Modelling population dynamics of banana plant-parasitic nematodes: A contribution to the design of sustainable cropping systems

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ABSTRACT

This article describes the biological background, the model-building methodology and some applications of SIMBA-NEM, a new model to simulate the population dynamics of two major plant-parasitic nematode species of banana, *Radopholus similis* and *Pratylenchus coffeae*. For each species, each generation is represented by one cohort. Cohorts of the same species form a chain representing the developmental stages of nematodes. A logistic function describes population growth in relation with: (i) an environmental carrying capacity (K) that depends on available banana root biomass, (ii) an intrinsic growth rate (c) and (iii) competition between nematode species. Soil water content and the quantity of nematicides used are considered to be the main variables influencing the intrinsic population growth rate of each species. SIMBA-NEM was calibrated and validated using datasets from banana cropping systems in Guadeloupe (French West Indies). By analysing the sensitivity of the model to the main parameters and performing simulations of validation for various cropping systems (banana monoculture with or without nematicide applications use and a banana/sugarcane rotation) we were able to test the ability of the model to predict nematode population dynamics under a range of conditions. SIMBA-NEM is able to predict long-term nematode population size, while taking interspecific competition into account. It also helped to define knowledge gaps in nematology and modelling. SIMBA-NEM was used to optimise the effect of nematicide applications. SIMBA-NEM can already be a very helpful tool for designing sustainable and more environment-friendly banana cropping systems. In the SIMBA global crop-modelling environment, SIMBA-NEM is a key sub-model which provides essential information concerning the sustainability of the simulated system and thus permits planning environmentally friendly cropping systems.

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1. Introduction

As in many intensive agrosystems, banana monocultures in the French West Indies are hampered by major parasitic factors (plant-parasitic nematodes, insect pests and soil-borne fungi) that seriously threaten the sustainability of these systems by decreasing yield, causing plant toppling or requiring intensive pesticide use. In these regions, plant parasitism by

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nematodes is characterised by high biodiversity of the communities, with various levels of affinity and harmfulness to the banana hosts (Gowen and Quénéhervé, 1990). According to the authors, *Radopholus similis* and *Pratylenchus coffeae* are plant-parasitic nematodes that generate extensive root lesions, and they are considered to be among the most detrimental pathogens of banana. Their worst consequence is a loss of the plant's soil anchoring capacity due to breakage of damaged roots, which can cause plants to topple over. Necrosis also have harmful trophic effects such as a reduction in plant growth and extension of the vegetative period due to less efficient water and mineral uptake and transport by the roots (Seinhorst, 1981; Gowen and Quénéhervé, 1990; Fogain, 2000).

In French West Indies and in most areas of production of export banana, up to the last decade, management of plant-parasitic nematodes was mainly based on the used of chemical nematicide, a practice that can have a very detrimental effect on the environment (Hallberg, 1989; Leistra and Boesten, 1989). Crop rotations and improved fallows (Chabrier and Quénéhervé, 2003) have recently been introduced to temporarily reduce populations of plant-parasitic nematodes by removing the host plant (banana), which is replaced by non-host or poor-host plants. These techniques are efficient but still need to be improved and tailored to farmers' economic potential.

Cropping system models such as CROPSYST (Stöckle et al., 2003), STICS (Brisson et al., 1998) or DSSAT (Jones et al., 2003) have given rise to new simulation approaches because many biophysical variables of the system are simulated, e.g. soil characteristics or the biomass of various crop organs. However, plant parasitism is rarely taken into account in these models, although it is a key point for agronomic, ecological and economic sustainability (Kropff et al., 1995). Most often however, pest progress over time is simply introduced as a forcing function (van Ittersum et al., 2003).

To understand parasite population dynamics and to draw up efficient pest management programmes, it is essential to pool plant pathologists' knowledge. The development of a disease in an agrosystem can be considered as a variety of interactions between a host plant population and a parasite population, which are influenced by environmental factors and cropping practices. Such interactions first need to be defined and hierarchized in pathosystem studies. Pest and host population models help to formalize and quantify these interactions and define the dynamic aspects. One of the main aims of these models is to simulate how pests affect the crop, as done by Colbach and Huet (1995), who modelled the frequency and severity of root and foot diseases in winter wheat monocultures and used this model to design more sustainable cropping systems (Colbach et al., 1999). Plant-parasitic nematode populations and their damage have been simulated on potato by Ehwaeti et al. (2000), where an initial population, the intrinsic growth rate and the maximum population were used to predict the final population after one crop cycle. Generally, simulation of an organism whose life cycle is characterised by different developmental stages, such as insects (Deaton and Winebrake, 2000), requires the use of 'partial life models' or more complex models, such as 'matrix models' (Oli, 2003). Cohort models are usually used to represent the population dynamics of organisms that have different developmental stages (Hannon and Matthias, 1999).

This article describes the development of SIMBA-NEM, a model aimed at simulating the dynamics of populations of banana plant-parasitic nematodes at field scale, in relation to environmental factors and banana root system. The model needs to have a sufficient precision to be used as a decision tool for helping the plant-parasitic nematodes control. SIMBA-NEM is a population model based on a cohort structure, which describes nematodes stages. The growth of the population is assumed to follow a logistic function with an intrinsic growth rate and a carrying capacity. The carrying capacity depends on the banana root biomass. We considered the soil water content and the nematicide concentration as the environmental factors that modify the intrinsic growth rate. SIMBA-NEM takes into account the competition between the two simulated species of nematodes for banana root biomass. The structure of SIMBA-NEM is presented in Fig. 1.

2. Biological background and derived postulates for model construction

2.1. Biology and life cycle of banana plant-parasitic nematodes

In French West Indies, banana production is seriously hampered by biotic constraints, including soil-borne parasites. These involve a root parasite complex that combines plant-parasitic nematodes and soil-borne fungi, such as the primary parasite *Cylindrocladium spathiphylli* (Loridat, 1989; Risède and Simoneau, 2004). Plant-parasitic nematodes attack simultaneously the banana root system and thus constitute communities of multiple species with different feeding habits and pathogenicity. Within these communities, plant-parasitic nematodes that induce lesions are the most damaging and include *P. coffeae*, and especially *R. similis*, which is considered to be the most abundant species in French West Indies and the most detrimental for banana crops (Sarah, 1993). These species perforate the pecto-cellulosic wall of host plant root tissues with a retractile stylet; enter the root cortical parenchyma, where they settle in an intercellular position (Gowen and Quénéhervé, 1990). Most of their life-cycle occurs inside the root tissues. In Pratylenchideae species like *P. coffeae* or *R. similis*, females lay eggs about 3 weeks after their own egg stage, but this period is longer if the temperature and moisture conditions are not favourable (Gowen and Quénéhervé, 1990).

Little information is available about the true length of a nematode life-cycle. However, on the basis of laboratory observations, plant nematologists estimate that it lasts approximately 6 weeks (Quénéhervé, personal communication). We thus assumed that our nematodes are mature 3 weeks after hatching (Assumption 1) and that the length of their life-cycle is 6 weeks (Assumption 2).

2.2. Banana population dynamics and banana/nematode interactions

Banana crops (*Musa* spp., AAA group, cv. Cavendish Grande Naine) are herbaceous perennials whose root system is characterised by an underground rhizome and adventitious roots
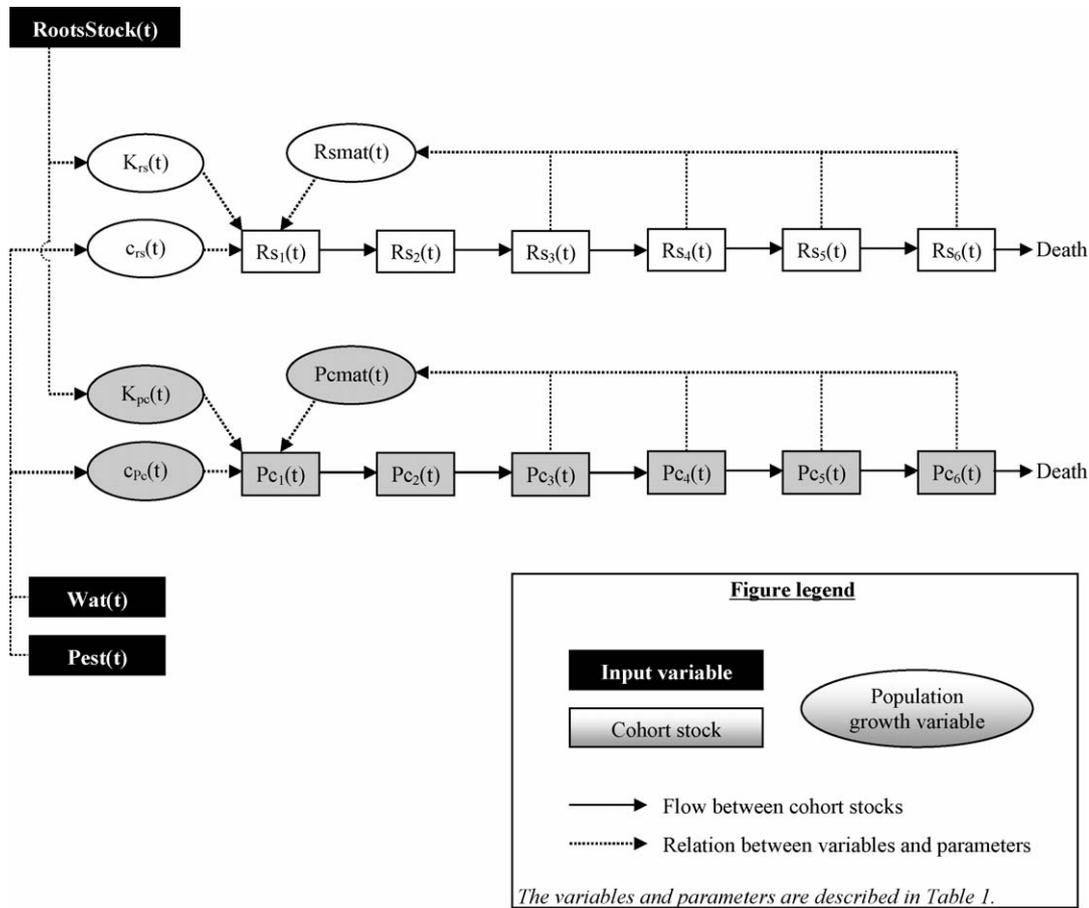
Fig. 1 – Structure of the SIMBA-NEM model. At each time step *t* of the model for each species, Rs$_i$(t) and Pc$_i$(t) represent the number of nematodes in cohort i, Rsmat(t) and Pcmat(t) represent the number of mature nematodes, K_{Rs}(t) and K_{Pc}(t) the carrying capacity and c_{Rs}(t) and c_{Pc}(t) the population growth parameter for *R. similis* (Rs) and *P. coffeae* (Pc) respectively and RootsStock(t), Wat(t) and Pest(t) represent the banana fresh root biomass, percentage of soil water and soil nematicide quantity, respectively.

and axillary buds (Turner, 1994). Roots are emitted mainly laterally, seldom vertically (Champion and Sioussaram, 1970). Axillary buds of the rhizome develop in lateral suckers. Root dynamics is characterised by successive flushes (Lavigne, 1987) in relation with shoot phenology. New roots are emitted until the flowering stage of the mother plant (Beugnon and Champion, 1966). Sucker roots are present and develop at the same time as those of the mother plant. The group of plants formed by the previous cycle plants, the actual mother plant and its suckers is called a 'mat'. In production conditions, only one sucker is usually selected per mat (the others are destroyed) and will become the mother plant for the next cropping cycle. Depending on sucker selection conditions (early or late), the number of suckers present at a given period of the cropping cycle may differ, thereby influencing overall banana root dynamics. The growth rate of banana roots depends on the physical and chemical properties of the soil, the age of the roots, and the root type (primary roots grow fast, secondary roots grow slower); the rate ranges from 1 to 5 cm/day (Lecompte et al., 2003). The spatial structure of the root system is also dependent on the physical and chemical properties of the soil (Delvaux and Guyot, 1989;

Lecompte et al., 2003). The root biomass of banana varies over time and depends on soil conditions, cultural practices (sucker selection) and plant population dynamics (Tixier et al., 2004a).

In a field, banana plants are managed individually and are not synchronised; after few cropping cycles, all developmental stages can consequently be present at the same time (Lassoudière, 1980). Physiological (root emission and growth), cultural (sucker selection) and structural (heterogeneity of developmental stages in a field) processes need to be integrated to characterise root dynamics on a field scale.

Quénéhervé (1989a,b, 1993) and Sarah (1986) showed that *R. similis* and *Helicotylenchus multicinctus* nematode populations on a banana plant can vary over time in line with banana root dynamics and the phenological stage of the mother plant, i.e. nematode populations grow until banana flowering, are stable during inflorescence development and decrease after bunch harvest. Nematode populations can be partially limited by reducing the total root biomass with chemical destruction of suckers (Mateille et al., 1984). It could thus be assumed that the plant-parasitic nematode carrying capacity of a field depends on total root biomass in the field (Assumption 3).

Hugon and Picard (1988) examined the behavioural patterns of nematodes when infesting, exploiting and destroying a banana root. They demonstrated that the most infested zones within a root are not those showing the most visible necrotic symptoms but rather their neighbouring zones that still appear healthy. This confirms that highly damaged roots are not used as a nutritional resource by plant-parasitic nematodes. In addition, it underlines the obligatory parasite status of these nematodes, which live and reproduce at the expense of living organic matter. Interspecific competition between plant-parasitic nematodes has been documented for different plant species (Duncan and Ferris, 1982; Shoener, 1983; Cadet and Debouzie, 1990; Umesh et al., 1994). For banana, Quénéhervé (1989a) demonstrated this competition between *R. similis*, *P. coffeae*, *H. multicintus* and *Hoplolaimus pararobustus*. Competition for the resource (feeding site) between these species leads to exclusion through a deterioration of the quality of the resource by other species. Plant-parasitic nematode species can be considered as being in competition for the banana root resource (Assumption 4).

Studies of *R. similis* and *P. coffeae* dynamics reported in the literature (Ganry, personal communication; Hugon et al., 1984; Quénéhervé, 1988, 1989a,b,c; Simon, personal communication) confirm that plant-parasitic nematodes of banana display population growth that follows logistics functions (Assumption 5). These dynamics can be characterised by an environmental carrying capacity (*K*) that is dependent on the root resource, the population of species in competition and the intrinsic growing rate (*c*). The growth rate is specific to each nematode species and to each cultivar of the banana. It may be affected by soil water content, soil temperature and quantity of nematicide in soil.

2.3. Influence of soil-climate conditions on plant-parasitic nematode population dynamics

Although roots can be considered as a protected (buffered) area for endoparasitic nematodes, environmental factors such as edaphic factors (soil texture and organic matter content) and soil climate (water content and temperature) have been shown to influence the dynamics of these nematodes (Hugon et al., 1984; Quénéhervé, 1988, 1989a,b,c). Fargette and Quénéhervé (1988) and Quénéhervé (1988) showed that variations in soil texture generated significant variations in nematode dynamics, and that light soil textures seemed to promote growth of nematode populations. Excess in soil water content and drought reduce nematodes population growth and affects their survival (Hugon et al., 1984; Mateille et al., 1988; Quénéhervé, 1988, 1989a,b,c; Vilardebo, 1984). The effect of water excess is enhanced in clayey soils, while drought is enhanced in light soils that infiltrate water fast. Soil temperature is also an important factor that could affect the nematode intrinsic growth rate (Hugon et al., 1984). In the geographical conditions of the study (tropical climate) the temperature amplitude is small (mean temperature at 250 m of altitude: 25.1 °C; standard deviation: 1.5 °C; maximum: 28.2 °C; minimum: 20.0 °C) but the rain variations are important (cumulated annual rainfall at 250 m of altitude: 3.05 m; maximum weekly rainfall: 0.25 m; minimum weekly rainfall: 0.00 m); hence we did not consider the temperature factor in this study.

Soil water content influence plant-parasitic nematode dynamics, i.e. over or under the optimum water content level, the nematode intrinsic growth rate decreases (Assumption 6).

2.4. Nematicide action on nematode populations

In intensive cropping conditions, nematode populations are mainly controlled by nematicide treatments (organophosphates and carbamates). These products have various effects on nematode physiology, i.e. they reduce reproduction (Cavelier, 1987; Bergé et al., 1980) and limit nematode root penetration. We assume that the quantity of nematicide in soil has a direct influence on the intrinsic growth rate of plant-parasitic nematodes (Assumption 7).

3. Material and methods

3.1. Model description

The structure of the model is based on a representation of nematode developmental stages by cohorts (Fig. 1). A cohort represents a pool of individuals at the same age in number of weeks. Successive cohorts are linked to each other and form a cohort chain. This cohort representation allows, at each step of the model, describing the age structure of the population of the simulated species. The variables and equations of the model are presented in Tables 1 and 2. On a field scale, *R. similis* and *P. coffeae* populations are characterised by two cohort chains that enabled the description of their different generations. SIMBA-NEM runs on a weekly time step t and all variables and parameters are considered according to that time step. The first cohort contained individuals of less than 1 week old. The model is based on six cohorts because all individuals died after 6 weeks. Mature individuals (cohorts 3, 4, 5 and 6 of each population) produce eggs that increment the first cohort. Egg production of each species follows a logistic function (Eqs. (4c) and (5c)), and is characterised by the carrying capacity $K_{Rs}(t)$ and $K_{Pc}(t)$ (maximum number of nematodes) and the intrinsic growth rate c_{Rs}pot and c_{Pc}pot. The total carrying capacity of the environment for the two species K_{nem}pot(t) is calculated with the banana root biomass RootsStock(t) and the maximal carrying capacity K_{nem}Max (Eq. (1)). The banana root biomass RootStock(t) varies over the simulation according to the growth of bananas. Carrying capacities $K_{Rs}(t)$ and $K_{Pc}(t)$ are calculated with the total carrying capacity K_{nem}pot(t) and to the total number of nematodes of other species Rstotal(t) and Pctotal(t) (Eqs. (2a) and (2b)). These equations describe the root resource sharing: e.g. the carrying capacity of *R. similis* at step t was equal to the total nematode carrying capacity at step t minus the total number of *P. coffeae* at step $t-1$. Eqs. (2a) and (2b) ensure that the sum of the total number of nematodes of both species never exceeds the total nematode carrying capacity.

The growth rates $c_{Rs}(t)$ and $c_{Pc}(t)$ are calculated at each step of the model using the intrinsic growth rate of each species c_{Rs}pot and c_{Pc}pot and correction factors relative to the soil water content and the quantity of nematicides in the soil (Eqs. (3a) and (3b)). The total population of nematodes is calculated in Eqs. (4a) and (5a). The logistic growth patterns correspond-

Table 1 – Variables and parameters of the SIMBA-NEM model, where t is the time step of the model (in weeks) and i is the cohort rank

	Meaning
Input variables	
$RootsStock(t)$	Banana root fresh biomass at step t ($g\,ha^{-1}$)
$Wat(t)$	Soil water content at step t in percentage of stock (%)
$Pest(t)$	Grams of nematicide active product in soil per hectare at step t ($g\,ha^{-1}$)
$Rs_1(1); Pc_1(1)$	Initial nematode number for Rs and Pc (in number of nematode per hectare, $nb\,ha^{-1}$)
Output variables	
$K_{nem}pot(t)$	Total carrying capacity in nematodes per hectare at step t (ha^{-1})
$K_{Rs}(t); K_{Pc}(t)$	Carrying capacity per hectare for Rs and Pc at step t (ha^{-1})
$c_{Rs}(t); c_{Pc}(t)$	Growth rate at step t for Rs and Pc
$FX_{pest}(t)$	Nematicide effect at step t
$FX_{wat}(t)$	Soil water content effect at step t
$Rs_i(t); Pc_i(t)$	Number of nematodes in cohort i per hectare at step t for Rs and Pc (ha^{-1})
$Rsmat(t); Pcmat(t)$	Total number of mature nematodes per hectare at step t for Rs and Pc (ha^{-1})
$Rstotal(t); Pctotal(t)$	Total number of nematodes per hectare at step t for Rs and Pc (ha^{-1})
$Rs(t); Pc(t)$	Nematode population per gram of root at step t for Rs and Pc (g^{-1})
Parameters	
$K_{nem}Max$	Maximum carrying capacity per gram of root (g^{-1})
$c_{Rs}pot; c_{Pc}pot$	Intrinsic growth rate for Rs and Pc
a_{pest}, b_{pest}	Parameters of the nematicide effect curve $FX_{pest}(t)$
$a_{wat}, b_{wat}, c_{wat}$	Parameters of the soil water content effect curve $FX_{wat}(t)$

Rs for *R. similis* and Pc for *P. coffeae*.

ing to new individuals (eggs) are shown in Eqs. (4c) and (5c). The passage of individuals from cohort i to cohort $i+1$ is described in Eqs. (4d) and (5d).

The effect of soil water content and the effect of nematicide are represented following to Assumptions 6 and 7. The nematicide effect on intrinsic growth rates $c_{Rs}(t)$ and $c_{Pc}(t)$ is accounted for through a corrective factor $FX_{pest}(t)$ ranging from 0 to 1, $FX_{pest}(t)$ follows a curve whose parameters are a_{pest} and b_{pest} (Eq. (7a)). The parameter a_{pest} define the quantity of nematicide at which the effect is maximum, and b_{pest} define the maximum reduction factor of the intrinsic growth rates.

The effect of the soil nematicide concentration on nematode population growth $FX_{pest}(t)$ is a linear response between the point of no effect, when nematicide concentration is nil, and the maximum reducing factor b_{pest} for nematicide concentration a_{pest} with maximum effect. The effect of soil water content on the intrinsic growth rates is accounted for through a corrective factor $FX_{wat}(t)$ ranging from 0 to 1, $FX_{wat}(t)$ follow a curve whose parameters are a_{wat}, b_{wat} and c_{wat} (Eq. (7b)). The parameter a_{wat} define the optimum soil water content, b_{wat} and c_{wat} are the maximum corrections for minimum and maximum soil water content respectively (drought and water

Table 2 – Equations of the SIMBA-NEM model, where t is the time step of the model (in weeks) and i is the cohort rank

Equations

$K_{nem}pot(t) = RootsStock(t) \times K_{nem}Max$	(1)
$K_{Rs}(t) = K_{nem}pot(t) - Pctotal(t-1)\,(\text{for } t > 1)$	(2a)
$K_{Pc}(t) = K_{nem}pot(t) - Rstotal(t-1)\,(\text{for } t > 1)$	(2b)
$c_{Rs}(t) = c_{Rs}pot \times FX_{pest}(t) \times FX_{wat}(t)$	(3a)
$c_{Pc}(t) = c_{Pc}pot \times FX_{pest}(t) \times FX_{wat}(t)$	(3b)
$Rstotal(t) = Rs_1(t) + Rs_2(t) + Rs_3(t) + Rs_4(t) + Rs_5(t) + Rs_6(t)$	(4a)
$Rsmat(t) = Rs_3(t) + Rs_4(t) + Rs_5(t) + Rs_6(t)$	(4b)
$Rs_1(t) = (c_{Rs}(t) \times Rsmat(t-1)) \times ((K_{Rs}(t) - Rstotal(t-1))/K_{Rs}(t))\,(\text{for } t > 1)$	(4c)
$Rs_i(t) = Rs_{i-1}(t-1)\,(\text{for } i > 1 \text{ and for } t > 1)$	(4d)
$Pctotal(t) = Pc_1(t) + Pc_2(t) + Pc_3(t) + Pc_4(t) + Pc_5(t) + Pc_6(t)$	(5a)
$Pcmat(t) = Pc_3(t) + Pc_4(t) + Pc_5(t) + Pc_6(t)$	(5b)
$Pc_1(t) = (c_{Pc}(t) \times Pcmat(t-1)) \times ((K_{Pc}(t) - Pctotal(t-1))/K_{Pc}(t))\,(\text{for } t > 1)$	(5c)
$Pc_i(t) = Pc_{i-1}(t-1)\,(\text{for } i > 1 \text{ and for } t > 1)$	(5d)
$Rs(t) = Rstotal(t)/RootsStock(t)$	(6a)
$Pc(t) = Pctotal(t)/RootsStock(t)$	(6b)
$FX_{pest}(t): \{\text{if } Pest(t) > a_{pest}\}, \{\text{then } b_{pest}\}, \{\text{otherwise}((b_{pest} - 1)/a_{pest}) \times Pest(t) + 1\}$	(7a)
$FX_{wat}(t): \{\text{if } Wat(t) < a_{wat}\}, \{\text{then } (((1 - b_{wat})/a_{wat}) \times Wat(t)) + b_{wat}\}, \{\text{otherwise}(((1 - c_{wat})/(a_{wat} - 1)) \times Wat(t)) + (c_{wat} - ((1 - c_{wat})/(a_{wat} - 1)))\}$	(7b)

For $t = 0$ $Pctotal(t-1)$ and $Rstotal(t-1)$ are considered equal to the initial nematodes populations. See Table 1 for variables and parameters description.

Table 3 – Presentation of all data used for calibration and validation of SIMBA-NEM

Field number	Species present	Dates of measurements	Number of data	Pesticides	Uses
1	Rs	15/05/77–05/03/78	28	No	Calibration
2	Rs	17/07/77–05/03/78	25	No	Calibration
3	Rs	07/12/88–28/08/89	11	Yes	Validation
4	Rs	28/06/88–08/07/91	22	Yes	Calibration
5	Rs	28/06/88–08/07/91	22	Yes	Calibration
6	Rs	28/06/88–08/07/91	22	Yes	Calibration
7	Pc	03/12/02–09/01/04	11	No	Calibration
8	Pc	03/12/02–09/01/04	11	No	Calibration
9	Pc	06/06/03–09/01/04	6	No	Calibration
10	Rs	20/08/03–28/11/03	8	No	Calibration
11	Rs and Pc	17/08/01–30/10/03	48	Yes	Validation

Datasets were constructed with the results of finished field experiments using nematicides (Aldicarb or Cadusaphos) or not (control), and with unpublished data derived from ongoing field experiments. For both species, the number of plant-parasitic nematodes was measured; extraction was carried out by the centrifugation–flotation method (Coolen and D'Herde, 1972).

excess). The effect of the soil water content on nematode population growth $FX_{wat}(t)$ is described by two linear responses between the optimum soil water content a_{wat} with no effect on nematode population growth, and the reducing factor b_{wat} for the nil soil water content and the reducing factor c_{wat} for a soil water content equal to 100%.

3.2. Experimental data

The data used for calibration and validation of SIMBA-NEM are derived from trials conducted to test the efficacy of nematicides in Guadeloupe between 1974 and 2004 (Table 3). The enumeration of each species of root plant-parasitic nematodes was carried out after extraction by the centrifugation–flotation method (Coolen and D'Herde, 1972). Nematode populations are expressed as the number of nematodes per gram of fresh root biomass. The intervals between measurements ranged from 1 week to 1 month. Datasets without nematicide applications were used to calibrate the model under optimum conditions, whereas datasets with nematicides were used to calibrate the effects of a nematicide application.

3.3. Calibration method

Parameters $c_{Rs}pot$, $c_{Pc}pot$ and $K_{nem}Max$ were calibrated separately for each studied nematode species and in situation with no nematicide application and non-limiting water content. The nematicide and soil water content effects were calibrated later. The datasets were used separately and then all the parameters were compared to obtain a calibration that was representative of the soil and climate situation.

The parameters and initial data used by SIMBA-NEM are given in Table 1. For each dataset, the initial number of nematodes for each species $Rs_1(1)$ and $Pc_1(1)$ was fixed to the first data of the dataset. The initial populations of each nematode species permits accounting the effect of the previous crop. The carrying capacity $K_{nem}pot$ was calibrated using the maximum value of each dataset. The intrinsic growth rates were calibrated using a procedure that minimised the mean square error between measured and simulated data (Wallach and Goffinet, 1989); they were calibrated separately for each species (in situations were only one nematode species was

present). The mean square error (MSE) and the root mean square error (RMSE) were calculated for each species in each simulation. The RMSE value provided information on the accuracy of the model for predicting the number of nematodes at each measurement point, in the same units as the model output (individuals per gram of fresh root). The curve parameters of the nematicide correction factor (a_{pest} and b_{pest}) and of the soil water content effect (a_{wat}, b_{wat} and c_{wat}) were also calibrated by reducing the mean square error between measured and simulated data.

3.4. Sensitivity analysis method

SIMBA-NEM has eight parameters and three input variables that have been estimated by measurements or by parameter fitting. The influence of parameters and inputs on outputs needs to be estimated in order to determine their degrees of accuracy. A sensitivity analysis was performed to estimate the influence of parameters or inputs on state variables or on model outputs. In the case of SIMBA-NEM, a simple output value is not sufficient to assess the accuracy of the model because the dynamics of the variables represent an important aspect of outputs. The sensitivity analysis has to take this aspect into account. We proposed a sensitivity analysis of dynamics whereby output values were presented at every time step of the model for each tested parameter value. For each tested parameter or input, three or four values included in its variation range were tested, while other parameters were set at the calibrated values. The analysis was performed under typical climatic conditions over a period of 50–70 weeks that was compatible with the tested phenomenon.

4. Results and discussion

4.1. Model calibration

Table 4 shows the mean and standard deviation for all the parameters of SIMBA-NEM, calculated with the fitted value for each dataset. The standard deviation is relatively high for the intrinsic growth rates ($c_{Rs}pot$ and $c_{Pc}pot$), which could be explained by the high variability in the measured values in

Table 4 – Presentation of model parameter values, standard deviations and the fields used for the calibration			
Parameter	Used fields	Mean value	Standard deviation
c_{Rs}pot	1; 2; 4	0.957	0.186
c_{Pc}pot	7; 8; 9	0.713	0.202
K_{nem}Max (g^{-1})	1; 2; 4; 7; 8; 9	521	59
a_{pest} (g ha^{-1})	4; 5; 6	1000	707
b_{pest}	4; 5; 6	0.1	0.0
a_{wat} (%)	10	0.4	–
b_{wat}	10	0.9	–
c_{wat}	10	1.0	–
The parameters are described in Table 1.			

similar conditions. The parameter a_{pest} has a large standard deviation but this needs to be compared to the variation range for the quantity of nematicide Pest(t) that could take values over 6000 g ha^{-1}.

The absence of replications and the difficulty in obtaining data considerably handicap studies on nematode population dynamics. This variability, however, is compatible with the overall goal of the model, i.e. to give an order of magnitude for nematode infestation over time.

4.2. Validation of SIMBA-NEM for two pest management strategies

SIMBA-NEM was validated in two situations: a banana monoculture with intensive use of nematicides and high rainfall (field 3), and a crop sequence involving banana after sugarcane with low use of nematicides and heterogeneous rainfall (field 11). These two situations were characterised by the initial number of nematodes in banana roots for each nematode species, nematicide use, soil humidity and the variation in banana root biomass. The banana monoculture was characterised by an absence of *P. coffeae* and a high initial population of *R. similis* in the banana roots. The case of banana after sugarcane was characterised by a high initial population of *P. coffeae* and a very small initial population of *R. similis*. Fig. 2 shows the simulated and measured populations of plant-parasitic nematodes per gram of fresh root biomass and the dynamics of banana fresh root biomass (g m^{-2}) for these two situations. RMSE values obtained for *R. similis* in "banana monocultures", *R. similis* and *P. coffeae* in "banana-after-sugarcane" cropping systems are 76 (*R. similis*), 63 (*R. similis*) and 118 (*P. coffeae*), respectively. These RMSE values are equal or less than 25% of the maximum observed values. It can be considered as a low accuracy, but this precision is enough to help the nematode population management because it allows determining the periods of low population, exponential growth or high population. The overall population dynamics is well simulated by the model, and the peaks of population of *R. similis* are correctly simulated as shown in weeks 48–52 and 72–75 (Fig. 2A) and in week 30 for populations of *P. coffeae* and *R. similis* (Fig. 2B). Furthermore, the rapid decrease of population due to nematicide application is well simulated in the period following the applications (week 48–52 and 114–116 (Fig. 2A and B, respectively). Additionally, this figure shows that the measured nematode populations and the banana root biomass follow the same trends. This is particularly noticeable when the populations
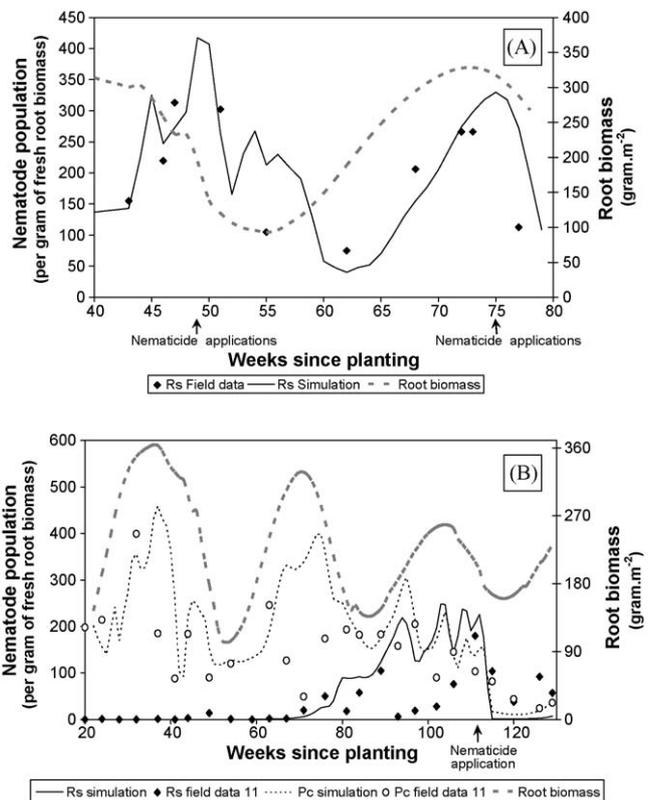

Fig. 2 – Measured and simulated time course variations in nematode densities of *R. similis* (Rs) and *P. coffeae* (Pc) expressed in number of nematodes per gram of fresh root biomass and the root biomass (g m^{-2}) for two pest management strategies, monocultures with pesticides (A) and banana after sugarcane with low pesticide inputs (B).

approach the carrying capacity (*R. similis* in Fig. 2A and *P. coffeae* in Fig. 2B). This corroborates Assumption 3 (plant-parasitic nematode carrying capacity depends on root biomass) made for the model construction.

4.3. Sensitivity analysis and limitations of the model

Fig. 3 presents the results of the sensitivity analysis for variations in c_{Rs}pot, K_{nem}pot, a_{pest}, and b_{pest}. These results show that population parameters (K_{nem}Max and c_{Rs}pot) have a substantial impact on nematode dynamics, while pesticide parameters (a_{pest}, and b_{pest}) have lower impact. When c_{Rs}pot
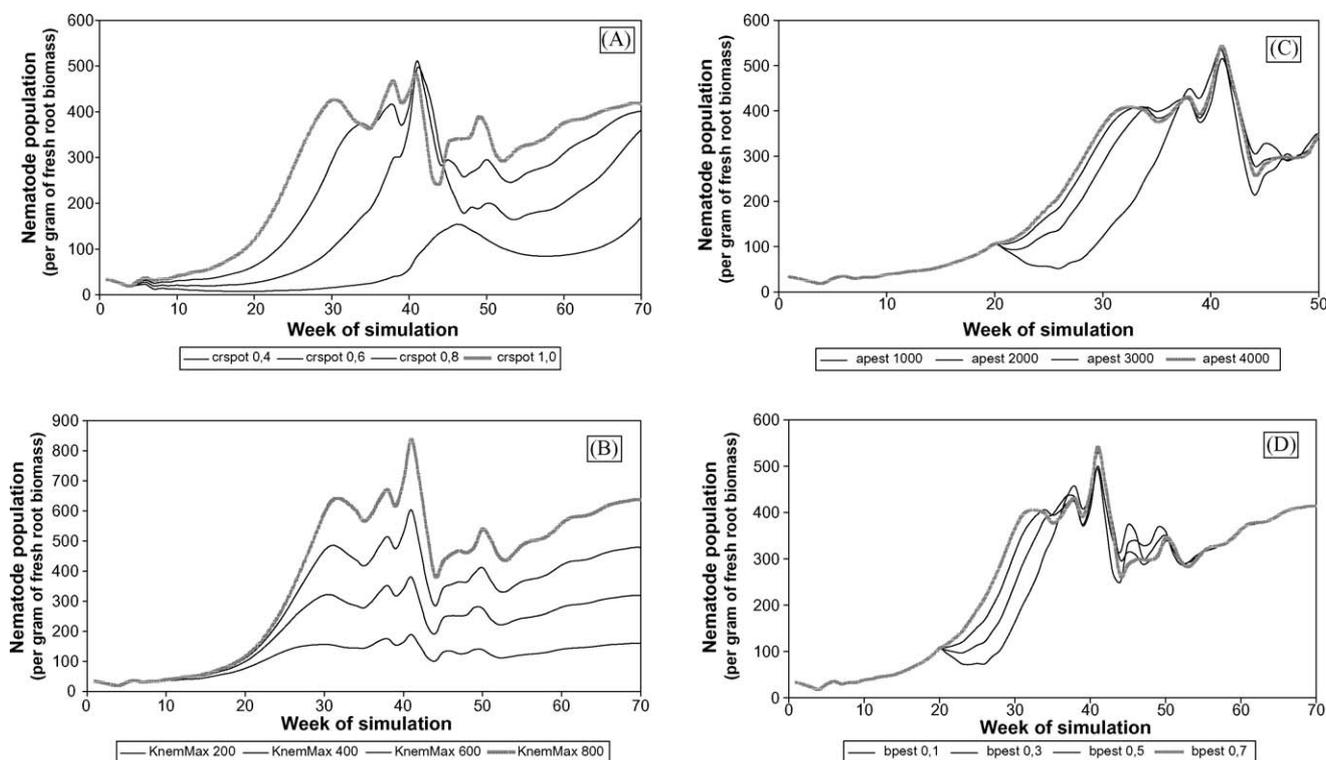
Fig. 3 – Simulation of R. similis nematode populations in a monospecies situation for different values of model parameters: c_{Rs}pot (A), K_{nem}Max (B), a_{pest} (C) and b_{pest} (D). In each analysis, untested parameters were set to their calibrated values. For (C) and (D) nematicide applications are realized in week 20.

increases, the population grows faster but is plateaued at the same level. When K_{nem}Max increases, the level at which the population is plateaued increase, but the time needed to reach this plateau is unchanged. The behaviour of the model to growth parameter variations follows an expected trend for a population model. For parameters related to the effect of pesticides, when a_{pest}, and b_{pest} (the quantity of nematicide at which the effect is maximum and the maximum reduction factor of the potential intrinsic growth rate, respectively) increase, the nematodes populations of are less reduced during the period following the nematicide application. It is noticeable that the calibrated values of parameters are included within intervals of values that are sensible for model's outputs.

4.4. Multispecies competition in long-term simulations

SIMBA-NEM was used to test different management strategies for plant-parasitic nematodes in the long term and the influence of the respective initial nematodes population level for both simulated species. Fig. 4 shows three simulations of R. similis population dynamics with the same R. similis initial nematode population but with three different P. coffeae initial populations. These simulations confirm that the model accurately accounted for interspecific competition for the root resource. This ability of the model may be very useful to help designing banana based cropping systems, where R. similis populations are controlled by crop rotations such as sugarcane, pineapple or other plants that are non-hosts or poor hosts for R. similis and where the initial population of

other plant-parasitic nematode species may be very important. SIMBA-NEM was able to simulate cropping systems with various initial situations. After many cropping cycles, the simulations indicate (as in Fig. 2) the coexistence of both simulated species, without any complete exclusion of one species. This is in line with our observations obtained in a long-standing banana field, where the root parasite complex included many nematode species. When a climax is reached, the ratio between the two simulated species is proportional to
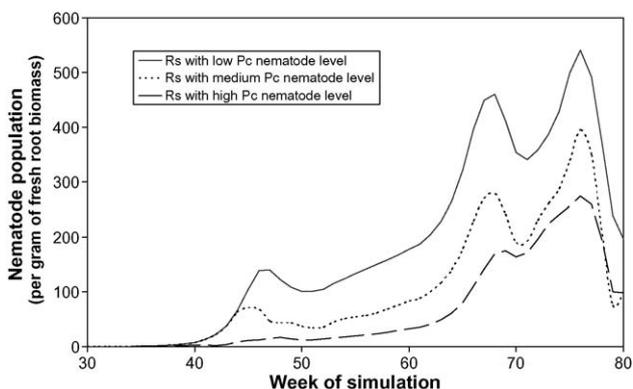

Fig. 4 – Simulations of R. similis populations with the same initial population (0.01 R. similis per gram) but with three different P. coffeae initial nematode populations (low: 0.00001 P. coffeae per gram; medium: 1 P. coffeae per gram; high: 100 P. coffeae per gram); both species were inoculated in week 7.

ratio between the two intrinsic growth rates. The correlation between parameters c_{Rs}pot and c_{Pc}pot is due to the fact that they partly represent their affinity for the host.

4.5. Optimisation of pest management strategies with SIMBA-NEM

We used SIMBA-NEM to optimise long-term nematicide applications in order to maximise their effects for a particular planting date and a specific soil and climate context. Over a 3-year simulation period (planting on January first and a mid-elevation climate), we tested conditional nematicide application rules where the R. similis population in banana roots is used as a control variable: when the R. similis population reaches a threshold, nematicide application is activated with a minimum interval between two applications of 12 weeks. We tested threshold values between 0 and 800 (nematodes per gram of fresh root biomass). The output values are the mean R. similis populations over the simulation period and the number of nematicide applications during the simulation. Table 5 shows, for each number of applications, the threshold that leads to the lowest R. similis population. SIMBA-NEM proved to be a powerful tool for tailoring nematicide applications to nematode populations. SIMBA-NEM help in choosing the best nematicide programme according to objectives, be they environmental (to reduce nematicide applications) or agronomic (to minimise R. similis populations).

We also used SIMBA-NEM to optimise the date of nematicide application in a 100-week simulation. Fig. 5 shows the mean R. similis population for each week of pesticide application (from 1 to 100) and the weekly R. similis population without nematicide application. Under these conditions, week 45 was found to be the best time to apply nematicides. This best period fits well with the time when nematode populations increase very fast, at the end of the pre-flowering period when root growth is maximum.

4.6. Comparison of SIMBA-NEM with other parasite models

Fabre et al. (2006) presented a stochastic population dynamics model of aphid Rhopalosiphum padi vector of Barley yellow dwarf virus (BYDV) vector in winter cereals. This model is based on a Bayesian statistical interference approach and use a density-independent exponential equation to describe
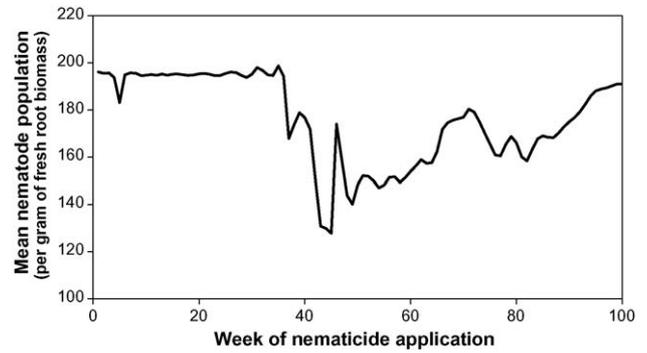

Fig. 5 – Mean R. similis population for each week of pesticide application (from 1 to 100) and the weekly R. similis population without nematicide application.

R. padi populations. The factor that affects the growth rate is the temperature. In SIMBA-NEM the main environmental factors affecting the growth rate are the soil water content and the presence of nematicide. This difference may be explained because in tropical conditions the temperature is relatively constant. Marín et al. (1998) proposed a model to simulate the population dynamics of Haematoloechus coloradensis, this fluke parasite includes three different hosts. Such a model highlights the importance of the population dynamics of hosts, as does SIMBA-NEM with banana root biomass. Also, as in SIMBA-NEM, these authors used a cohort approach to describe the different stages of H. coloradensis in its hosts. Multi-host parasite models are a complex case of parasite–host relation, on which the precision is relatively low but they can be used to examine effects of variation of initial population and of environmental factors on parasite population dynamics. The use of host–parasite models to highlight trends in population dynamics was also well shown by Salles et al. (2006) with a qualitative modelling approach of interactions between populations of ant's garden (ants, their cultivated fungi, bacteria, and a virulent parasitic fungus), these approaches complement the numerical models and permit to test different hypothesis without a complex calibration. Choi et al. (2004) presented a population model that simulates slug (Deroceras reticulatum) population dynamics according to climatic inputs. More recently, Choi et al. (2006) developed an individual based, spatially explicit, simulation framework

Table 5 – Optimisation, over a 3-year simulation, of the nematode population threshold to activate nematicide application. Presentation, for each total number of nematicide applications, of the optimum nematode threshold, and the associated mean R. similis population in banana roots (in number of nematodes per gram of fresh root biomass; g^{-1})

Number of nematicide applications	Nematode population threshold (g^{-1})	Mean weekly nematode population (g^{-1})
1	480	224
2	460	220
3	–	–
4	440	209
5	–	–
6	360	175
7	240	158
8	150	144
9	140	140

for *D. reticulatum* population dynamics, with a strong emphasis on environmental stochasticity, time delay and movement behaviour patterns of slugs. Such an improvement may present an interesting perspective for SIMBA-NEM, especially by accounting for the spatial variability of soil water content and for banana root biomass. Especially because the spatial arrangement of nematodes in roots around the banana mat can vary according to species biology and parasitism specificities (Quénéhervé, 1990). It can also be used to help designing diversified agro-ecosystems that manipulate the spatial dynamics of parasites by adding a trap crop that attracts and retains them in the non-crop area or by adding a disruptive crop that induces an emigration response as suggested by Potting et al. (2005) for herbivorous insects. Compared to other host–parasite model, SIMBA-NEM presents an original structure (cohort chains and logistic growth) that is particularly suitable for banana–nematode system because it takes into account competition between species of nematodes, the model structure recreate the nematode's biology and environmental factors are specifically implemented.

5. Conclusion

SIMBA-NEM should be considered as a model proposed for simulating nematode population dynamics, in relation to the host and to environmental factors. Undoubtedly it needs improving, especially by taking into account more environmental factors such as soil temperature or soil physical and chemical. These improvements of SIMBA-NEM should rise to the capacity to simulate wider range of soil and climate situations. Nevertheless SIMBA-NEM can already be a very helpful tool for designing sustainable and more environment-friendly banana cropping systems. SIMBA-NEM can also be used in a global cropping system modelling environment, called SIMBA, which includes sub-models that simulate plant growth, plant population structure, physical soil properties and water balance (Tixier et al., 2004b). In this global simulation context, SIMBA-NEM provides essential information on cropping system constraints, functioning and sustainability. In addition to conventional innovations such as cover crops, genetic improvement, etc., the model approach can jointly assess time-course patterns concerning cultural practices and the natural dynamics of the agrosystem in order to optimise yield, preserve soil fertility and minimise environmental risks. Pest dynamic models are rarely included in cropping system models or crop models, due to their complexity. Nevertheless, they are essential for prototyping more sustainable cropping systems. SIMBA-NEM will be used in the future to determine the best trade-off between nematicide use and environmental risks when linked to SIMBA and environmental assessment indicators. It could also be used to test biological hypotheses regarding competition between species, the role of root growth in nematode development, or other factors.

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REFERENCES

Bergé, J.B., Cuany, A., Bride, J.M., 1980. Mode d'action des nématicides. Phytiatrie-Phytopharm. 29, 149–160.

Beugnon, M., Champion, J., 1966. Etude sur les racines du bananier. Fruits 21, 309–327.

Brisson, N., Mary, B., Ripoche, D., Jeuffroy, M.H., Ruget, F., Nicoullaud, B., Gate, P., Devienne-Barret, F., Antonielli, R., Durr, C., Richard, G., Beaudoin, N., Recous, S., Tayot, X., Plenet, D., Cellier, P., Machet, J.M., Meynard, J.M., Delécolle, R., 1998. STICS: a generic model for the simulation of crops and their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. Agronomie 18, 311–346.

Cadet, P., Debouzie, D., 1990. Evolution spatio-temporelle d'un peuplement de nématodes parasites de la canne à sucre. Rev. Nématol. 13, 79–88.

Cavelier, A., 1987. Le mode d'action des nématicides non-fumigants. Agronomie 7, 747–762.

Chabrier, C., Quénéhervé, P., 2003. Control of the burrowing nematode (*Radopholus similis* Cobb) on banana: impact of the banana field destruction method on the efficiency of the following fallow. Crop. Prot. 22, 121–127.

Champion, J., Sioussaram, D., 1970. L'enracinement du bananier dans les conditions de la station de Neufchâteau (Guadeloupe). Fruits 25, 847–859.

Choi, Y.H., Powers, S., Bohan, D., Wiltshire, C., Glen, D., Semenov, M.A., 2004. Modelling *Deroceras reticulatum* (Gastropoda) population dynamics based on daily temperature and rainfall. Agric. Ecosyst. Environ. 103, 519–525.

Choi, Y.H., Bohana, D.A., Potting, R.P.J., Semenov, M.A., Glen, D.M., 2006. Individual based model of slug population and spatial dynamics. Ecol. Model. 190, 336–350.

Colbach, N., Huet, P., 1995. Modelling the frequency and severity of root and foot diseases in winter wheat monocultures. Eur. J. Agron. 4, 217–227.

Colbach, N., Meynard, J.-M., Duby, C., Huet, P., 1999. A dynamic model of the influence of rotation and crop management on the disease development of eyespot. Proposal of cropping systems with low disease risk. Crop. Prot. 18, 451–461.

Coolen, W.A., D'Herde, C.J. (Eds.), 1972. A Method for the Quantitative Extraction of Nematodes from Plant Tissue. Ministry of Agriculture of Belgium. Agricultural Research Administration, Belgium, p. 77.

Deaton, M.L., Winebrake, J.J., 2000. Modeling mobile source air pollution inventories. In: Deaton, M.L., Winbrake, J.J. (Eds.), Dynamic Modeling of Environmental Systems. Springer Verlag, New York, pp. 142–157.

Delvaux, B., Guyot, P., 1989. Caractérisation, de l'enracinement du bananier au champ. Incidences sur les relations sol-plante dans les bananeraies intensives de la Martinique. Fruits 44, 633–647.

Duncan, L.W., Ferris, H., 1982. Interactions between phytophagous nematodes. In: Freckman, D.W. (Ed.), Nematodes in Soil Ecosystems. University of Texas Press, Austin, pp. 29–51.

Ehwaeti, M.E., Elliott, M.J., McNicol, J.M., Phillips, M.S., Trudgill, D.L., 2000. Modelling nematode population growth and damage. Crop. Prot. 19, 739–745.

Fabre, F., Pierre, J.S., Dedryver, C.A., Plantegenest, M., 2006. Barley yellow dwarf disease risk assessment based on Bayesian

modelling of aphid population dynamics. Ecol. Model. 193, 457–466.

Fargette, M., Quénéhervé, P., 1988. Population of nematodes in soils under banana, cv. Poyo, in the Ivory Coast. 1. The nematofauna occurring in the banana producing areas. Rev. Nématol. 11, 239–244.

Fogain, R., 2000. Effect of Radopholus similis on plant growth and yield of plantain (Musa, AAB). Nematology 2, 129–133.

Gowen, S., Quénéhervé, P., 1990. Nematode parasites of bananas, plantains and acaba. In: Luc, M., Sikora, A., Bridge, J. (Eds.), Plant Parasitic Nematodes in Subtropical Agriculture. CAB International, pp. 431–460.

Hallberg, G.R., 1989. Pesticide pollution of groundwater in the humid United States. Agric. Ecosyst. Environ. 26, 299–367.

Hannon, B., Matthias, R., 1999. Multistage insect model. In: Hannon, B., Ruth, M. (Eds.), Modelling Dynamic Biological Systems. Springer Verlag, New York, pp. 170–180.

Hugon, R., Ganry, J., Berthe, G., 1984. Dynamique de population du nématode Radopholus similis en fonction du stade de développement du bananier et le climat. Fruits 39, 251–253.

Hugon, R., Picard, H., 1988. Relations spatiales entre taches et nécroses racinaires et nématodes endoparasites chez le bananier. Fruits 33, 491–498.

Jones, J.W., Hoogenboom, G., Porter, C.H., Boote, K.J., Batchelor, W.D., Hunt, L.A., Wilkens, P.W., Singh, U., Gijsman, A.J., Ritchie, J.T., 2003. The DSSAT cropping system model. Eur. J. Agron. 18, 235–265.

Kropff, M.J., Teng, P.S., Rabbinge, R., 1995. The challenge of linking pest and crop models. Agric. Syst. 49, 413–434.

Lassoudière, A., 1980. Comportement du bananier Poyo au second cycle. III. Etude d'une population. Fruits 35, 3–17.

Lavigne, C., 1987. Contribution à l'étude du système racinaire du bananier. Mise au point de rhizotrons et premiers résultats. Fruits 42, 265–271.

Lecompte, F., Ozier-Lafontaine, H., Pages, L., 2003. An analysis of growth rates and directions of growth of primary roots of field-grown banana trees in an andisol at three levels of soil compaction. Agronomie 23, 209–218.

Leistra, M., Boesten, J.J.T.I., 1989. Pesticide contamination of groundwater in western Europe. Agric. Ecosyst. Environ. 26, 369–389.

Loridat, P., 1989. Etude de la microflore fongique et des nématodes associés aux nécroses de l'appareil souterrain du bananier en Martinique. Mise en évidence du pouvoir pathogène du genre Cylindrocladium. Fruits 44, 587–597.

Marín, S.L., Grant, W.E., Dronen, N.O., 1998. Simulation of population dynamics of the parasite Haematoloechus coloradensis in its three host species: effects of environmental temperature and precipitation. Ecol. Model. 105, 185–211.

Mateille, T., Cadet, P., Quénéhervé, P., 1984. Influence du recépage du bananier Poyo sur le développement des populations de Radopholus similis et d'Helicotylenchus multicinctus. Rev. Nématol. 7, 355–361.

Mateille, T., Foncelle, B., Ferrer, H., 1988. Lutte contre les nématodes du bananier par submersion du sol. Rev. Nématol. 11, 235–238.

Olì, M.K., 2003. Partial life-cycle models: how good are they? Ecol. Model. 169, 313–325.

Potting, R.P.J., Perry, J.N., Powell, W., 2005. Insect behavioural ecology and other factors affecting the control efficacy of agro-ecosystem diversification strategies. Ecol. Model. 182, 199–216.

Quénéhervé, P., 1988. Population of nematodes in soils under banana, cv. Poyo, in the Ivory Coast. 2. Influence of soil texture, pH and organic matter in nematode populations. Rev. Nématol. 11, 245–251.

Quénéhervé, P., 1989a. Population of nematodes in soils under banana, cv. Poyo, in the Ivory Coast. 3. Seasonal dynamics of populations in mineral soil. Rev. Nématol. 12, 149–160.

Quénéhervé, P., 1989b. Population of nematodes in soils under banana, cv. Poyo, in the Ivory Coast. 4. Seasonal dynamics of populations in organic soil. Rev. Nématol. 12, 161–170.

Quénéhervé, P., 1989c. Population of nematodes in soils under banana, cv. Poyo, in the Ivory Coast. 5. Screening of nematicides and horticultural results. Rev. Nématol. 14, 231–249.

Quénéhervé, H., 1990. Spatial arrangement of nematodes around the banana plant in the Ivory Coast: related comments on the interaction among concomitant phytophagous nematodes. Acta Œcologica 11, 875–886.

Quénéhervé, P., 1993. Nematode management in intensive banana agrosystems: comments and outlook from the Côte d'Ivoire experience. Crop. Prot. 13, 164–172.

Risède, J.M., Simoneau, P., 2004. Pathogenic and genetic diversity of soilborne isolates of Cylindrocladium from banana cropping systems. Eur. J. Plant Pathol. 110, 139–154.

Salles, P., Bredeweg, B., Bensusan, N., 2006. The ants' garden: qualitative models of complex interactions between populations. Ecol. Model. 194, 90–101.

Sarah, J.L., 1986. Répartition spatiale des infestations racinaires de Radopholus similis (COBB) en relation avec la croissance et le développement du bananier Poyo en Côte d'Ivoire. Fruits 41, 427–435.

Sarah, J.L., 1993. Variabilité du pouvoir pathogène de Radopholus similis entre populations provenant de différentes zones de production du monde. Info Musa 2, 6.

Shoener, T.W., 1983. Field experiment on interspecific competition. Am. Nat. 122, 240–285.

Seinhorst, J.W., 1981. Water consumption of plants attacked by nematodes and mechanisms of growth reduction. Nematologica 27, 34–51.

Stöckle, C.O., Donatelli, M., Nelson, R., 2003. CropSyst, a cropping systems simulation model. Eur. J. Agron. 18, 289–307.

Tixier, P., Malézieux, E., Dorel, M., 2004a. SIMBA-POP: a cohort population model for long-term simulation of banana crop harvest. Ecol. Model. 180, 407–417.

Tixier, P., Malézieux, E., Dorel, M., Wery, J., 2004b. SIMBA: a comprehensive model for agro-ecological assessment and prototyping of banana based cropping systems. An application to the banana cropping systems in French West Indies. In: Proceedings of the Fourth International Crop Science Congress, Brisbane, September.

Turner, D.W., 1994. Banana and plantain. In: Environmental Physiology of Fruit Crops, vol. 2, No. 37–64. CRC Press, pp. 206–229.

Umesh, K.C., Ferris, H, Bayer, D.E., 1994. Competition between the plant-parasitic nematodes Pratylenchus neglectus and Meloidogyne chitwoodi. J. Nematol. 26, 286–295.

van Ittersum, M.K., Leffelaar, P.A., van Keulen, H., Kropff, M.J., Bastiaans, L., Goudriaan, J., 2003. On approaches and applications of the Wageningen crop models. Eur. J. Agron. 18, 201–234.

Vilardebo, A., 1984. Problèmes scientifiques posés par Radopholus similis et Cosmopolites sordidus en cultures bananières des zones francophones de production. Fruits 39, 227–233.

Wallach, D., Goffinet, B., 1989. Mean squared error of prediction as a criterion for evaluating and comparing system models. Ecol. Model. 44, 299–306.