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, \textit{Radopholus similis} and \textit{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...
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 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 (Stockle 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 characterized 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; Risede and Simonneau, 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 Pratylenchidae 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, $R_s(t)$ and $P_c(t)$ represent the number of nematodes in cohort $i$, $R_{smat}(t)$ and $P_{cmat}(t)$ 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 $\text{RootsStock}(t)$, $\text{Wat}(t)$ and $\text{Pest}(t)$ 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 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 (Lassoudièere, 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. multicinctus and Hoplolaimus pararobustus. Competition for the resource (feeding site) between these species leads to an exhaustion 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) examined the behavioural patterns of nematodes and 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 nematode 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 Kc(t) and Kc(t) (maximum number of nematodes) and the intrinsic growth rate cRspot and cRpot.

The total carrying capacity of the environment for the two species Kc(t) is calculated with the banana root biomass Rspot and the maximal carrying capacity Knc(t) (Eq. (1)). The banana root biomass Rspot(t) varies over the simulation according to the growth of bananas. Carrying capacities Kc(t) and Kc(t) are calculated with the total carrying capacity Kc(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 cR(t) and cR(t) are calculated at each step of the model using the intrinsic growth rate of each species cRpot and cRpot 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-
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 concentration on nematode population growth \( F_{\text{pest}}(t) \) is a linear response between the point of no effect, when nematicide concentration is nil, and the maximum reducing factor \( b_{\text{pest}} \) for nematicide concentration \( a_{\text{pest}} \) with maximum effect. The effect of soil water content on the intrinsic growth rates is accounted for through a corrective factor \( F_{\text{wat}}(t) \) ranging from 0 to 1, \( F_{\text{wat}}(t) \) follows a curve whose parameters are \( a_{\text{wat}} \) and \( b_{\text{wat}} \) (Eq. (7b)). The parameter \( a_{\text{wat}} \) define the optimum soil water content, \( b_{\text{wat}} \) and \( c_{\text{wat}} \) are the maximum corrections for minimum and maximum soil water content respectively (drought and water excess).

### 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

<table>
<thead>
<tr>
<th>Input variables</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>RootsStock((t))</td>
<td>Banana root fresh biomass at step ( t ) (g ha(^{-1}))</td>
</tr>
<tr>
<td>Wa((t))</td>
<td>Soil water content at step ( t ) in percentage of stock (%)</td>
</tr>
<tr>
<td>Pest((t))</td>
<td>Grams of nematicide active product in soil per hectare at step ( t ) (g ha(^{-1}))</td>
</tr>
<tr>
<td>Rs(<em>{1}(i)), Pc(</em>{1}(i))</td>
<td>Initial nematode number for Rs and Pc (in number of nematode per hectare, nb ha(^{-1}))</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Output variables</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K_{\text{smax}})pot((t))</td>
<td>Total carrying capacity in nematodes per hectare at step ( t ) (ha(^{-1}))</td>
</tr>
<tr>
<td>( K_{R_{\text{s}}}), ( K_{P_{\text{c}}})</td>
<td>Carrying capacity per hectare for Rs and Pc at step ( t ) (ha(^{-1}))</td>
</tr>
<tr>
<td>( c_{\text{bas}}), ( c_{\text{PC}})</td>
<td>Growth rate at step ( t ) for Rs and Pc</td>
</tr>
<tr>
<td>( F_{\text{Xpest}}(t))</td>
<td>Nematicide effect at step ( t )</td>
</tr>
<tr>
<td>( F_{\text{Xwat}}(t))</td>
<td>Soil water content effect at step ( t )</td>
</tr>
<tr>
<td>Rs(<em>{1}), Pc(</em>{1})</td>
<td>Number of nematodes in cohort ( i ) per hectare at step ( t ) for Rs and Pc (ha(^{-1}))</td>
</tr>
<tr>
<td>Rstotal((t)), Pctotal((t))</td>
<td>Total number of nematodes per hectare at step ( t ) for Rs and Pc (ha(^{-1}))</td>
</tr>
<tr>
<td>Rs(<em>{1}), Pc(</em>{1})</td>
<td>Nematode population per gram of root at step ( t ) for Rs and Pc (g(^{-1}))</td>
</tr>
</tbody>
</table>

### 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

<table>
<thead>
<tr>
<th>Equations</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K_{\text{smax}})pot((t) = \text{RootsStock}(t) \times K_{\text{smax}})Max</td>
<td>Maximum carrying capacity per gram of root (g(^{-1}))</td>
</tr>
<tr>
<td>( K_{R_{\text{s}}}) = ( K_{\text{smax}})pot((t) - \text{Pctotal}(t - 1) ) (for ( t &gt; 1 ))</td>
<td>Intrinsic growth rate for Rs and Pc</td>
</tr>
<tr>
<td>( K_{P_{\text{c}}}) = ( K_{\text{smax}})pot((t) - \text{Rstotal}(t - 1) ) (for ( t &gt; 1 ))</td>
<td>Parameters of the nematicide effect curve ( F_{\text{Xpest}}(t) )</td>
</tr>
<tr>
<td>( c_{\text{bas}}) = ( c_{\text{PC}}\pot \times F_{\text{Xpest}}(t) \times F_{\text{Xwat}}(t) )</td>
<td>Parameters of the soil water content effect curve ( F_{\text{Xwat}}(t) )</td>
</tr>
</tbody>
</table>

\( Rs_{1}, Pc_{1} = \) Parameters of the soil water content effect curve \( F_{\text{Xwat}}(t) \)

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.
The effect of the soil water content on nematode population growth $F_{\text{wat}}(t)$ is described by two linear responses between the optimum soil water content $a_{\text{wat}}$ with no effect on nematode population growth, and the reducing factor $b_{\text{wat}}$ for the nil soil water content and the reducing factor $c_{\text{wat}}$ 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–floation 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 $c_{\text{Rspot}}, c_{\text{Pcpot}}$ and $K_{\text{emMax}}$ 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 $R_{s_1}(1)$ and $P_{c_1}(1)$ 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 $K_{\text{empot}}$ 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 ($k_{\text{pest}}$ and $b_{\text{pest}}$) and of the soil water content effect ($a_{\text{wat}}, b_{\text{wat}}$ and $c_{\text{wat}}$) 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 ($c_{\text{Rspot}}$ and $c_{\text{Pcpot}}$), which could be explained by the high variability in the measured values in

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

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–floation method (Coolen and D’Herde, 1972).
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 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 $c_{Rspot}$, $K_{nemMax}$, $a_{pest}$, and $b_{pest}$. These results show that population parameters ($K_{nemMax}$ and $c_{Rpot}$) have a substantial impact on nematode dynamics, while pesticide parameters ($a_{pest}$ and $b_{pest}$) have lower impact. When $c_{Rpot}$
increases, the population grows faster but is plateaued at the same level. When \( K_{\text{nemMax}} \) 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 \( a_{\text{pest}} \), and \( b_{\text{pest}} \) (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 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...
ratio between the two intrinsic growth rates. The correlation between parameters $c_{R'}$ and $c_{R''}$ 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 $R. padi$ 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$^{-1}$)

<table>
<thead>
<tr>
<th>Number of nematicide applications</th>
<th>Nematode population threshold (g$^{-1}$)</th>
<th>Mean weekly nematode population (g$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>480</td>
<td>224</td>
</tr>
<tr>
<td>2</td>
<td>460</td>
<td>220</td>
</tr>
<tr>
<td>3</td>
<td>–</td>
<td>–</td>
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<tr>
<td>4</td>
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<td>150</td>
<td>144</td>
</tr>
<tr>
<td>9</td>
<td>140</td>
<td>140</td>
</tr>
</tbody>
</table>

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.
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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