cuillé, 1950; Treverrow et al., 1992). Authors disagree on the possible effect of age on egg laying (Gold et al., 2001). Yet it is agreed that egg laying depends mainly on two processes. First, egg laying probability and fecundity increase over banana phenologic stages (Cuillé, 1950; Vilardebo, 1973); the maximal probability of egg laying and fecundity occurs at the post-flowering stage, see Table 1 (Koppenhofer, 1993; Abera-Kalibata et al., 1999). Second, egg laying activity declines when the number of adults per plant increases (Cuillé, 1950; Koppenhofer, 1993; Abera-Kalibata et al., 1999).

In our model, mating and the effect of age on egg laying are not considered. Egg laying occurs for each female once a week, according to the period found in the literature (Koppenhofer, 1993), and follows a binomial distribution with a probability depending on the stage of the host plant (flowering, preflowering and maiden sucker) as estimated by Abera-Kalibata et al. (1999). If conditions for egg laying are fulfilled, the fecundity of each female is assumed to be Poisson-distributed (in accordance with Hilker et al. (2006)), with parameter equal to 2.7 if the adult density exceeds a given threshold (DE, Table 1) and 0.8 otherwise.

The maximal lifespan of adult of *C. sordidus* was estimated to be 748 days (Froggatt, 1925; Gold et al., 2001). The mortality rate of adults is often considered as constant during their lifespan (Godfray and Hassell, 1989; Berec, 2002; Potting et al., 2005). To our knowledge, no data are available on the predation rate of *C. sordidus* adults in the field.

Following Bousquet et al. (2001), MR was calculated assuming a discrete decreasing process, as a function of the maximum lifespan (ML , in days, Table 1; Eq. (2)). We assumed a high mortality rate (0.99) of adults from emergence to the maximum lifespan and a constant daily mortality (MR). The shape of the survival schedule exponentially decreases in those conditions and is convex (Carey,

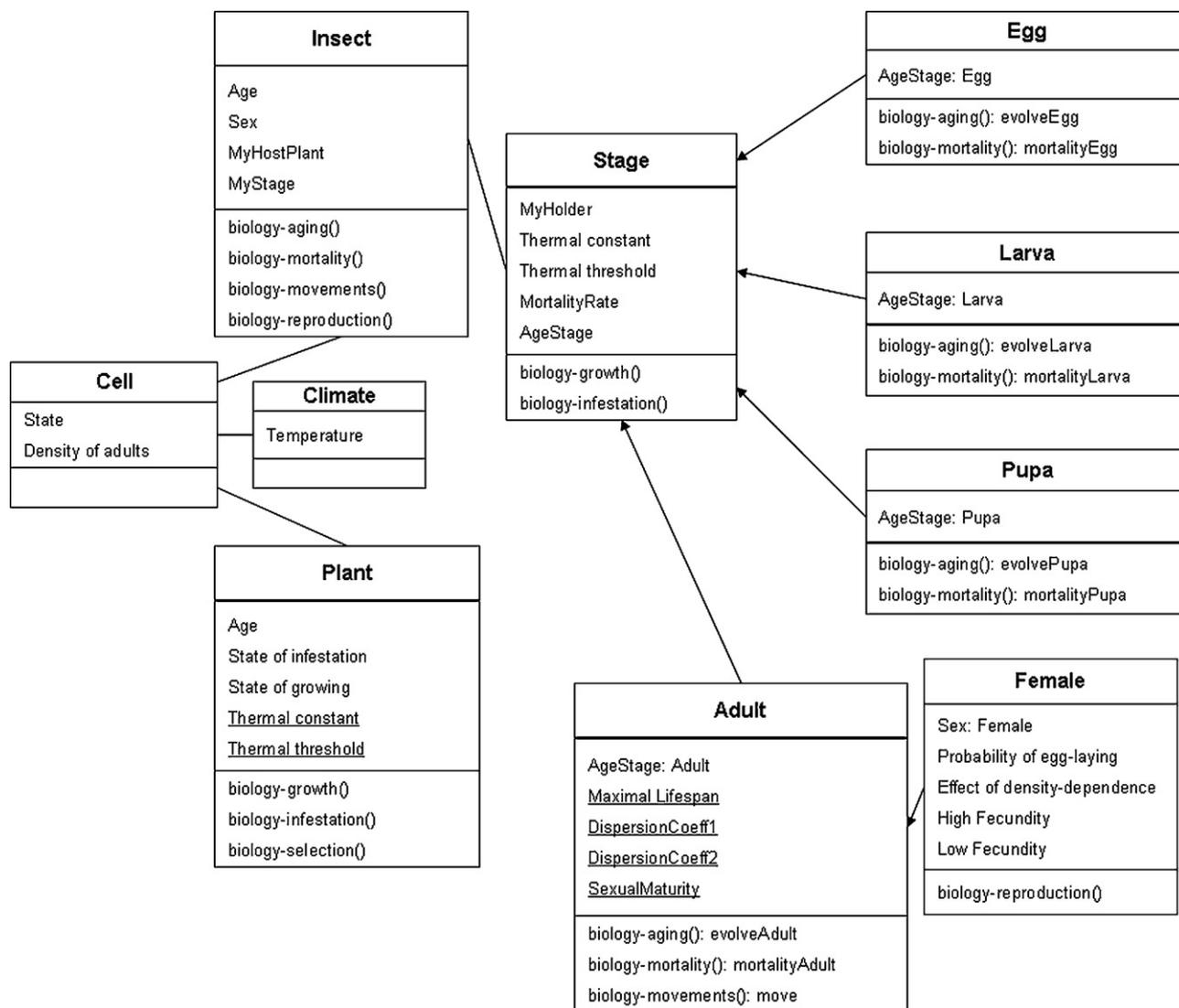


Fig. 1. Static structure of the spatially explicit model COSMOS in Unified Modeling Language (UML). Each box contains the name of a class in the first part, its key attributes in the second part, and the rules in the third part. For example, an individual of class Adult moves according to the rule `biology-movements()` and the key attributes `DispersionCoeff1` and `DispersionCoeff2`. Class attributes are shared for all the individuals of the class (underlined names) and instance attributes have a specific value for each instance (non-underlined names). Arrows between boxes signify inheritance, and simple links signify association. For example, an individual of class Adult inherits from class Stage and is associated with class Insect.

2001):

$$MR = 1 - (0.01)^{1/ML} \quad (2)$$

2.4. Development and mortality of immature stages

The development of *C. sordidus* is driven by temperature (Kiggundu et al., 2003a). Eggs, larvae, and pupae have different intrinsic mortality rates; larvae are the most susceptible stage (Traore et al., 1993, 1996; Kiggundu et al., 2003b). However, eggs laid on the surface of the corm are exposed to additional mortality by predators, e.g. ants (Koppenhofer, 1993; Abera-Kalibata et al., 2007, 2008). Mortality rates of immatures and additional mortality resulting from predators are shown in Table 1.

In the model, the physiological age for each juvenile stage i increases each day, at a rate determined by the difference between the daily temperature and a thermal threshold corresponding to stage i . Daily temperature was calculated as the mean between minimum and maximum temperature. Table 1 presents the thermal constants, i.e. the number of degree-days above the thermal

threshold required to complete development from stage i to the $i + 1$ th stage. Mortality at stage i follows a binomial distribution based on a constant mortality rate, because the literature gives only cumulative mortality rates at the end of each stage.

2.5. Development of banana plants

The thermal threshold for banana-plant development was estimated to be 14 °C (Ganry, 1980), and the duration in degree-days of each stage from planting to harvesting was determined by Abera-Kalibata (1997) and Tixier et al. (2004) (Table 1). In the COSMOS model, flowering rate follows a normal distribution (mean = 2350 degree-days; $\sigma = 200$ degree-days), adapted from Tixier et al. (2004). The sucker of the following cycle is selected after 2180 degree-days (Tixier et al., 2004).

2.6. Infestation of banana plants

Damage resulting from adult *C. sordidus* feeding is negligible compared to that resulting from larvae (Gold et al., 2001). When

Table 1
Model parameters, their values and ranges for sensitivity analyses, and corresponding references.

Description	Code	Value	Range used for the first sensitivity analysis	References
Egg				
Thermal constant to reach next stage (degree-days)	TCE	89	80.1–97.9	Gold et al. (2001)
Thermal threshold for development (°C)	TTE	12	10.8–13.2	Gold et al. (2001)
Mortality rate for eggs	MRE	0.11	0.09–0.12	Kiggundu et al. (2003a,b)
Proportion of eggs removed by predators	PE	0.6	0.33–0.68	Koppenhofer (1993) and Abera-Kalibata et al. (2008)
Larva				
Thermal constant to reach next stage (degree-days)	TCL	537.9	484.1–591.7	Traore et al. (1996)
Thermal threshold for development (°C)	TTL	8.8	7.9–9.7	Traore et al. (1996)
Mortality rate for larvae	MRL	0.48	0.32–0.64	Kiggundu et al. (2003a,b)
Diameter of gallery (in cm)	G	1	0.8–1.2	Montellano (1954) and Sponagel et al. (1995)
Pupa				
Thermal constant to reach next stage (degree-days)	TCP	120.7	108.6–132.8	Traore et al. (1996)
Thermal threshold for development (°C)	TTP	10.1	9.09–11.11	Traore et al. (1996)
Mortality rate for pupae	MRP	0.18	0.095–0.265	Traore et al. (1996)
Adult				
Sex-ratio (male:female)	–	1:1	–	Gold et al. (2001)
Sexual maturity for females after emergence (days)	SM	34.5	33–36	Cuillé (1950)
Probability of egg-laying on maiden sucker compared to flowered plants	OPMS	0.11	0.08–0.13	Estimated from Abera-Kalibata (1997)
Probability of egg-laying on preflowered plants compared to flowered plants	OPPF	0.41	0.39–0.46	Estimated from Abera-Kalibata (1997)
Number of adults per week necessary for density-dependent effect on fecundity	DE	20	10–33	Abera-Kalibata (1997)
Number of eggs per week per female without density-dependent effect	FH	2.7	1.7–3.2	Koppenhofer (1993)
Number of eggs per week per female with density-dependent effect	FL	0.8	0.6–1.1	Koppenhofer (1993)
Proportion of individuals moving 2 m per time step (%)	DC1	1.4	1.5–6.6	Delattre (1980)
Proportion of individuals moving 4 m per time step (%)	DC2	0.3	0.0–3.0	Delattre (1980)
Maximum lifespan of adult (days)	ML	748	520–900	Estimated from Froggatt (1925)
Banana plant				
Interval planting–maiden sucker (degree-days)	–	800	–	Estimated from Abera-Kalibata (1997)
Interval planting–preflowering (degree-days)		1600		Estimated from Abera-Kalibata (1997)
Interval planting–post-flowering (degree-days)		2350		Tixier et al. (2004)
Standard deviation for flowering rate (degree-days)		200		Adapted from Tixier et al. (2004)
Appearance of first sucker (degree-days)		2180		Tixier et al. (2004)
Interval planting–harvesting (degree-days)		3250		Tixier et al. (2004)
Thermal threshold (°C)		14		Ganry (1980)
Maximal circumference of plant at harvesting (cm)		60		

larvae are ready to pupate, they burrow toward the outer surface of the corm (Froggatt, 1925). The attacked circumference (AC), measured at the outer surface of the corm of each banana plant, is a common indicator of damage; it is assumed to be proportional to the number of galleries bored by the larvae. When the whole circumference of the corm is attacked, eggs and larvae die because of resource limitation (Koppenhofer and Seshu Reddy, 1994).

In the model, at each time step, the attacked circumference (AC) is estimated as the total number of larvae that have reached emergence multiplied by the mean diameter of a gallery (i.e. 1 cm

according to Montellano (1954) and Sponagel et al. (1995)). The maximum value of AC is equal to the maximum circumference of the banana plant at harvest.

3. Materials and methods

3.1. Field data

Damages of *C. sordidus* on banana plants were measured on 18 plots during two cropping cycles at the CIRAD experimental station,

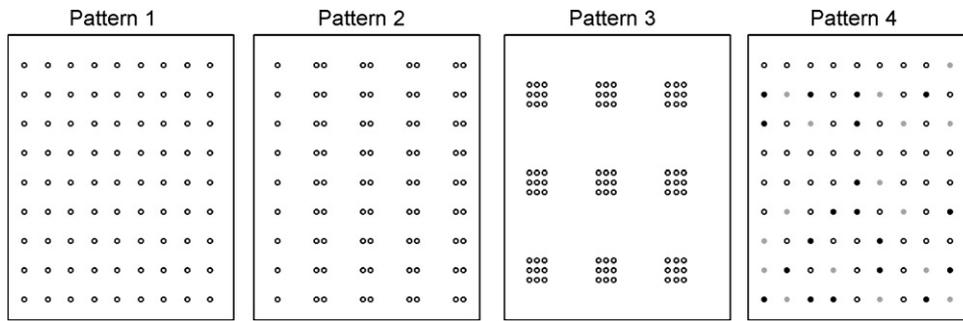


Fig. 2. Spatial arrangements of banana plants used in simulations: regular planting (1), double row planting (2), patch planting (3), regular planting with heterogeneity of banana stages (4). Color gradation figures from white to black the different banana stages from the youngest to the oldest, respectively. Planting density is 1750 plants/ha everywhere.

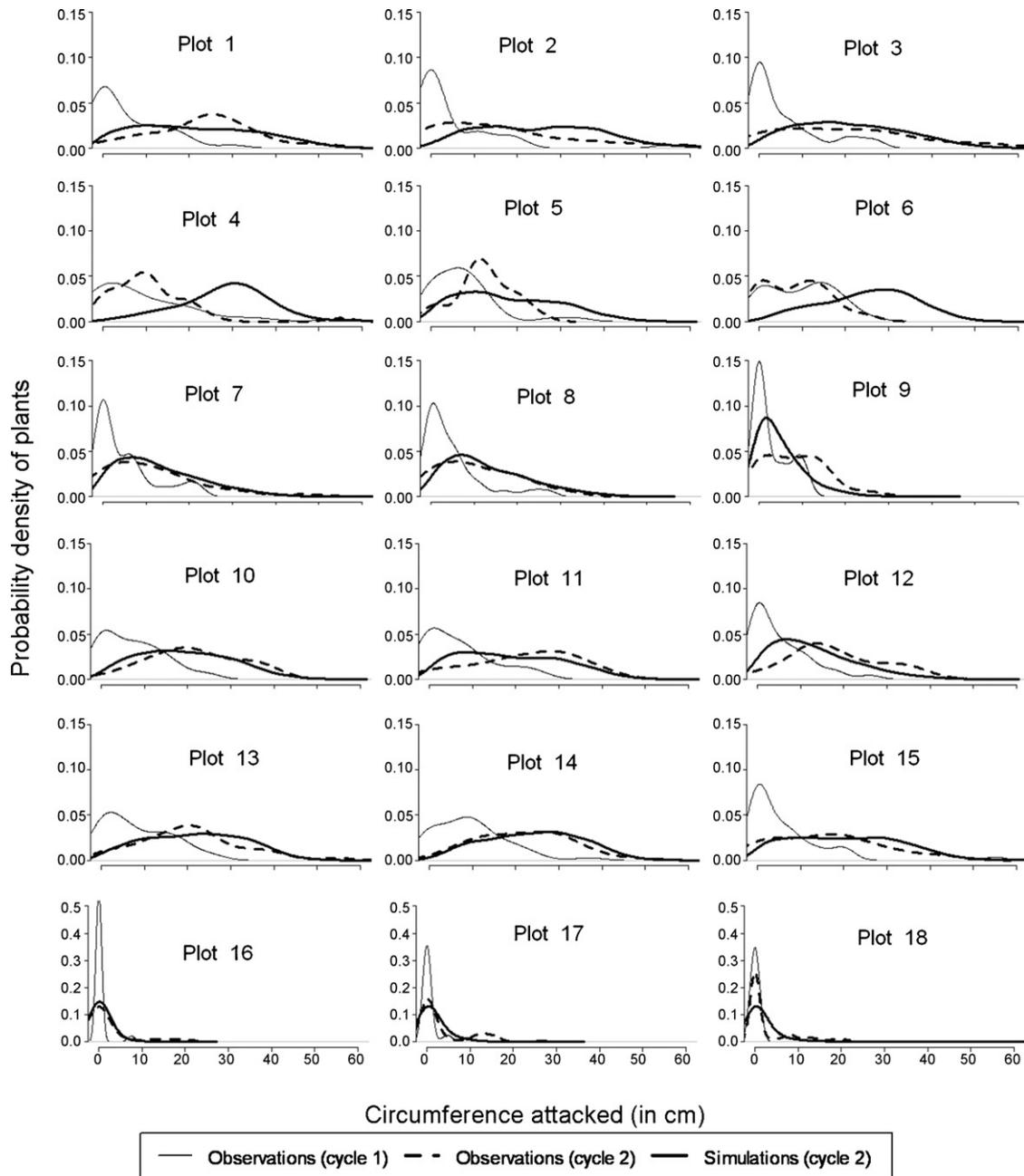


Fig. 3. Observed and simulated distribution of banana damages in 18 plots infested by *Cosmopolites sordidus* in Guadeloupe. Distributions are depicted by probability densities. Simulated probability densities were obtained over 100 runs for each plot. The solid thin line represents the distribution of attacks at the end of the first cycle (initialization). Bold lines represent the observed (dotted) and simulated (solid) distributions. Note that y-scale is different for plots 16–17–18.

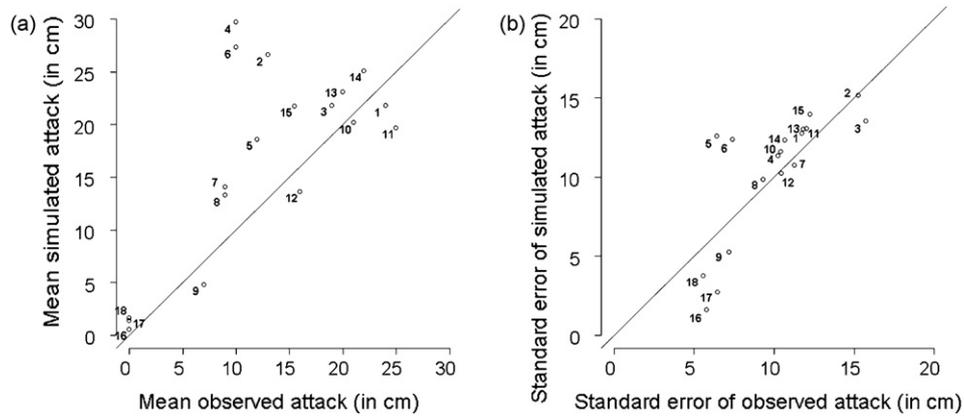


Fig. 4. Comparison of observed vs. simulated (a) mean and (b) standard deviation of distributions for each plot. Solid line indicates a perfect fit between observation and simulation. Numbers correspond to plot numbers.

Neufchâteau, Guadeloupe (French West Indies, 16°15'N, 61°32'W, altitude 250 m) between 1990 and 1995. The plots contained 30–42 banana plants (2174 plants/ha, *Musa* spp., AAA group cv. Cavendish Grande Naine) and were separated by a row without plants. Initial inoculums of *C. sordidus* arrived from previous banana crops. At each harvest, damages caused by larvae inside the corm were evaluated on each banana plant by removing 10 cm of topsoil around the corm and a band of tissue 7 cm wide and 0.5 cm deep across the corm at its widest point. The circumference of the corm with galleries was measured using a tape measure.

3.2. Simulation procedures

3.2.1. Model validation

The simulation area was a 15 × 15 to 18 × 21 cell grid (cell dimension: 0.8 m × 0.8 m), according to the number of banana plants in each field. Each banana plant belonged to one cell and was separated from other plants by two empty cells. Simulations were run

over 200 days, corresponding to the period between two consecutive harvests. Model inputs consisted of daily mean temperature from a five-year dataset and of initial populations (see below). Because of the model stochasticity, we performed 100 replicates for each situation and averaged the results.

For each of the 18 plots used for model validation, the model was initialised using populations of individuals distributed in the plot, estimated according to the attacks recorded at the end of the first cycle for each plant, i.e. the attacked circumference (AC). For this estimation, we first established a relation to calculate the number of adults per plant from AC using data from a capture-recapture study performed in a banana field in Neufchâteau (1996–1997). In this study, populations had been trapped using pseudostem traps (Gold et al., 2002), and AC had been measured for each banana plant. The ratio of the abundance of *C. sordidus* adults (square-root-transformed to stabilise the variance) to AC was 0.22 ± 0.07 ($F = 18.85$; $P < 0.01$; $df = 50$). Having calculated the number of adults at the end of the first cropping cycle in each cell of the 18 grids by

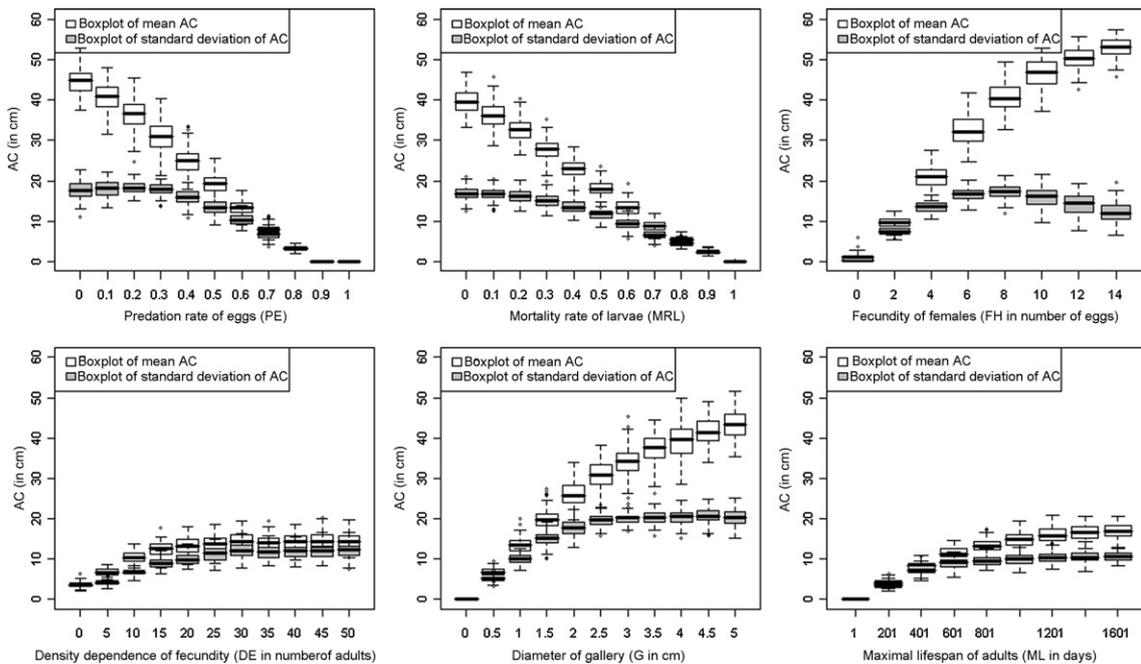


Fig. 5. Analyses of the COSMOS model sensitivity to the most influent insect biological parameters, focusing on two main parameters of the distribution of attacks on plot 8: mean (white boxes), standard deviation (grey boxes). A range of values was tested for each parameter, the other parameters being held constant. The output of 100 runs was computed in a boxplot. Each boxplot contains the lower whisker, the lower hinge (first quartile), the median, the upper hinge (third quartile) and the extreme of the upper whisker. The whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box.

using this ratio, we set the population age structure, using ratios of 0.24, 0.48, 0.10, and 0.18 for egg, larvae, pupae, and adults, respectively (Koppenhofer, 1993). Within each stage the age was considered to follow a uniform distribution. Then, the model simulated the epidemiology of *C. sordidus* during the second cropping cycle.

3.2.2. Simulation of spatial arrangements of banana plants

We simulated different spatial arrangements of banana plants thought to have an effect on the time necessary for *C. sordidus* to colonise a plot and to cause damage. First, we simulated three planting patterns with synchronous banana stages (Fig. 2): (1) regular planting (2.4 m × 2.4 m), (2) double row planting (0.8 or 4 m × 2.4 m) and (3) patches of nine banana plants (5.6 m × 5.6 m between each patch). The age of banana plants at initialisation was 1 month. Then, we simulated a regular planting pattern with asynchronous banana plant stages (4; Fig. 2), i.e. with different stages of plants in the same plot at the same time. In pattern 4, plant stages were randomly set from 1 month (planting) to 9 months (harvest); this situation is representative of old banana plots, which are unsynchronised because of the common practice of repeated sucker selection (Tixier et al., 2004; Lassoudière, 2007). For all patterns, 81 banana plants were distributed over a grid of 27 × 27 cells with a cell size of 0.8 m × 0.8 m, yielding a planting density of 1750 plants/ha.

At initialisation, different populations of adults of random age were equally distributed over the first column of the grid, representing the beginning of a rapid invasion due to putting an infested plot in fallow near the tested grid. For each pattern, we computed the time necessary for at least one adult to reach the column on the opposite side of the grid, the time-series of the mean intensity of attacks of each plant (AC), and the time-series of the percentage of plants with severe attacks (more than 20 cm of AC) over the entire period of simulation (600 days). Boundaries of grid were closed. Top and bottom edges represented a barrier; left edge the source of contamination that is unidirectional. As simulation stopped when one adult reached the last column of the grid, effect of right edge is absent. This experimental design allowed low edge effects, based on an infestation from one side to the other.

3.3. Sensitivity analyses

In a first step, we used the Morris method (Morris, 1991; Cariboni et al., 2007; see Appendix A) to discriminate the model parameters having the highest influence on the variability of mean and standard deviation of attacks, on four plots with different level of attacks (plots 8, 9, 10 and 16). Two ranges of parameter values were defined for this analysis, the first one corresponding to the uncertainty of estimates according to the literature, the other equally proportioned from –20 to 20% of the value in Table 1. Parameters equally discriminated using the two ranges were considered as the most influential.

In a second step, the parameters that were the most influential according to the first discrimination were tested one by one using a simple sensitivity analysis, the other parameter values being held constant. The model outputs were as before the variability of mean and standard deviation of attacks. For each parameter, different ranges of values were set, from 0 to 1 for biological rates and from 0 to an extreme value empirically defined (when model outputs no longer responded to parameter variations) for the other parameters. For each parameter value, 100 simulations were performed and the results arranged as boxplots showing the quartiles of the output distribution (Arrignon et al., 2007). For all the sensitivity analyses, plot 8 was chosen as representative of the studied plots, after examination of the first simulations (data not shown).

3.4. Statistical methods

For each plot used for model validation, smoothed distributions of the simulated attacks were plotted using 100 replicates of each simulation and compared with observations; this smoothing method is issued from Sheater and Jones (1991). Plotting smoothed distributions instead of histograms allow a better comparison between simulations and observations. The average distribution of the simulated attacks was compared to the observed attacks for each plot using the Kolmogorov–Smirnov (ks) test (Mellin et al., 2006). If the value of the probability associated to the ks test is greater than the level of significance (commonly 0.05), the null hypothesis of conformity (similar distributions) cannot be rejected. For each plot, the simulated mean and standard deviation of the distribution of attacks were compared to the observations over 100 replicates. The mean difference between observation and simulation was calculated using the root mean squared error (RMSE (Wallach and Goffinet, 1989)).

All statistical analyses were performed with the R software (R Development Core Team, 2008) using basic packages: “lattice” (for plotting the distributions of attacks using the kernel density estimate) and “sensitivity” (for sensitivity analysis using the Morris method).

4. Results

4.1. Model validation

Fig. 3 shows a good agreement between observed and simulated smoothed distributions of attacks for most plots. However, observed and simulated distributions were different for plots 2, 4, 6, 9, and 17 according to the Kolmogorov–Smirnov test ($P < 0.05$). For plots 2, 4, and 6, the model overestimated the frequency of high levels of attacks while it underestimated low levels of attacks (Fig. 4). For these plots, mean observed and simulated attack circumference (AC) were 10–15 and 25–30 cm, respectively. For plots 9 and 17, the model could not simulate the bimodal distribution of observed attacks. The model predicted well when the level of attacks at initialisation was relatively low (e.g. on plots 16 and 18, where the mean observed AC was 0 and 2 cm, respectively); and relatively high (plots 1, 11, 14, where the observed AC was 23–25 cm). The RMSE between the observed and simulated mean AC of the 18 plots was 7.7 cm; it improved when excluding plots 2, 4, and 6 (3.7 cm). The RMSE of the standard deviation was 2.6 cm for the 18 plots.

4.2. Sensitivity analysis

The Morris method showed that six parameters had a major influence on mean and standard deviation of the distribution of attacks: *DE*, *FH*, *ML*, *MRL*, *PE* (demographic parameters), and *G* (diameter of gallery; Appendix A, Table 1). Since the six parameters were similarly highlighted for the four tested plots, only the results for plot 8 were showed in Appendix A. *PE*, *MRL*, *G* and *FH* had a greater influence than *DE* and *ML*. On an extended range of variation, the increase in *PE* and *MRL* linearly decreased the mean level of attacks. The influence of *FH* (female fecundity) on the standard deviation of attacks decreased for more than eight eggs per week. For increasing values of *FH*, *DE*, *G*, and *ML*, the mean values of attacks increased linearly and then plateaued (Fig. 5).

4.3. Simulated effect of spatial arrangements of banana plants

The time necessary to cross the field was considerably higher for pattern 3 than for the other patterns, while a shorter time was found for pattern 4 (Table 2). This result remained the same when

Table 2

Time to cross the plot and mean level of attacks at 300 and 500 time steps for the four spatial arrangements of banana plants illustrated in Fig. 2 (initial population: 50 adults).

	Time to cross the plot (in days) \pm SE	Mean AC at 300 days (in cm) \pm SE	Mean AC at 500 days (in cm) \pm SE
Pattern 1	184 \pm 8	2.44 \pm 0.08	6.89 \pm 0.3
Pattern 2	197 \pm 8	2.41 \pm 0.09	7.03 \pm 0.2
Pattern 3	395 \pm 14	2.55 \pm 0.08	7.47 \pm 0.3
Pattern 4	170 \pm 7	6.22 \pm 0.16	16.24 \pm 0.46

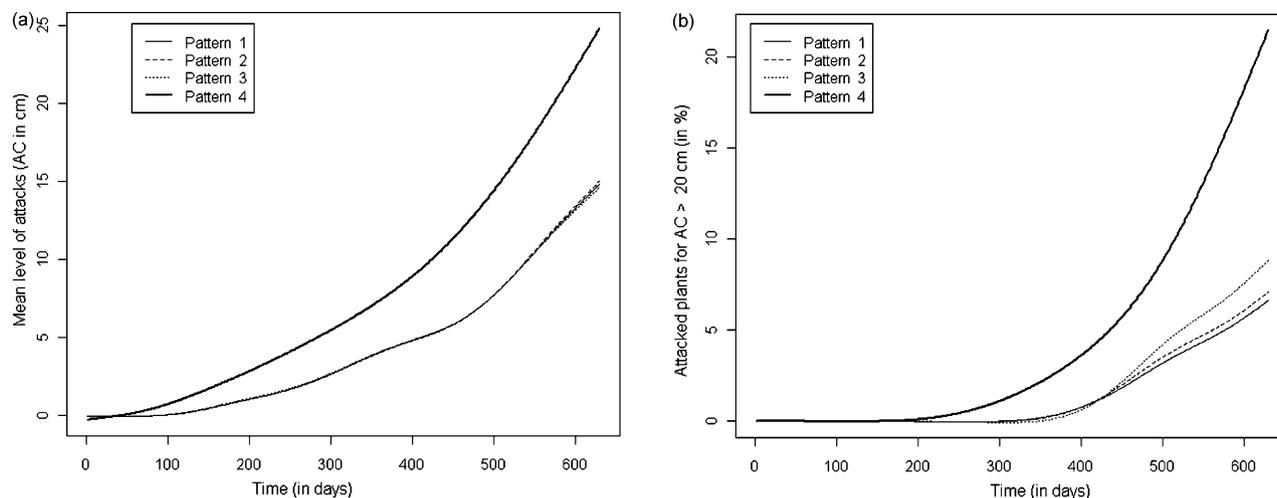


Fig. 6. Evolution of the mean intensity of attacks (a) and percentage of severe attacks (AC greater than 20 cm) (b), resulting from *C. sordidus* infestation of a plot. Initialization of the model was done for 50 individuals at one side of the plot, figuring a massive infestation from a neighboring field.

the initial population varied; times were reduced by half when the population varied from 50 to 400 individuals (data not shown). Mean levels of attacks at 300 days (harvest of first cycle) and 500 days (harvest of second cycle) were similar for planting patterns 1, 2 and 3 and twice as high for pattern 4.

Fig. 6 shows that the mean level of attacks increased to a higher level for pattern 4 than for patterns 1, 2, and 3. For patterns 1, 2, and 3, we observed a small inflexion of the mean level of attacks between 300–350 days and 500–550 days after planting (Fig. 6a). The percentage of plants with severe attacks (AC > 20 cm) increased faster for planting pattern 4, followed by patterns 3, 2, and 1 (Fig. 6b).

5. Discussion and conclusion

The individual-based COSMOS model accurately predicted the distributions of attacks of *C. sordidus* on banana plants for 13 out of 18 plots. This quality of prediction is attested for a large range of initial levels of attacks. The RMSE value of mean attacked circumference (7.7 cm) may be the consequence of overestimation of three validation plots and/or measurement error in the field. Furthermore, in the tested range of attacks, the standard deviation of the attacks in the plot was well maintained. Measurement error in the field could be due to an overlapping of some galleries in the same plant or to the presence of some galleries above or below the observation area. For three validation plots out of 18, the model overestimated the mean level of attacks. This overestimation could be explained by a greater predation of eggs in these plots than is accounted for by the model, predation of eggs being a major parameter according to the results of the sensitivity analyses. A highly variable density of *Pheidole* spp., a possible predator of *C. sordidus* eggs, was found among sites in a field trial in Uganda, ranging from 3.1 to 38.4 individuals per trap (Abera-Kalibata et al., 2008). Based on a recent survey in French West Indies, it seems that several species of ants are present in banana fields, including *Pheidole* spp. (Duyck, P.-F., pers. com.).

COSMOS compiles almost all of the existing knowledge about the biology of *C. sordidus*, benefiting from many experimental studies (Gold et al., 2001 and references therein). Nevertheless, our sensitivity analyses highlight the importance of better specifying key biological parameters to improve predictions, such as egg predation, adult mortality, and density-dependent effects. The level of egg predation is a key factor but is variable (Abera-Kalibata et al., 2008), which calls for further investigations. As explained by Carey (2001), little is known about mortality and longevity of insects, whereas they are fundamental epidemiological processes. The effect of density dependency of egg laying is also an influential parameter (Cuillé, 1950; Koppenhofer, 1993; Abera-Kalibata et al., 1999), but further studies should explore the whole range in which density dependency is established. It is also important to fill the lack of available data on predation rate of adults in the field, following the example of Sutherst et al. (2000) on ticks. For that purpose, field and laboratory experiments are currently conducted in French West Indies to identify the main predators of *C. sordidus*, and quantify their predation rates (Duyck, P.-F., pers. com.).

Our simulations on the effect of different spatial arrangements of banana plants on the epidemiology of *C. sordidus* show that planting in patches with a large distance between patches should limit the time necessary for the pest to colonise a new field. Indeed, in this case, only a small proportion of individuals is able to invade new patches. In contrast, the simulations indicate that the severity of attacks may increase when banana plants are planted in patches. Potting et al. (2005) in a modeling study on herbivores, found the same result, with a higher level of damages in patches than in rows. The pattern 3 figures patches with high concentration of plants. The hypothesis of resource concentration has been studied by Levine and Wetzler (1996). They have tested with an individual-based model the effect of planting decisions on attack frequencies by herbivorous insect pests, and they concluded that probability of host plant attack emerged partly as function of density of plants within patches. Furthermore, they estimate that probability of attack is function of radial distance

detection of host by insect. In COSMOS, radial detection is defined by weak dispersal abilities of adults, as defined by literature. These weak abilities contribute also to increase intensity of attacks inside patches. Planting banana regularly or in double rows resulted in similar simulated colonisation time and intensity of attacks. This is probably because in the case of double row spacing, the slow spreading of *C. sordidus* in large interstices between rows was compensated by fast spreading in small interstices inside rows. Unsynchronised banana plantation decreased the time of colonisation of the plot by *C. sordidus* and increased the severity of attacks. In this pattern, at every time step, *C. sordidus* can find stages of banana plant suitable for egg laying. In contrast for the other patterns, the inflexion of mean AC observed at $t=300$ – 350 days and $t=500$ – 550 days may be explained by the lack of stages of banana plant suitable for egg laying after harvest. For management purposes at the landscape scale, farmers should avoid transforming a heavily infested field into fallow close to an unsynchronised field free of *C. sordidus*. At the field scale, planting in patches would limit the time of colonisation but after two or three cropping cycles, attacks might be severe. Such a strategy might be suitable for cropping systems with a limited number of cropping cycles. For cropping systems with more cropping cycles, regular and double row planting patterns of plantation would be more suitable.

The choice of the model type is governed by both spatial characteristics of habitat and insect traits. In a spatial insect model figuring infestation of melon by aphids, Lopes et al. (Lopes et al., 2009) introduced space implicitly because they consider local movement as negligible. In that model, populations of aphids are described by partial differential equations, figuring the continuous development of populations. In our case, weak dispersal abilities of *C. sordidus* have required to introduce space explicitly. Populations of *C. sordidus* are described at individual level because of its discontinuous development and the presence of all stages with different behaviour at the same time. These results show that COSMOS is an interesting tool to design planting schemes for the control of banana weevil. IBM models have rarely been used for such purposes on pests. Generally, they have dealt with spatial heterogeneity as a means of controlling pests by simulating the incorporation of non-attractant crops in the field (Potting et al., 2005; Choi et al., 2006).

The basic principles of the epidemiology of *C. sordidus* were successfully integrated in the COSMOS model. Further steps in developing this model should consist of integrating more management practices able to influence the epidemiology of this pest and to contribute to Integrated Pest Management (Huffaker and Gutierrez,

1999, p. 682), such as the use of resistant varieties, traps, and biological control agents, as suggested by Gold et al. (2001). This could be done by designing a sub-model that accounts for trapping. For this, existing algorithms (Byers, 1993; Branco et al., 2006) may be adapted to COSMOS. Furthermore, to design IPM schemes at the farm scale, the next step will be to upscale the model to a group of fields and to account for interfaces between fields.

The COSMOS model, by capturing the population trend of a tropical pest, is a powerful tool to analyse population processes of this pest in various management conditions. COSMOS can be seen as a 'virtual laboratory' (Charnell, 2008) for studying different agricultural practices that can influence the epidemiology of a pest. Emergence of population spatial properties from individual biology is the main driver of our study, as we consider that these practices will influence the individual behaviour of pests. In that way, IBMs can be applied to several pests, for which the spatial heterogeneity of agricultural practices influences biological parameters of individuals.

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Appendix A.

Twenty biological parameters of the insect (k "factors", according to the Morris method) were tested, considering their possible influence on the variability of mean and standard deviation of attacks. Each tested range was divided into four levels, corresponding to the resolution (Δ) at which the factor was examined. Following the method, for each factor, one of the four possible levels was randomly chosen, leading to a first sample. A first sensitivity run was done on this sample that consisted of 100 replicates of a one cropping cycle (200 time steps) simulation (see Section 3.2); the results were further averaged over the 100 replicates. Starting from the first factor sample, similar sensitivity runs were performed by considering successively each factor and increasing (or decreasing) its value by the quantity Δ . The combination of these ($k+1$) sensitivity runs is called a trajectory and has to be repeated r times, thus leading to $r(k+1)$ sensitivity runs.

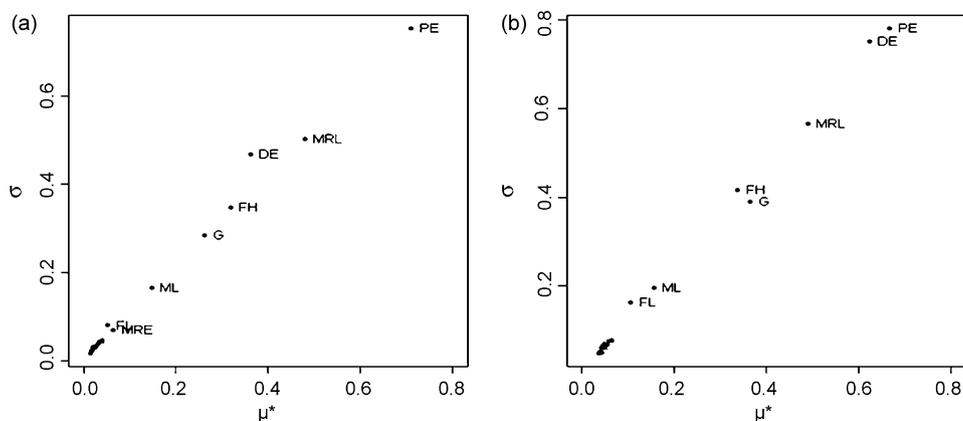


Fig. A.1. Sensitivity analysis on mean (a) and standard deviation (b) of attacks of *C. sordidus*. For each parameter, the tested range was defined according to the uncertainty of estimates according to published experimental studies.

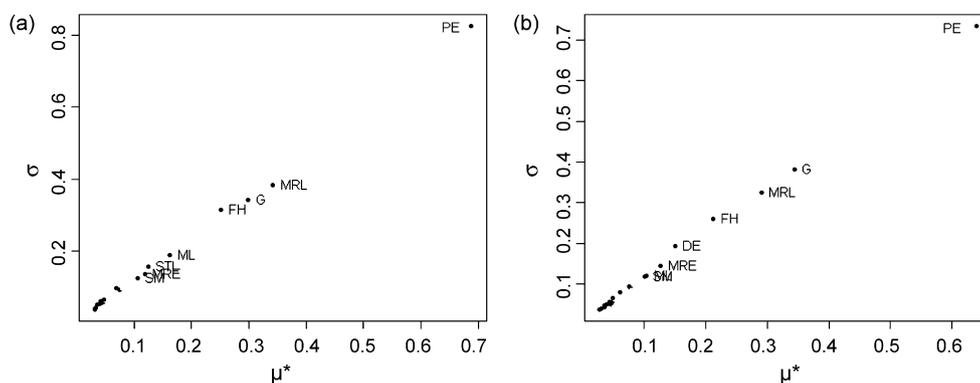


Fig. A.2. Sensitivity analysis on mean (a) and standard deviation (b) of attacks of *C. sordidus*. For each parameter, the tested range was equally proportioned (-20 , -10 , 10 , 20% of the value in Table 1).

The elementary effect (EE_i) of a parameter θ on a trajectory j was calculated as:

$$EE_{i,j}(\theta) = \frac{y_j(\theta + e_i \Delta) - y_j(\theta)}{\Delta} \quad (\text{A.1})$$

with $e_i = \pm 1$ and y_j the model output, here the mean or variance of attacks in the plot.

Thus, we generated a design experiment of 20 levels of parameters on 30 trajectories, which corresponded to a series of 630 sensitivity runs. The mean μ and the standard deviation σ of the absolute values of the elementary effects over the trajectories were used as sensitivity measures to ascertain the importance of the factors. A large μ indicates a large overall influence of the parameter and a large σ implies a dependency of the parameter on the value of the other parameters through non-linear or interaction effects (Figs. A.1 and A.2).

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