

Generalized Linear Dynamics of a Plant-Parasitic Nematode Population and the Economic Evaluation of Crop Rotations

W. VAN DEN BERG¹ AND W. A. H. ROSSING²

Abstract: In 1-year experiments, the final population density of nematodes is usually modeled as a function of initial density. Often, estimation of the parameters is precarious because nematode measurements, although laborious and expensive, are imprecise and the range in initial densities may be small. The estimation procedure can be improved by using orthogonal regression with a parameter for initial density on each experimental unit. In multi-year experiments parameters of a dynamic model can be estimated with optimization techniques like simulated annealing or Bayesian methods such as Markov chain Monte Carlo (MCMC). With these algorithms information from different experiments can be combined. In multi-year dynamic models, the stability of the steady states is an important issue. With chaotic dynamics, prediction of densities and associated economic loss will be possible only on a short timescale. In this study, a generic model was developed that describes population dynamics in crop rotations. Mathematical analysis showed stable steady states do exist for this dynamic model. Using the Metropolis algorithm, the model was fitted to data from a multi-year experiment on *Pratylenchus penetrans* dynamics with treatments that varied between years. For three crops, parameters for a yield loss assessment model were available and gross margin of the six possible rotations comprising these three crops and a fallow year were compared at the steady state of nematode density. Sensitivity of mean gross margin to changes in the parameter estimates was investigated. We discuss the general applicability of the dynamic rotation model and the opportunities arising from combination of the model with Bayesian calibration techniques for more efficient utilization and collection of data relevant for economic evaluation of crop rotations.

Key words: Crop rotation, economic evaluation, gross margin, population dynamics, *Pratylenchus penetrans*, sensitivity analysis, stability, steady state, yield loss assessment.

Crop rotation is a tool for managing population levels of nematodes (Dropkin, 1988). Cyst nematodes associated with a single host crop can be controlled by choosing a rotation with a low frequency of this host crop. Species like *Meloidogyne* or *Pratylenchus*, having a wide range of host crops, are harder to control with crop rotations alone. Additional management tools are resistant or tolerant cultivars, nematicides, or biological treatments (Oostenbrink, 1964; Struik and Bonciarelli, 1997).

Data from experiments in which nematode dynamics were studied under different rotations may be analyzed in terms of mean nematode density per rotation, yield of each crop per rotation, or initial nematode density per crop in each rotation (e.g., Fortnum et al., 2001; Johnson et al., 1995; Weaver et al., 1989). With such results, qualitative ratings of host suitability and tolerance may be given for each crop or cultivar and these judgements can be used to choose suitable crop rotations (Hijink and Oostenbrink, 1968; Molendijk and Mulder, 1996). A more quantitative approach is to regress final population density on initial density and use the so-obtained single-year parameter estimates to simulate nematode dynamics in different rotations (Kinloch, 1986; Noe et al., 1991). Others model multiplication (final over initial density) as function of initial density (Ogallo et al. 1999). However, to analyze multi-

year experiments, it is more appropriate to use a multi-year model, as is done by Mol et al. (1995) to analyze *Verticillium dahliae* dynamics in crop rotations. Mol et al. (1995) fitted their model to data by minimizing the residual sum of squares with respect to each of the parameters one at a time. A drawback of this heuristic method is that no standard errors of the parameters are obtained.

Rather than estimating parameters from experiments, they may be derived from literature (Been et al., 1995; Burt and Ferris, 1996; Ehwaeti et al., 2000). When the same sequence of crops is grown again and again in consecutive years, one wants to know if stable steady states exist. If so, it will be possible to predict for a given rotation future densities for a nematode species. The stability of steady states was studied numerically by Kinloch (1986), Noe et al. (1991), Ehwaeti et al. (2000), and Mol et al. (1995), as well as analytically. Burt and Ferris (1996) presented a model with analytical expressions for stable steady states in a dynamic model for nematodes with one host crop. In this paper, we show that with the model of Burt and Ferris (1996) analytical expressions for stable steady states can also be obtained for rotations with more than one host crop in the rotation by logarithmic transformation of the model.

Various models have been proposed to relate the final density, P_f (number of nematodes g^{-1} soil), at the end of the growing season after harvest of the crop to initial density, P_i (number of nematodes g^{-1} soil), before the crop is planted or sown. A common structure in many of these models is

$$P_f = \frac{P_i}{\alpha + \beta P_i} \quad (1)$$

in which $1/\alpha$ represents the slope of the curve in the

Received for publication 4 March 2004.

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The authors thank J. Grasman, H. Ferris, and Y. H. Choi for critical reading of the manuscript and L. P. G. Molendijk, T. van Galen-van Beers, and E. Brommer for making available the data for the case study.

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This paper was edited by D. A. Neher.

origin and $1/\beta$ defines the horizontal asymptote. Jones et al. (1978) presented a model for potato cyst nematode, using the work of Jones (1966) and Trudgill (1967),

$$P_f = \frac{\varphi HP_i}{1 + \frac{\gamma HP_i}{h}} = \frac{P_i}{\frac{1}{\varphi H} + \frac{\gamma P_i}{h\varphi}}, \quad (2)$$

where h is root length per weight of soil, H is proportion of the initial nematode density P_i that invades the roots, γ is the ratio of males to females, and φ is the average number of eggs produced per female nematode. Equation [2] is identical to Eq. [1] by taking $1/\varphi H$ equal to α and $\gamma/h\varphi$ equal to β . Jones et al. (1978) introduced intraspecific competition into Eq. [2] by making h a decreasing function of P_i such that P_f decreased when P_i attained high values.

Equation [1] was found to be valid for other cyst nematodes with one synchronous generation per growing season and for *M. naasi*, a species that also has one synchronous generation per year (Seinhorst, 1970). For beet cyst nematode with multiple, non-overlapping generations per year, Eq. [1] must be applied to each generation (Seinhorst, 1970).

Migratory nematodes live in soil or roots of different plant species (e.g., *P. penetrans*) or exclusively in the soil (e.g., *Tylenchorhynchus dubius*) and have overlapping generations and multiply continuously during growth of a host crop. Dynamics of these nematodes can be described by the logistic equation

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{E} \right), \quad (3)$$

where r represents the intrinsic rate of increase and E is the carrying of a given environment for the population. The solution of the differential equation [3] is

$$P_f = \frac{aEP_i}{E + (a-1)P_i} = \frac{P_i}{\frac{1}{a} + \frac{(a-1)}{aE}P_i}, \quad (4)$$

in which a is equal to e^{rt} and t is the end of the growing season. Note that the structure of Eq. [4] is similar to Eq. [1] by taking when $1/a$ equals α and $(a-1)/aE$ equals β .

So Eq. [1] applies to dynamics of a range of nematodes (Seinhorst, 1970) and will be used in this study to develop a dynamic model for a single nematode species that interacts with more than one host crop in the rotation. Analytical expressions for the stable steady states of this dynamic model are derived. The population dynamics model is combined with a yield loss assessment model to enable evaluation of steady states in economic terms. The model is fitted to data from an experiment with *P. penetrans* using the Metropolis algorithm (Gelman et al., 1996), which allows estimation of the stan-

dard errors of the parameter estimates. Results are used to assess mean gross margin of a number of crop rotations and to estimate the contribution of parameter uncertainty to uncertainty in model output.

THEORY

Single-year nematode dynamics in the presence of a host: In single-year experiments nematode density is usually measured in spring before a crop is sown or planted to establish the initial density, P_i (number of nematodes g^{-1} soil), and in autumn when the crop is harvested to establish final density, P_f (number of nematodes g^{-1} soil). In this study, Eq. [1] will be used to describe the relation between P_f and P_i in the presence of a host crop. We ignore population decrease at high initial population levels, a finding well known for potato cyst nematode (Seinhorst, 1970); thus, the model should be applied only where rotations maintain density of nematodes at relatively low levels, as may be expected in economically feasible cropping systems.

Single-year nematode dynamics in the absence of a host: We assume a fraction of the nematodes will survive during growth of a non-host crop. The surviving fraction can be estimated with Eq. 1 as $1/\alpha$ by setting β to 0.

$$P_f = \frac{P_i}{\alpha}. \quad (5)$$

During a period without a host crop, a non-host crop may be present or the field may be fallow. Equation [5] is also relevant for estimating the fraction of the nematode population that survives a control measure. Examples of control measures include soil fumigation by chemical or biological (Blok et al., 2000) means, growing a trap crop (Scholte, 2000), or growing a crop with nematicidal properties such as *Tagetes* spp. (Dropkin, 1988).

Yield loss and financial results: Relative yield expresses the yield in nematode-infested soil relative to the yield in soil without infestation of nematodes. Several models have been proposed to describe the relative yield (Y) of a crop as function of P_i . All models describe a similar pattern. Relative yield is 1 for $0 < P_i < \theta$. For $P_i > \theta$, Y declines because of damage to the root system of the crop (Seinhorst, 1965). Above θ , the rate of decline in Y decreases with increasing P_i and Y goes to a horizontal lower asymptote. Often estimation of parameter θ does not improve the fit of the yield loss assessment model and parameter θ is assumed to be 0 (e.g., Elston et al., 1991).

The inverse linear model was used in a study of relative potato yield (Y) as function of initial density of potato cyst nematodes (Elston et al., 1991):

$$Y = \left[\nu + (1 - \nu) \frac{1}{1 + \lambda P_i} \right]. \quad (6)$$

Parameter ν is the minimum relative yield when P_i

tends to infinity and λ is a rate parameter. The fit of the model did not decrease when ν was set to zero; therefore, Elston et al. (1991) proposed the simpler model

$$Y = \frac{1}{1 + \lambda P_i}, \quad (7)$$

which we also assumed valid in this study to describe relative yield Y as a function of P_i . Gross margin (GM , expressed in euros $\text{ha}^{-1} \text{year}^{-1}$) of a crop in absence of nematodes is equal to financial output (FO , euros $\text{ha}^{-1} \text{year}^{-1}$), the product of yield, and value of the crop minus the specific costs (SC , euros $\text{ha}^{-1} \text{year}^{-1}$) of the crop

$$GM = FO - SC. \quad (8)$$

Yearly updated averages for FO and SC are available in handbooks (e.g., Dekkers, 2001). For specific fields or farms where advice is to be given, farmers could provide these data. When nematodes are present it is assumed yield is a function of P_i ; therefore FO in Eq. [8] is multiplied with relative yield Y from Eq. [7]:

$$GM(P_i) = \frac{FO}{1 + \lambda P_i} - SC. \quad (9)$$

Nematode dynamics in rotations: In a crop rotation, n crops are grown on the same field for n consecutive years. This process is repeated every n years, so the period of the rotation is n years. Each crop is denoted as a phase of the rotation, with crop 1 being phase 1, crop 2 being phase 2, and so on (Yates, 1954). The size of nematode population at the start of year t is P_t . The dynamics are modeled by the equation

$$P_{t+1} = f(t, P_t) = \frac{P_t}{\alpha(\tau(t)) + \beta(\tau(t))P_t} \quad P_1 = \pi_0, \quad (10)$$

in which $\tau(t) = t(\text{mod})n$ and $1 \leq \tau \leq n$. Function $t(\text{mod})n$ is such that $\tau(t)$ is equal to 1 in year 1, equal to 2 in year 2, equal to n in year n , and again equal to 1 in year $n + 1$, and so on. The nematode density before the first crop is grown for the first time, π_0 , is a field-specific parameter of the model. The parameters $\alpha(\tau(t))$ and $\beta(\tau(t))$ are dependent on the crop grown in year $t(\text{mod})n$. When P_t and P_{t+1} in Eq. [10] are replaced by their reciprocal R_t and R_{t+1} and $\rho_0 = 1/\pi_0$, Eq. [10] becomes

$$R_{t+1} = f(t, R_t) = \beta(\tau(t)) + \alpha(\tau(t))R_t \quad R_1 = \rho_0. \quad (11)$$

Analytical expressions for the density can be obtained with three crops growing on the same field in consecutive years. If the initial density before the first crop is grown is equal to P_1 , then the reciprocal of the population density in the following years will be

$$R_2 = \beta(1) + \alpha(1)R_1 \quad R_1 = \rho_0, \quad (12)$$

$$R_3 = \beta(2) + \alpha(2)R_2 = \beta(1)\alpha(2) + \beta(2) + \alpha(1)\alpha(2)R_1, \quad (13)$$

$$R_4 = \beta(3) + \alpha(3)R_3 = \beta(1)\alpha(2)\alpha(3) + \beta(2)\alpha(3) + \beta(3) + R_1 \prod_{s=1}^3 \alpha(s). \quad (14)$$

Continuing this iteration process, it can be shown that in year 7

$$R_7 = (\beta(1)\alpha(2)\alpha(3) + \beta(2)\alpha(3) + \beta(3)) \left[1 + \prod_{s=1}^3 \alpha(s) \right] + R_1 \prod_{s=1}^3 \alpha(s)^2, \quad (15)$$

and after another 3 years

$$R_{10} = (\beta(1)\alpha(2)\alpha(3) + \beta(2)\alpha(3) + \beta(3)) \left[1 + \prod_{s=1}^3 \alpha(s) \right]^2 + R_1 \prod_{s=1}^3 \alpha(s)^3. \quad (16)$$

If the product of the of the $\alpha(s)$, $\prod_{s=1}^3 \alpha(s)$, is larger than 1, the product of the maximum multiplication rates, $1/\prod_{s=1}^3 \alpha(s)$ will be smaller than 1 and the nematode will become extinct in the rotation. Because only persistent organisms are relevant, $\prod_{s=1}^3 \alpha(s)$ is postulated to be smaller than 1. In that case, the term in square brackets in Eq. [16], being a finite geometric series (Mood et al., 1974), remains bounded for $t \rightarrow \infty$. For a finite geometric series,

$$\sum_{i=0}^{q-1} x^i = \frac{1 - x^q}{1 - x}. \quad (17)$$

so Eq. [16] now can be written in a general form for a rotation of n crops and p repetitions ($p = 0, \dots, \infty$) with $t = pn + 1$, the time in years

$$R_{t=pn+1} = \left(\sum_{k=1}^{n-1} \beta(k) \prod_{m=k+1}^n \alpha(m) + \beta(n) \right) \frac{1 - \prod_{s=1}^n \alpha(s)^p}{1 - \prod_{s=1}^n \alpha(s)} + R_1 \prod_{s=1}^n \alpha(s)^p. \quad (18)$$

Steady states of a rotation: When a rotation is maintained for an indefinite period of time, the inverse nematode densities R_t tend to an equilibrium level, or steady state. Using Eq. [18] and letting p tend to infinity, the steady state of each phase or crop in the rotation may be calculated:

$$\bar{R}_1 = \lim_{p \rightarrow \infty} R_{pn+1} = \frac{\sum_{k=1}^{n-1} \beta(k) \prod_{m=k+1}^n \alpha(m) + \beta(n)}{1 - \prod_{s=1}^n \alpha(s)} \quad (19)$$

$$\bar{R}_2 = \beta(1) + \alpha(1)R_1 \quad (20)$$

and so on, until

$$\bar{R}_n = \beta(n-1) + \alpha(n-1)\bar{R}_{n-1}. \quad (21)$$

The steady state of nematode densities associated with phase (or crop) j is indicated by \bar{R}_j whereas R_p represents density at the start of year t . The earlier assumption $\prod_{s=1}^n \alpha(s) < 1$ is necessary to calculate the limit in Eq. [19] because only then does $\prod_{s=1}^n \alpha(s)^p$ tend to 0 when p tends to infinity. An alternative way to obtain the expressions for $\bar{R}_j, \dots, \bar{R}_n$ is given in Appendix A. In steady state the gross margin associated with crop j , is equal to

$$GM(\bar{R}_j) = \frac{FO(j)}{1 + \frac{\lambda(j)}{\bar{R}_j}} - SC(j), \quad (22)$$

and the mean gross margin GM_R of the n crops in a rotation R is equal to

$$GM_R = \frac{1}{n} \sum_{j=1}^n GM(\bar{R}_j). \quad (23)$$

Once gross margins have been calculated, the issue of stability of the steady states becomes relevant. When the inverse of nematode density is disturbed from the steady state (for example in the case of crop 1, \bar{R}_1), it will return to the steady state only when the derivative of the function g to R , given $R = \bar{R}_1$, is smaller than unity, where function g is such that $R_{(p+1)n+1} = g(R_{pn+1})$. According to Eq. [18] and using the fact that $\prod_{s=1}^n \alpha(s)^p$ tends to 0 when p tends to infinity:

$$\begin{aligned} R_{(p+1)n+1} &= g(R_{pn+1}) \\ &= \sum_{k=1}^{n-1} \beta(k) \prod_{m=k+1}^n \alpha(m) + \beta(n) + R_{pn+1} \prod_{s=1}^n \alpha(s). \end{aligned} \quad (24)$$

In steady state $R_{(p+1)n+1} = R_{pn+1} = \bar{R}_1$ and (Edelstein-Keshet, 1988)

$$\left. \frac{dg}{dR} \right|_{R=\bar{R}_1} = \prod_{s=1}^n \alpha(s). \quad (25)$$

The steady state is stable when equation [25] is in absolute value smaller than 1 (Edelstein-Keshet, 1988), which is exactly the case under study. It can be shown that Eq. [25] is equal to $\prod_{s=1}^n \alpha(s)$ given $R = \bar{R}_j, j = 1, \dots, n$. Therefore, it may be concluded that in the present model formulation, a stable steady state exists for each phase in the rotation. It can also be shown that after perturbation of nematode density from the steady state, the velocity of return to the steady state depends on $\prod_{s=1}^n \alpha(s)$ but is independent of the $\beta(k)$'s, $k = 1, \dots, n$. Combining equations [18] and [19] R_{pn+1} can be written as

$$R_{pn+1} = \bar{R}_1 \left(1 - \prod_{s=1}^n \alpha(s)^p \right) + R_1 \prod_{s=1}^n \alpha(s)^p. \quad (26)$$

When p tends to ∞ , R_{pn+1} tends to \bar{R}_1 . For example, with soil fumigation population density can be reduced to a new starting value $R_1 + c\bar{R}_1$ and time t is set back to zero, from this time on R_{pn+1} can be written as

$$\begin{aligned} R_{pn+1} &= \bar{R}_1 \left(1 - \prod_{s=1}^n \alpha(s)^p \right) + c\bar{R}_1 \prod_{s=1}^n \alpha(s)^p \\ &= \bar{R}_1 + (c-1)\bar{R}_1 \prod_{s=1}^n \alpha(s)^p. \end{aligned} \quad (27)$$

Parameter estimation and sensitivity analysis: When a crop rotation experiment is performed and the density of the nematodes is measured on each experimental unit each spring before crops are planted, parameter π_{0i} is the initial nematode density in field i . This parameter, π_{0i} is used in Eq. [10] to predict P_{2i} the density in spring of year 2. The prediction of P_{2i} is used to predict P_{3i} and so on. Such a model may be fitted to data with the Metropolis algorithm. With this algorithm, first an initial estimate for each parameter is chosen and the likelihood for the initial set of parameters is calculated. Subsequently, a new parameter set is generated, for example, by adding a sample from the standard normal distribution to the logarithm of each parameter. The new parameter set replaces the old set when the likelihood of the new set is greater than the likelihood of the old set or when, the likelihood of the new set over the likelihood of the old set is greater than a randomly generated number from the interval (0, 1). With this algorithm, the sampled estimates for each parameter tend to the distribution for each of the parameters. Population density is measured by counting nematodes, and the variance of these counts may be assumed to be proportional to the expected value of the counts, which is called quasi-likelihood (McCullagh and Nelder, 1989). The estimation procedure is made more stable by estimating the logarithm of the positive parameters. Unfortunately, residuals of the analysis are usually large and have spatial and temporal correlation. The parameters α, β , and π were assumed to have prior distributions $N(\mu_\alpha; \sigma_\alpha^2)$, $N(\mu_\beta; \sigma_\beta^2)$, $N(\mu_\pi; \sigma_\pi^2)$, and the parameters of these distributions were estimated with the Metropolis algorithm, a technique called empirical Bayes (Carlin and Louis, 2000). The reciprocal of the parameters α of fallow, *Tagetes*, and anaerobic were assumed to be uniformly distributed on the interval (0, 1).

With the Metropolis algorithm, data from crop rotation experiments can be used to estimate parameters α and β . However, data from large-scale experiments in which whole-farm systems are compared (Dent and Walton, 1997) also can be used. Because a rigorous experimental design is not strictly necessary to estimate the parameters, data from farmer's fields may be used,

e.g., as collected during a “prototyping” project (Vereijken, 1997). The analysis of data from 1-year experiments with measurement of density in spring before planting or sowing a crop and in autumn after harvest of the crop corresponds to orthogonal regression analysis (Carrol et al., 1995). In addition, parameters for treatment effects can be estimated with the model. When, for example, the soil is fumigated after a crop is grown, the difference Eq. [10] becomes

$$P_{t+1} = \frac{\omega P_t}{\alpha(\tau(t)) + \beta(\tau(t))P_t} = \frac{P_t}{\frac{\alpha(\tau(t))}{\omega} + \frac{\beta(\tau(t))}{\omega} P_t}, \quad (28)$$

in which $\tau(t) = t(\text{mod})n$ and where P_t is the nematode density prior to the crop, P_{t+1} the density prior to the next crop, and ω is the proportion of nematodes surviving soil fumigation. Eventually $\alpha(j)/\omega$ and $\beta(j)/\omega$ may be replaced by new parameters $\alpha'(j)$ and $\beta'(j)$. When nematode density is measured in spring and autumn, density-dependent multiplication during summer can be modeled with Eq. [10] and the fraction surviving during winter with Eq. [10] but parameter β set to zero.

Uncertainty in parameter estimates is due to imperfect fit of the model. Further uncertainty in the data arises from measurement error and true variation in the field (e.g., Rossing et al., 1994). Parameter uncertainty is summarized in the standard error of the estimate. Sensitivity of model outcome to each of the parameters is calculated by taking the derivative of the model outcome with respect to each of the parameters of the model (Saltelli et al., 2000). The influence of uncertainty in a parameter on a particular model outcome then is the product of the standard error of the parameter estimate and the value of the derivative of the outcome to this parameter. Analytical derivatives of \bar{R}_j and $GM(\bar{R}_j)$, the major outputs of our model, to each of the parameters are listed in Appendix B.

A CASE STUDY

Pratylenchus penetrans in field-grown vegetable rotations: An experiment was performed from spring 1998 until autumn 2002 in the southeast of The Netherlands on a sandy soil infested with *P. penetrans* to study dynamics and yield loss of the nematode when different arable crops and vegetables were grown. During 1998–2002, a total of 38 treatments of crops or land-use types (i.e., crop species as well as different types of fallow) were grown on 96 experimental plots. In 1998, there were 22 land-use types each on four plots and lettuce on eight plots to establish host suitability of these land-use types. In 1999, there were eight land-use types each on eight plots to establish host suitability and two land-use types each on 16 plots to establish host suitability and yield loss assessment. In 2000, there were four land-use types

each on 20 plots for yield loss assessment and four land-use types each on four plots for establishing host suitability. In 2001, peas were grown on all 96 plots for yield loss assessment. Following harvest of peas in 2001 six different green manure crops were grown in autumn cropping, and in 2002 different potato cultivars were grown for yield loss assessment.

In this case study, the nematode density measured in spring 1998, 1999, and 2000 on all 96 plots were used to estimate parameters α and β of Eq. [10] for each of the 26 land-use types in 1999 and 2000. Nematode density was measured by taking a soil sample of about 2 kg. The soil was mixed and specific weight was measured. A subsample with weight corresponding to 100 cm³ soil was taken, and nematodes were extracted into a suspension of 100 ml. From this suspension two subsamples of 10 ml were taken. The statistical analysis was performed on the total number counted in the two subsamples. However nematode densities are reported as number per 100 cm³ soil.

In total, 288 data points were available to estimate the 151 parameters of the non-linear model, including 96 parameters ρ_0 (one for each plot), 26 parameters α (one for each land-use type), and 23 parameters β (one for each crop; for fallow, fallow with anaerobic conditions and *Tagetes*, with nematicidal effect on *P. penetrans*, β was assumed to be zero; and six parameters μ_α , σ_α^2 , μ_β , σ_β^2 , μ_π , σ_π^2 of the prior normal distribution of the parameters α , β and π). The parameters were estimated by programming the Metropolis algorithm within the Genstat statistical package (Windows 6th edition, Payne et al., 2002).

For lettuce, leek, and carrot parameters λ were estimated in yield loss assessment experiments also carried out in the southeast of the Netherlands. Financial output, specific costs, and gross margin (Dekkers, 2001) of the three crops and bare fallow are shown in Table 1. With n land-use types $(n-1)!$ rotations of n years can be constructed. We evaluated the six rotations of 4 years that result from all permutations of the land-use types in Table 1. For each rotation, densities of *P. penetrans* before planting each of the four crops were calculated assuming the population in steady state. For each crop in each rotation the corresponding yield and financial output were calculated as well as the financial output per rotation.

TABLE 1. Financial output (FO), specific costs (SC), and gross margin (GM) for land-use types lettuce, leek, fallow, and carrot in euros per hectare.

Crop	FO	SC	GM
Lettuce (<i>Lactuca sativa</i> L.)	15,072	6,645	8,427
Leek (<i>Allium porri</i> L.)	18,408	10,158	8,249
Fallow	*446	85	361
Carrot (<i>Daucus carota</i> L.)	13,616	5,438	8,178

* EU fallow premium.

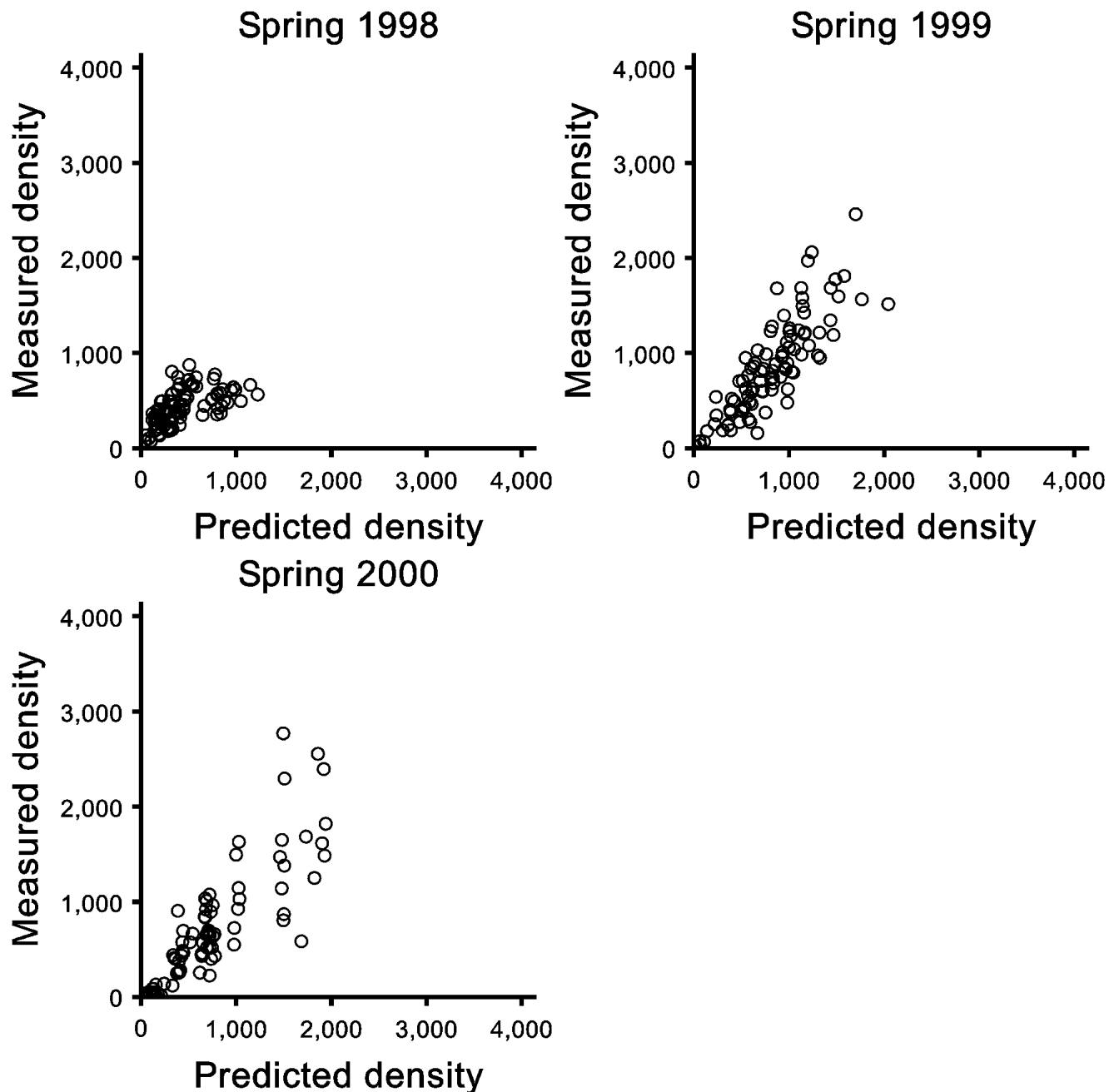


FIG. 1. Measured and predicted density (nematodes/100 cm³ soil) in spring 1998, 1999, and 2000.

Results: The predictions of the model were closer to observations in spring 1998 than in spring 1999 and 2000 (Fig. 1). Density of the nematodes also rose from 1998 to 1999 and 2000. For lettuce, leek, fallow, and carrot, the land-use types that were combined to rotations and the relation between initial and final densities were well predicted by the model across the range of initial densities (Table 2, Fig. 2). Yield decline caused by *P. penetrans* was moderate for each of the three vegetable crops, but lettuce was more susceptible than carrot and leek, and there was a wide range of yields around the predicted value (Fig. 3).

Without nematodes present, predicted mean gross

margin of the six rotations based on lettuce, leek, fallow, and carrot was 6,304 euro ha⁻¹ yr⁻¹. With *P. penetrans* in the steady state for each crop, gross margins

TABLE 2. Estimates α ((nematodes/100 cm³ soil)/(nematodes/100 cm³ soil), β (100 cm³ soil/nematodes), and λ (100 cm³ soil/nematodes) and associated standard errors in parentheses for land-use types lettuce, leek, fallow, and carrot.

Crop	α	β	λ
Lettuce	0.1248 (0.1092)	0.00078 (0.00440)	0.00098 (0.00019)
Leek	0.0348 (0.0635)	0.00184 (0.00592)	0.00004 (0.00004)
Fallow	2.5233 (0.2970)	0	0
Carrot	0.0391 (0.1728)	0.00142 (0.00144)	0.00007 (0.00003)

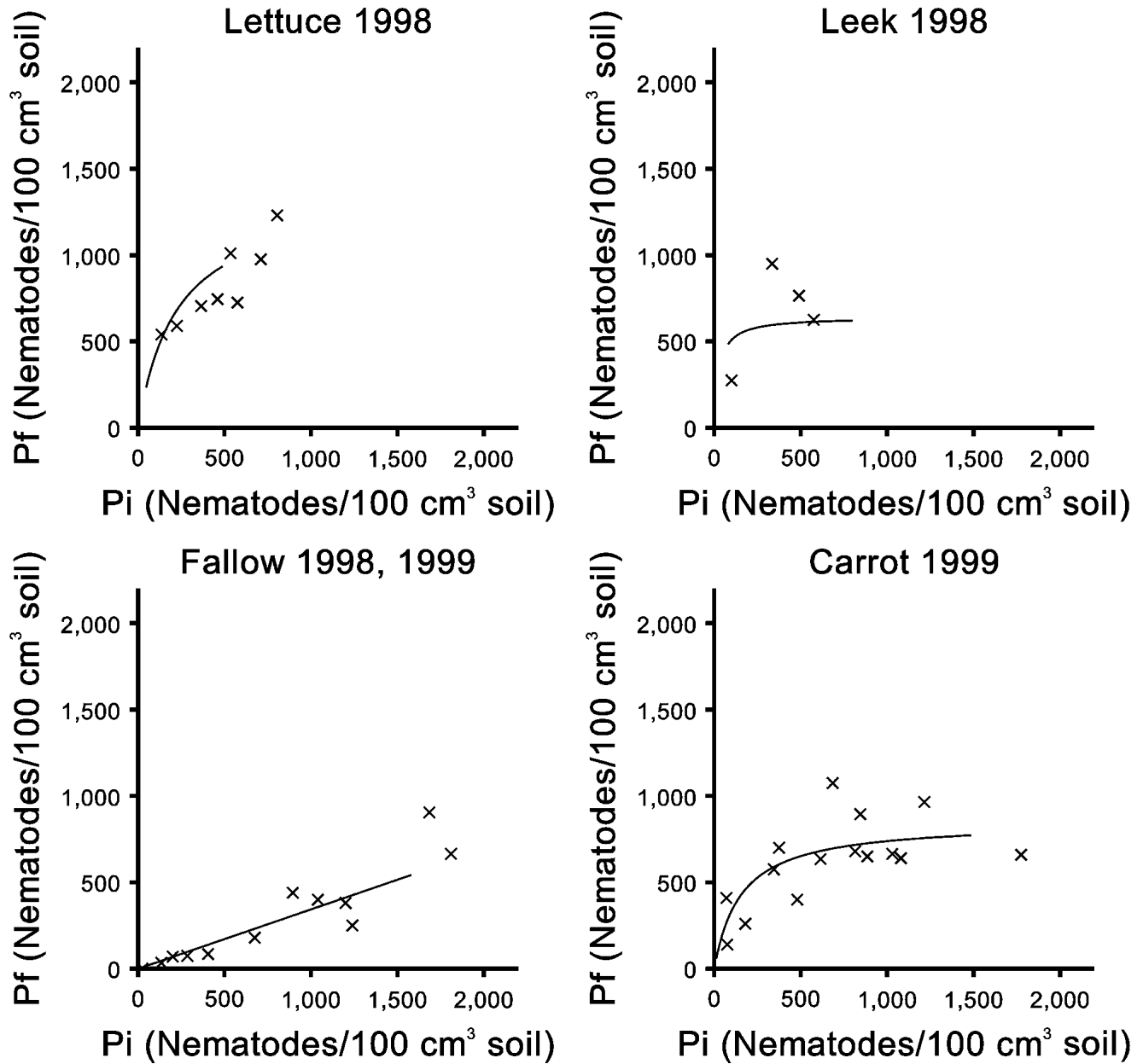


FIG. 2. Measured (x) and predicted (—) response (nematodes/100 cm³ soil) of *P. penetrans* to growth of lettuce, leek, fallow, and carrot.

decreased by more than 1,000 euro ha⁻¹ yr⁻¹ for rotation LE-LK-CT-FW and by nearly 2,000 euro ha⁻¹ yr⁻¹ for rotation LE-FW-LK-CT (Table 3). Because lettuce was the most susceptible crop in the rotation, mean gross margin for the rotation was greatest when lettuce was grown after fallow (Fig. 4). The derivatives of the mean gross margin for α , β , and λ that were calculated using GM and specific cost from Table 1 and estimates of the parameters from Table 2 were greater for parameter β than for parameter α but greatest for parameter λ (Table 3). The products of the standard error and the derivatives show that the contribution to the uncertainty in the mean gross margin increases from α to β to λ , indicating that the damage relation is relatively more uncertain than the

population dynamics relation. This indicates that collecting additional information for estimating parameter λ is more urgent than for parameters α and β .

DISCUSSION

We promote the general applicability of a dynamic rotation model and opportunities arising from a combination of the model with Bayesian calibration techniques for more efficient utilization and collection of data. To model the dynamics of nematodes in a rotation of n crops (or, more generally, land-use types), equations are needed to describe dynamics during

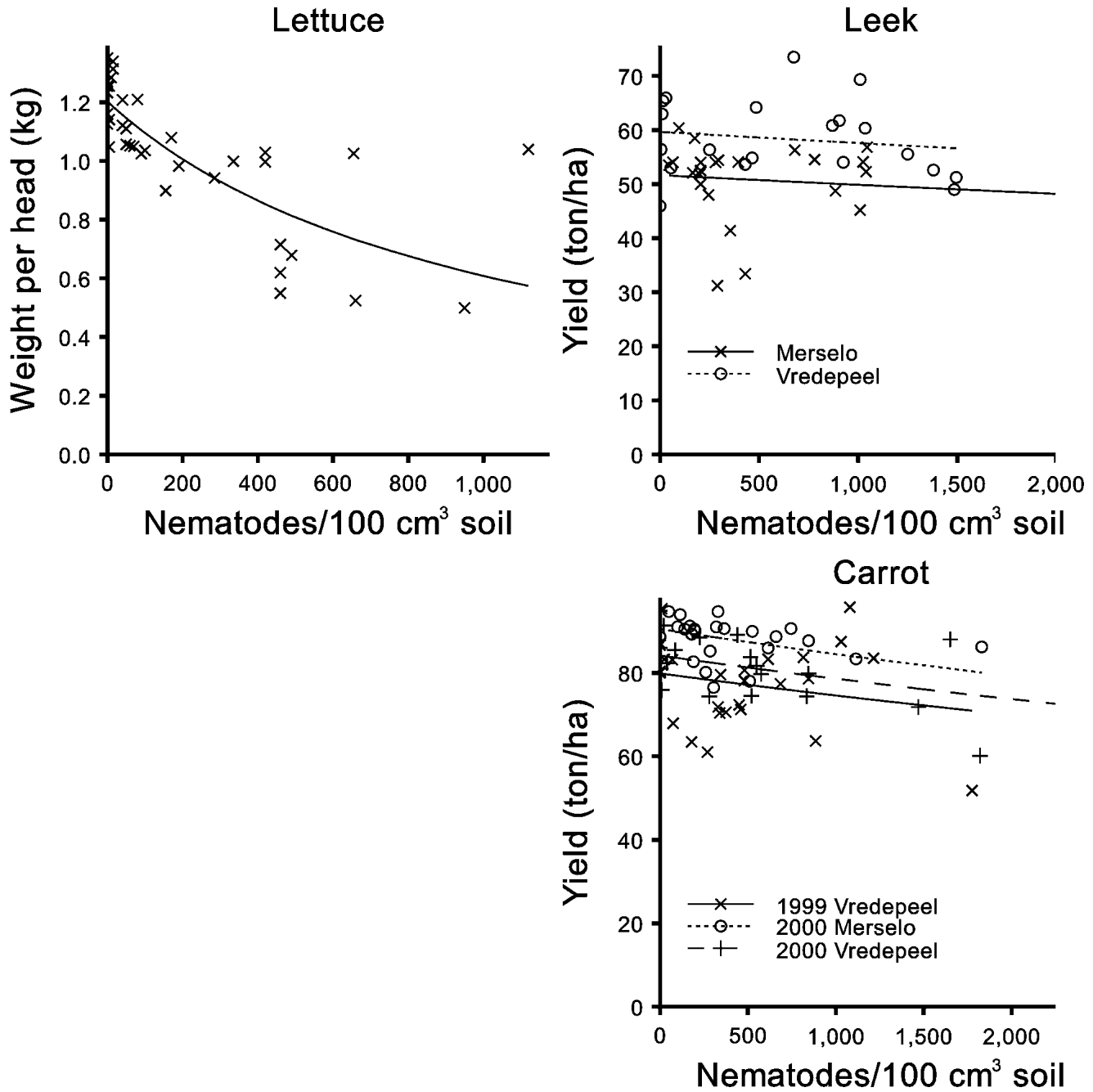


FIG. 3. Measured (x,o,+) and predicted (—) yield of carrot, leek, and lettuce as function of initial nematode density (nematodes/100 cm³ soil).

growth of each of the n crops. We have studied the case where the same equation applies to each of the crops, and differences between crops are reflected in parameter estimates only. Our analysis showed that when the equation is of the form

$$g(P_{t+1}) = f(t, P_t) = \beta_0 (\tau(t)) + \beta_1 (\tau(t)) g(P_t), \quad P_1 = \pi_0 \quad (29)$$

or can be transformed to this form, analytical expressions can be obtained for the initial nematode densities for each crop in the rotation. In Eq. [29], $\tau(t) = t(\text{mod})n$ describes the pattern of crop alternation and $g(x)$ may be a transformation of x such as $1/x$, $\log(x)$, or

$\logit(x)$. Eq. [29], therefore, provides a generic description of rotational nematode dynamics that we denote as generalized linear dynamics in analogy to the theory of Generalized Linear Models where non-linear statistical models are transformed to linear models (McCullagh and Nelder, 1989). Eq. [29] provides a summary for a range of models proposed in the literature. For example, Ferris and Greco (1992) and Burt and Ferris (1996) used the difference equation

$$P_{t+1} = f(t, P_t) = \delta(\tau(t)) P_t^{\delta(\tau(t))}, \quad P_1 = \pi_0 \quad (30)$$

By taking logarithms of both sides and replacing

TABLE 3. Mean gross margin (euro ha⁻¹ yr⁻¹), and derivative of mean gross margin with respect to parameter α , β , and λ (Appendix B), given the estimates of these parameters for the six different rotations with land-use types lettuce (LE), leek (LK), fallow (FW), and carrot (CT).

Crop rotation	GM_R	$dGM_R/d\alpha$	$dGM_R/d\beta$	$dGM_R/d\lambda$
LE-LK-FW-CT	4610	1303	3107678	-19540038
LE-LK-CT-FW	5285	1713	1216991	-20912440
LE-CT-LK-FW	5421	1430	1012535	-20685392
LE-FW-LK-CT	4508	5805	3418425	-23231111
LE-FW-CT-LK	4756	3868	2580331	-25239269
LE-CT-FW-LK	4821	1302	2399295	-23565259

$\log(P_{t+1})$ and $\log(P_t)$ by L_{t+1} and L_t and letting $\rho_0 = \log(\pi_0)$, Eq. [30] becomes

$$L_{t+1} = f(t, R_t) = \log \delta(\tau(t)) + \kappa(\tau(t)) L_t. \quad L_i = \rho_0 \quad (31)$$

which is in the same form as Eq. [29]. A similar reasoning may be applied to the models where $\log(P_t)$ is related to $\log(P_i)$. In Eq. [31] P_{t+1} continues to increase as function of P_t , whereas in the hyperbolic response through the origin (Eq. [1]), P_{t+1} tends to the horizontal asymptote $1/\beta$. The hyperbolic response Eq. [1] has a stronger basis in biological principles (Jones, 1966; Jones et al., 1978; Seinhorst, 1970; Trudgill, 1967) than Eq. [29] used by Ferris and Greco (1992) and Burt and Ferris (1996) and was therefore preferred in this study. Seinhorst (1970) concluded that Eq. [4] describes the relation between P_j and P_i fairly accurately and can be used for all practical purposes.

We have shown that for equations that can be written as Eq. [29] not only is an analytical expression for the steady states available but also these steady states are stable. This means that future densities can be predicted and these predictions can be used to predict mean gross margins of rotations. The time required to

(nearly) reach the steady state from some initial state can be found only by simulation. However, it was shown that the rate at which nematode density tends to the steady state is proportional to $\prod_{s=1}^n \alpha(s)^p$. For advisory purposes, steady states will be directly relevant for species with high intrinsic growth rates, such as *Meloidogyne* spp. that reach steady states within one cropping period. For slowly growing species such as *Trichodorus* spp., information on the steady states provides a reference for comparison of experiments or treatments.

The model contains a number of simplifying assumptions. At greater initial densities, final population density in Eq. [10] tends to a horizontal asymptote, $1/\beta$, also called the carrying capacity of the crop for the nematode. The model does not consider decline of the carrying capacity that will occur when density becomes very high (Jones et al., 1978). In the yield loss assessment model, a threshold value below which no yield decline occurs and a minimum yield at high initial densities are not considered. For datasets other than the one used here, this may be an invalid assumption. For example, fields with recent infestations may have spots with high population levels and areas without nematodes (Been et al., 1995). Extension of the yield loss model for this purpose will not affect the basic approach presented in this paper. The present model simply may be extended to deal with more than one nematode species as long as interactions between the population dynamics of the species may be ignored. Because changing the crop loss model does not affect the basic approach, more complex interactions between nematode species and crop can be accommodated.

Establishing parameter estimates for nematode dynamics and crop loss in rotation models using classical statistical experimental design requires much time and space and is often prohibitively costly. In addition, new developments in cultivars or land-use practices would

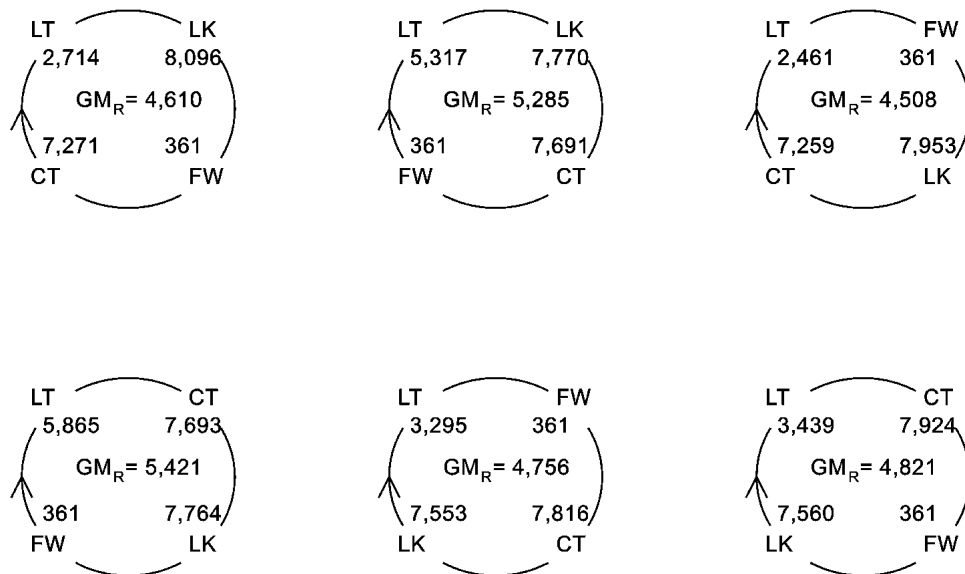


FIG. 4. Gross margin per crop in each of the six crop rotations and mean gross margin of the rotation (GM_R) in euro ha⁻¹, year⁻¹. LT = Lettuce, LK = Leek, FW = Fallow, CT = Carrot.

require repetition of these rotation experiments. Recent advances in Bayesian calibration methods, such as the Metropolis algorithm and other MCMC methods, provide the opportunity to combine information from different experiments to estimate the frequency distribution of parameters of rotation models. Starting from a uniform frequency distribution, application of these algorithms results in posterior distributions that may be used as input (prior distributions) in subsequent calibration steps based on other data sets. More research is needed to develop guidelines about combining information sources. Nevertheless, our results show how experimental data collected for different purposes can be combined that until now could be collated only in a qualitative way by invoking experts.

The Metropolis algorithm and other MCMC methods allow evaluation of the sensitivity of mean gross margin for each of the parameters in the model. Such analysis supports setting research priorities by revealing parameters for which additional information is most valuable. In our illustration, sensitivity of the mean gross margin was highest for parameter λ , indicating a current priority for crop loss studies over population dynamics studies.

Design of crop rotations involves evaluation of the performance of alternative crops, cultivars, and fallows as well as their sequence and management in terms of a range of objectives, one of which may be related to nematode dynamics. Other objectives may be related to economic performance, nutrient dynamics, erosion, or labor demand and, for many of these, quantitative approaches have been developed. To date, assessment of nematological aspects is mostly semiquantitative (Molendijk and Mulder, 1996). The approach presented in this paper represents a step toward quantitative nematological assessment of crop rotations, either to directly support farmer decision making or as part of integrated whole farm models (e.g., Dogliotti et al., 2004).

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APPENDIX A

For three crops in a rotation ($n = 3$) in steady state Eq. [19], [20], and [21] can be written in matrix notation:

$$\begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \bar{R}_1 \\ \bar{R}_2 \\ \bar{R}_3 \end{pmatrix} = \begin{pmatrix} \beta(3) \\ \beta(1) \\ \beta(2) \end{pmatrix} + \begin{pmatrix} 0 & 0 & \alpha(3) \\ \alpha(1) & 0 & 0 \\ 0 & \alpha(2) & 0 \end{pmatrix} \begin{pmatrix} \bar{R}_1 \\ \bar{R}_2 \\ \bar{R}_3 \end{pmatrix}, \quad (\text{A1})$$

where \bar{R}_1 is made a function of \bar{R}_3 , with solution

$$\begin{pmatrix} \bar{R}_1 \\ \bar{R}_2 \\ \bar{R}_3 \end{pmatrix} = \begin{pmatrix} 1 & 0 & -\alpha(3) \\ -\alpha(1) & 1 & 0 \\ 0 & -\alpha(2) & 1 \end{pmatrix}^{-1} \begin{pmatrix} \beta(3) \\ \beta(1) \\ \beta(2) \end{pmatrix}. \quad (\text{A2})$$

According to paragraph [4.4] in (Searle, 1966) this can be written as

$$\begin{pmatrix} \bar{R}_1 \\ \bar{R}_2 \\ \bar{R}_3 \end{pmatrix} = \frac{1}{1 - \prod_{s=1}^3 \alpha(s)} \begin{pmatrix} 1 & \alpha(2)\alpha(3) & \alpha(3) \\ \alpha(1) & 1 & \alpha(1)\alpha(3) \\ \alpha(1)\alpha(2) & \alpha(2) & 1 \end{pmatrix} \begin{pmatrix} \beta(3) \\ \beta(1) \\ \beta(2) \end{pmatrix}, \quad (\text{A3})$$

which is identical to Eq. [19], [20], and [21] for $n = 3$. Now GM_R can be calculated as

$$GM_R = \begin{pmatrix} 1 & 1 & 1 \end{pmatrix} \begin{pmatrix} FO(1)\bar{Y}_1 - SC(1) \\ FO(2)\bar{Y}_2 - SC(2) \\ FO(3)\bar{Y}_3 - SC(3) \end{pmatrix}, \quad (\text{A4})$$

where

$$\bar{Y}_j = \frac{1}{1 + \frac{\lambda(j)}{\bar{R}_j}} \quad (\text{A5})$$

APPENDIX B

Let

$$\psi = \left(1 - \prod_{s=1}^n \alpha(s) \right)^{-1} \quad (\text{B1})$$

Then the derivative of \bar{R}_1 in Eq. [19] with respect to $\alpha(j)$ for $j = 1, \dots, n$ equals

$$\frac{d\bar{R}_1}{d\alpha(1)} = \Psi \bar{R}_1 \prod_{k=2}^n \alpha(k) \quad (\text{B2})$$

$$\frac{d\bar{R}_1}{d\alpha(j)} = \Psi \left(\sum_{k=1}^{j-1} \beta(k) \prod_{m=j+1}^n \alpha(m) \right) + \frac{\Psi \bar{R}_1 \prod_{s=1}^n \alpha(s)}{\alpha(j)} \quad (\text{B3})$$

$$j = 2, \dots, n-1$$

$$\frac{d\bar{R}_1}{d\alpha(n)} = \Psi \left(\left(\sum_{k=1}^{n-2} \beta(k) \prod_{m=k+1}^{n-1} \alpha(m) \right) + \beta(n-1) \right) + \frac{\Psi \bar{R}_1 \prod_{s=1}^n \alpha(s)}{\alpha(n)} \quad (\text{B4})$$

The derivative of \bar{R}_1 in Eq. [19] with respect to $\beta(j)$ for $j = 1, \dots, n$ equals

$$\frac{d\bar{R}_1}{d\beta(j)} = \Psi \prod_{k=j+1}^n \alpha(k) \quad j = 1, \dots, n-1, \quad (\text{B5})$$

$$\frac{d\bar{R}_1}{d\beta(n)} = \psi \quad (\text{B6})$$

Let

$$\Omega(j) = \left(1 + \frac{\lambda(j)}{\bar{R}_j} \right)^{-2} \quad (\text{B7})$$

The derivative of $GM(\bar{R}_j)$ in Eq. [22] with respect to $\alpha(j)$, $\beta(j)$, and $\lambda(j)$ equals

$$\frac{dGM(\bar{R}_j)}{d\alpha(j)} = \Omega(j) FO(j) \frac{\lambda(j)}{\bar{R}_j^2} \frac{d\bar{R}_j}{d\alpha(j)} \quad (\text{B8})$$

$$\frac{dGM(\bar{R}_j)}{d\beta(j)} = \Omega(j) FO(j) \frac{\lambda(j)}{\bar{R}_j^2} \frac{d\bar{R}_j}{d\beta(j)} \quad (\text{B9})$$

$$\frac{dGM(\bar{R}_j)}{d\lambda(j)} = - \frac{\Omega(j) FO(j)}{\bar{R}_j} \quad (\text{B10})$$