Quantification of dynamics of soil-borne pathogens and their consequences for yield in crop rotations

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Contents

Abstract

In The Netherlands crop rotation experiments were performed that required a continuation over many years so that long term effects of treatments and rotations may build up. Usually, analysis of variance is performed on within year data or on data from the final years when treatment/rotation effects are maximal. In this thesis the scope is on rotation experiments in the presence of soil-borne pathogens. Instead of estimating the mean densities of these pathogens and the mean yields of the crops over the whole duration of the experiment, dynamics of the pathogens and yield were registered yearly. Two types of dynamical models were applied. In the first model the dependence of the final (end of the season) pathogen density upon the initial density was represented by a monotonically rising function. The model was applied to an experiment on the dynamics of *Pratylenchus penetrans* in vegetable crops. In the second model with a Ricker type of functional relation between initial and final pathogen densities, the dynamics of *Globodera pallida* on 6 cultivars of potato was studied. In both models the pathogen density tended to a stable steady state in the long term. For this steady state an economic evaluation of crop rotations was made. In a third study potato tuber yield was predicted taking into account the presence of three nematode species and the fungus *V. dahliae*. Also the effect of abiotic factors such as pH and the P content of the soil were taken in consideration. Based on information theory the results of a large class of feasible models was combined by using a suitable method of averaging values of parameters of the different models. Moreover, this method also ranks the predictors with respect to their predictive power. In a fourth study, optimum designs of experiments on pathogen dynamics and yield loss were derived for one of the cultivars already tested in the second study. Furthermore, a measure for the efficiency of a design was introduced so that designs can be compared.

Chapter 1: General introduction

The subject of this thesis is the dynamics of soil borne pathogens in crop rotations and the yield loss caused by the presence of these organisms. In this introduction, first some remarks about the use of crop rotations throughout agricultural history will be made. The role of crop rotation experiments in agricultural research will be discussed. In particular attention will be given to the statistical methods that are used to estimate the yield and to evaluate the presence of pathogens in those experiments. Finally a short review of crop rotation research in The Netherlands will be given, resulting in the formulation of the aim and structure of this thesis.

1.1 Rotation of crops in agriculture

Crop rotation is one of the oldest management strategies applied by farmers to conserve chemical, physical and biological soil fertility. Fertile soils enhance the production of agricultural crops, and crop rotation stimulates soil fertility by pest suppression and nutrient cycling. In conventional agriculture soil fertility is maintained by external inputs in the form of fertilizers, soil tillage or crop protection agents in order to maintain high yield levels. Integrated farming strategies have rediscovered crop rotation as a means to increase or at least maintain soil fertility to increase profits by reducing production costs and to improve the environment by cutting down emissions of nutrients and pesticides (Vereijken, 1997).

Shifting cultivation is probably the earliest type of crop rotation, still practiced in a part of the world where technology is limited and land relatively abundant. The natural vegetation is removed and crops are grown until soil fertility is depleted and yields are low. Farmers then move to a new piece of land (Ponting, 1991). On the deserted parcel chemical, physical and biological processes restore soil fertility when given sufficient time. Depending on conditions, up to fifteen years may be needed for restoration of soil fertility. If this restoration period cannot be maintained, e.g. due to increased human population pressure, this type of agriculture is not sustainable as successive cropping cycles increasingly deplete the soil (Zadoks and Schein, 1979).

In ancient Greece a winter crop was grown each other year. Also in the Roman Empire cultivation of a crop usually was alternated with a fallow year. On fertile soils or with manure application a crop could be grown each year; for example wheat in one year and a legume crop in the other year (White, 1970). In the medieval Islamic world crops were grown continuously in summer as well as in winter. Soil fertility was restored with manure. Much effort was spent growing crops suited to the local weather conditions. Therefore, a range of crops were introduced into new areas within the

Islamic world (Watson, 1983). At the end of the Middle-Ages the three-fields system prevailed in Western Europe. During two consecutive years grain crops were grown; the third year was a fallow year. The fallow year was considered to be necessary for restoring biological soil fertility. However, soil-borne pathogens of grain crops decline during cultivation of a fodder crop just as well as during a fallow year. Replacing the fallow year in the rotation by cultivation of fodder crops increased the amount of feed for keeping more animals, providing larger quantities of manure for fertilizing the soil, which increased the yield level of the wheat crops. In case a legume fodder crop was grown extra nitrogen was fixed from the atmosphere. In England the abolishment of the fallow year was completed during the start of the industrial revolution: the rise of productivity in agriculture enabled more people to work outside agriculture. A substantial part of the population moved from the countryside to become labourers in the urban industrial areas (Mazoyer and Roudart, 2005).

During the 20th century farmers in industrialized countries specialized in either animal husbandry or crop production, and limited the number of crops on a farm. Pollan (2006) describes how in the 1950s mixed farms dominated the state of Iowa in the US, with hogs, poultry, cattle and draught horses. There were pastures for animal feeding fenced by shrubs and trees, besides a variety of arable crops. Soil fertility was maintained by growing legume crops and by manuring the soil. Nowadays the landscape is more open and farms have specialized in growing corn and soybean in a two year rotation. The main source of soil fertility are chemical fertilizers and the soil is left bare from October until May, resulting in major erosion events. Effects of these changes in crop rotation extend beyond the farms. Leached fertilizer nitrogen is transported via ground and surface water to the Gulf of Mexico where it gives rise to algal bloom and anoxia events (Pollan, 2006).

In Europe agricultural production was transformed during the 20th century from small-scale and extensive to large-scale and intensive. Agricultural areas were consolidated by rationalizing farm layouts and improving road and drainage networks. Wooded banks were uprooted, ditches and brooks were straightened or filled in (Vitikainen, 2004). This intensification resulted in emissions of nutrients and pesticides to the environment and a decrease of biodiversity (Almekinders et al., 1995). In the second half of the twentieth century Europe became an exporter of agricultural products, while it had been an importer since the start of the Industrial Revolution.

1.2 Start of crop rotation research

The term crop rotation is used to describe a planned repeated sequence of crops with their associated management, which takes place in the same field (time dimension). This idealized structure is also reflected in space; each year all the crops of the sequence are present in the farm (space dimension) with more or less the same area. If there is a repetitive sequence of crops c_1, c_2 … c_n, c_1, c_2 … c_n a single repetition is termed a cycle and the number of years (or other time units) in the cycle is termed its period (Yates, 1954). Sequences starting at different points in the same cycle are said to be in different phase (e.g. c_2, c_3…c_n, c_1). There are thus n phases of a cycle of period n. The term phase is also used to denote the different components of the cycle. If two or more cycles differing in period length are included in an experiment then the whole experiment will follow a cycle whose period is the lowest common multiple of all periods. When the period of the longest rotation equals n years, the first n-1 years are the preliminary years and have to be discarded from the analysis because only after $n-1$ years for the first time the crops of the longest rotation follow after all preceding crops of the rotation.

During the nineteenth century agricultural research evolved in several European countries. Crop rotation experiments were set up by farmers and by agricultural departments at universities. Especially research on soil fertility became a scientific discipline. In Germany Justus von Liebig worked on a theory of organic chemistry. His ideas stimulated experiments with organic and chemical fertilizers in other countries (Maat, 2001). Around 1845 in Rothamsted England, experiments were laid out resulting in a refutation of Liebigs theory that all nitrogen taken up by plants originates from the atmosphere. By alternating nitrogen fertilizer application on two experimental plots in consecutive years, yields on the plot receiving nitrate fertilizer in the current year were shown to be higher than those on the unfertilized plot that had received nitrate fertilizer in the previous year. For further investigations ten experiments were laid out each with only one crop grown to compare the long-term effect of several fertilizing strategies. These experiments are continued until today and give insight in long-term effects of chemical and organic fertilizers on soil fertility and crop production. Rasmussen et al., (1998) mention a number of such long-term experiments in the United States, Western-Europe and Australia. All are inspired by the Rothamsted experiments and were started before 1930 and continue until today. These trials are called classicals when continued for more than 50 years. From time to time, cultivar choice, soil tillage and disease control were adapted to match practices in the surrounding agriculture. Such adaptations were made in such a way that long term effects were still measurable and the experiments remained valid for contemporary agriculture. Thus, growing conditions in the experiments were kept optimal according to agricultural practice in the specific country and time (Frye and Thomas, 1991).

In Rothamsted, the huge amount of data established in the long-term, non-replicated experiments stimulated the development of statistical techniques. The relation between yield and amount of precipitation was studied by Fisher (1924). To obtain information about size of the variance of the measurement in future experiments, randomization and replication of treatment levels across experimental units was introduced (Fisher, 1948; Fisher 1949). Design and analysis of crop rotation experiments with one or more crop sequences and with different treatments was a special topic (Yates, 1954; Jenkinson, 1991).

Yates (1954) distinguished experiments on the effects of treatments applied to a fixed rotation of crops, e.g. Cochran (1939), and experiments comparing the effects of different rotations, e.g. Patterson (1964). Often analysis of variance is performed on the data, per test crop per year (Scholte, 1990; and Scholte and s'Jacob, 1990). Analysis of data from all years induces spatial and temporal correlation of residuals. Analysis of this type of data has been facilitated by availability of computer software enabling the use of linear mixed models (Richter and Kroschewski, 2006). The last thirty years a number of new rotation experiments were laid out in accordance with a sound statistical design. These rotations were executed for many years and produced important agroecological insights (Cook, 2006; Mäder et al., 2002; Poudel et al., 2002; Tilman et al., 2002).

1.3 Crop rotation in farming system research

Until the 1970's crop rotations experiments were considered as a device to test efficacy and sustainability of crop sequences and their management treatments in the long term. Awareness of the detrimental effects of emissions of pesticides to the environment and the exhaustibility of natural resources stimulated the development of new production methods reducing inputs of pesticides and chemical fertilizers (Carson, 1962; Meadows et al., 1972). Factorial treatments applied within crop rotation experiments were replaced by a small number of production systems, e.g. conventional, integrated and biological farming. These systems differed in treatments such as cultivar choice, dose of fertilizer and pesticide use. A separate analysis of the effect of each treatment level was not possible; instead, the traits established per system were compared. Information of each year was used for improvement of the systems in the next year, called searching for sustainable production methods by prototyping (Vereijken, 1985). Crop rotation was one of the tools for developing sustainable farming systems (e.g. Struik and Bonciarelli, 1997; Vereijken, 1997; Rossing et al., 1997; Dogliotti et al., 2003, 2004). Design of a so-called multifunctional crop rotation constituted the first step in the 'prototyping' approach to farming systems development (Vereijken, 1997). The method was applied in agricultural research in a number of West European countries (Wijnands and Sukkel, 2000). During this step, relevant information was collated to assess alternative crop rotations with respect to objectives such as economics, weed and nutrient management, soil structure impact, and damage by nematodes and soil borne diseases. The ensuing phase of empirical testing on commercial and experimental farms was usually accompanied by field monitoring and provided substantial information on the actual performance of the rotations. In this research approach experiments were not always laid out in replications.

1.4 The use of dynamic models in crop rotation research

Crop rotation experiments are expensive because treatment effects must be established by measuring a number of traits during several years on a number of plots. Measurements on each plot form a time series and dynamic models can be applied to these measurements. To save money and time these dynamic models can also be used to extrapolate the effect of treatments in one-year experiments to effects in the long term. This paragraph presents reviews on some of the dynamic models used in crop rotation research.

In one of the first quantitative models soil fertility was expressed in units of agricultural product that could be produced from the soil (Von Wulfen, 1823). Each crop used a part from the soil fertility, which could be restored by manuring. In the long term, the level of manure application and the crop production level were in equilibrium. A model of phosphate dynamics in three long-term experiments each with only one crop growing all years is described by Wolf et al. (1987) and Janssen et al. (1987). Phosphate was present in the soil in a stable form and a less stable form. The latter form, was dissolved in the soil water. Yang and Janssen (1997) studied dynamics of organic matter in a dominant rotation in China with winter wheat followed by summer maize, and describes the effect of yield level, application of farm yard manure and straw on the long term dynamics of organic matter in the soil.

Also for soil-borne pest and pathogen dynamics models were developed. Pekrun et al. (2004) used a simple mechanistic model for seedbank dynamics of *Brassica napus* influenced by rotation and soil tillage. Burt and Ferris (1996) and Taylor and Rodriguez-Kábana (1999) integrated biological knowledge of soil-borne pathogens into economic evaluation of rotations. Ward et al. (1985) developed a mechanistic model for dynamics of *Globodera pallida* on potato and growth of the crop that could be used to predict yield of potato in a crop rotation. In the analysis yield was a function of the density of the pathogen in the soil when the crop is sown.

1.5 Experiments on soil borne pathogens in The Netherlands

In 1964 in the Netherlands a crop rotation experiment, called ‘de Schreef’ was laid out in the province of Flevoland on recently reclaimed soil. Soil-borne pathogens were not present at the start of the experiment, in which crop rotations differing in frequency of sugar-beets and potatoes were compared. Soil fungi showed up during the experiment and turned out to be a mayor cause of differences in yield level of potato, the most profitable arable crop (Hoekstra, 1989). Their intensity depended on the potato frequency in the crop rotation. Inspired by this experiment more crop rotation experiments were laid out in The Netherlands, to assess the dynamics of soil borne pathogens and associated yield loss (Scholte, 1990; Scholte and s’Jacob, 1990). A statistical investigation of the results of these experiments was performed by analysis of variance of data per crop and per year, and regression analysis was used for the prediction of yield loss caused by the soil borne pathogens (Scholte and s’Jacob, 1990). Also models for dynamics of soil borne pathogens and yield loss were formulated and fitted to experimental data (Seinhorst, 1965, Seinhorst, 1970, Mol et al., 1996).

1.6 Objectives

The overall objective of this thesis is to contribute to a methodological toolkit for designing and analyzing crop rotation experiments. A subsidiary aim is to apply methods for the analysis of specific soil borne pathogens in Dutch rotation experiments. In this approach five direct goals can be discerned:

- to develop dynamic models and yield loss relations for different host-pathogen systems and compare these for different crop rotations;
- to analyse the stationary states of the dynamic models and predict yield loss at the stable steady states;
- to develop a method for parameter estimation that uses data from heterogeneous sources;
- to predict yield loss when more than one soil borne pathogen is present using multimodel inference;
- to design optimum crop rotation experiments based on models and prior information on population and yield loss parameters.

1.7 Outline of the thesis

In Chapters 2 and 3, different dynamic models are introduced and applied to various pathogen-host systems in crop rotations. Nonlinear regression models are used to describe final nematode density as a function of the initial density. Formulating the nonlinear regression model as a difference equation with a yearly time step, a dynamic model for nematodes on different host crops is developed. In case studies on *Pratylenchus penetrans* and *Globodera pallida* the dynamics of these species and the associated yield loss within different rotations are modelled

In Chapter 4 soil fertility measurements and counts of several soil-borne pathogens are used to predict the yield level and the presence of disease symptoms of potato in a two-year crop rotation experiment. Model selection and multimodel inference is used to combine the predictive power of a large class of descriptive models.

Rotation experiments last many years. Therefore, it is important to choose an experimental design that enables an accurate estimation of parameters in dynamical models of pathogen densities and in yield loss models, see Chapters 2 and 3. For the case that pathogens and yield loss are covered by these models for only one year optimum designs were obtained in Chapter 5.

Finally, in Chapter 6 the contributions of the thesis to the methodology of designing and analyzing crop rotation experiments are discussed with a view to implications for future research.

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Chapter 2: Generalized linear dynamics of a plant-parasitic nematode population and the economic evaluation of crop rotations[1]

W. van den Berg and W.A.H. Rossing

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 only be possible on a short time-scale. 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, steady state, yield loss assessment.

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2.1 Introduction

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 of 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 e.g. 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 will 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

$$P_f = \frac{P_i}{\alpha + \beta P_i}\,. \tag{1}$$

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

$$P_f = \frac{\varphi H P_i}{1 + \frac{\gamma H P_i}{h}} = \frac{P_i}{\frac{1}{\varphi H} + \frac{\gamma P_i}{h\varphi}}, \tag{2}$$

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 *Meloidogyne 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. *Pratylenchus 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

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

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

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

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] taking $1/a$ equal to α and $(a\text{-}1)/aE$ equal to 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 standard 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.

2.2 Theory

Single year nematode dynamics in the presence of a host: In one-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 presence of a host crop. We ignore population decrease at high initial population levels, a finding well known for *e.g.* 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.

$$P_f = \frac{P_i}{\alpha}. \tag{5}$$

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):

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

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 and therefore Elston et al. (1991) proposed the simpler model

$$Y = \frac{1}{1+\lambda P_i}, \tag{7}$$

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 ha^{-1} year^{-1}) of a crop in absence of nematodes is equal to financial output (FO, euros ha^{-1} year^{-1}), the product of yield and value of the crop, minus the specific costs (SC, euros ha^{-1} year^{-1}) of the crop

$$GM = FO - SC . \tag{8}$$

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, so FO in Eq. [8] is multiplied with relative yield Y from Eq. [7]:

$$GM\left(P_i\right) = \frac{FO}{1+\lambda P_i} - SC \,. \tag{9}$$

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, crop 1 being phase 1, crop 2 being phase 2 and so on (Yates, 1954). The density of the nematode population at the start of year t is P_t. The dynamics are modeled by the equation

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

in which $\tau(t)=t(\text{mod})n$ and $1\le\tau\le n$. 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

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

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

$$R_2 = \beta(1) + \alpha(1)R_1 \qquad R_1 = \rho_0 \,, \tag{12}$$

$$R_3 = \beta(2) + \alpha(2)R_2 = \beta(1)\alpha(2) + \beta(2) + \alpha(1)\alpha(2)R_1 \,, \tag{13}$$

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

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

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

and after another three years

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

If the product of the α(*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 $t \to \infty$. For a finite geometric series,

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

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

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

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:

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

$$\overline{R}_2 = \beta(1) + \alpha(1)\underline{R}_1 \qquad (20)$$

and so on until

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

The steady state of nematode densities associated with phase (or crop) *j* is indicated by $\overline{R}_j$ whereas R_t, 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 $\overline{R}_j$, …, $\overline{R}_n$ is given in Appendix A. In steady state the gross margin associated with crop *j*, is equal to:

$$GM\left(\overline{R}_j\right) = \frac{FO(j)}{1+\frac{\lambda(j)}{\overline{R}_j}} - SC(j), \tag{22}$$

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

$$GM_R = \frac{1}{n}\sum_{j=1}^{n} GM\left(\overline{R}_j\right). \tag{23}$$

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, $\overline{R}_1$), it will return to the steady state only when the derivative of the function *g* to *R*, given $R=\overline{R}_1$, 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:

$$R_{(p+1)n+1} = g\left(R_{pn+1}\right) = \sum_{k=1}^{n-1}\beta(k)\prod_{m=k+1}^{n}\alpha(m) + \beta(n) + R_{pn+1}\prod_{s=1}^{n}\alpha(s). \tag{24}$$

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

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

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 $R = \overline{R}_j$, $j = 1,\ldots,n$. 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 β(k)'s, $k = 1,\ldots,n$. Combining equations [18] and [19] R_{pn+1} can be written as

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

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

$$R_{pn+1} = \overline{R}_1\left(1 - \prod_{s=1}^{n} \alpha(s)^p\right) + c\overline{R}_1 \prod_{s=1}^{n} \alpha(s)^p = \overline{R}_1 + (c-1)\overline{R}_1 \prod_{s=1}^{n} \alpha(s)^p . \tag{27}$$

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 the 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 $N(\mu_\alpha;\sigma^2_\alpha)$, $N(\mu_\beta;\sigma^2_\beta)$, $N(\mu_\pi;\sigma^2_\pi)$, 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 one-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

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

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 in 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, 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 $\overline{R}_j$ and $GM(\overline{R}_j)$, the major outputs of our model, to each of the parameters are listed in Appendix B.

2.3 A case study

Pratylenchus penetrans in field grown vegetable rotations: An experiment was performed from spring 1998 until autumn 2002 in the south-east 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 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 of 1998, 1999 and 2000 on all 96 plots will be 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 sub-sample with weight corresponding to 100 cm^3 soil was taken and nematodes were extracted into a suspension of 100 ml. From this suspension, two sub-samples of ten 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 cm^3 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 $\mu_\alpha, \sigma_\alpha^2, \mu_\beta, \sigma_\beta^2, \mu_\pi, \sigma_\pi^2$ of the prior normal distribution of the parameters α, β and π. The parameters were estimated by programming the Metropolis algorithm within Genstat (Genstat Committee, 2004).

For lettuce, leek and carrot parameters λ were estimated in yield loss assessment experiments also carried out in the south-east 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.

2.4 Results

The predictions of the model were closer to observations in spring 1998 than in spring of 1999 and 2000 (Figure 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, the relation between initial and final densities was well predicted by the model across the range of initial densities (Table 2, Figure 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 (Figure 3). Without nematodes present, predicted mean gross margin of the 6 rotations based on lettuce, leek, fallow and carrot was 6304 euro ha^{-1} yr^{-1}. With *P. penetrans* in the steady state for each crop, gross margins decreased by more than 1000 euro ha^{-1} yr^{-1} for rotation LE-LK-CT-FW and by nearly 2000 euro ha^{-1} yr^{-1}

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 (*Lactua sativa* L.)	15072	6645	8427
Leek (*Allium porri* L.)	18408	10158	8249
Fallow	*446	85	361
Carrot (*Daucus carota* L.)	13616	5438	8178

* EU fallow premium

Table 2. Estimates α ((nematodes/100 cm^3 soil)/(nematodes/100 cm^3 soil), β (100 cm^3 soil/nematodes) and λ (100 cm^3 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)

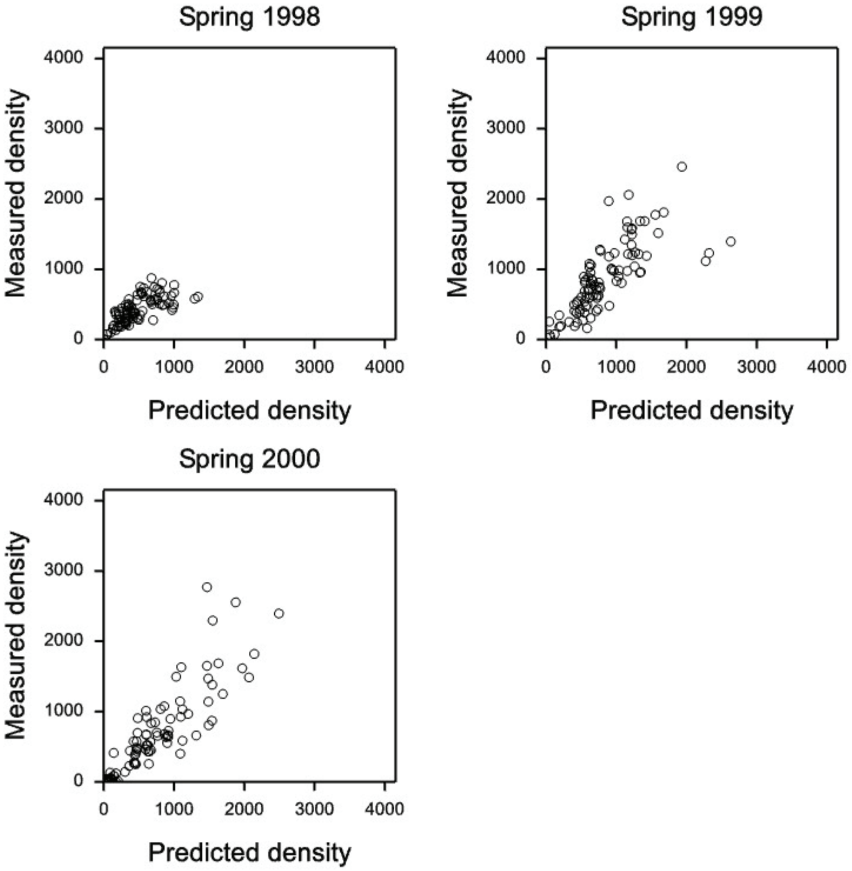

Fig. 1. Measured and predicted density (nematodes/100 cm^3 soil) in spring 1998, 1999 and 2000.

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 highest when lettuce was grown after fallow (Figure 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 higher for parameter β than for parameter α but highest 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.

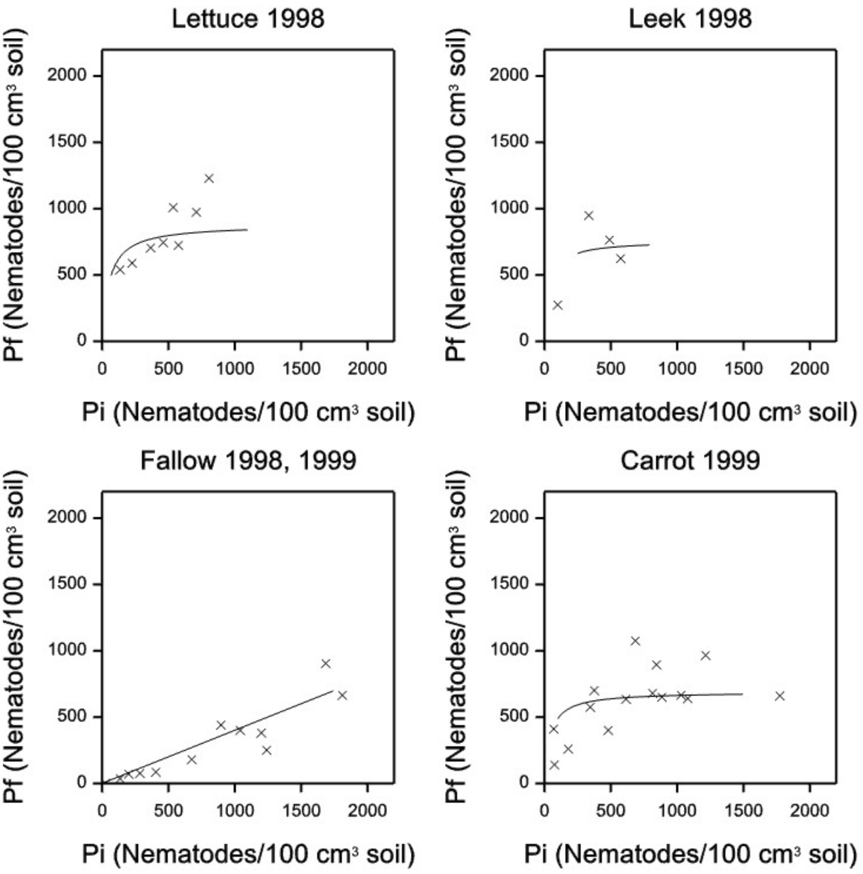

Fig. 2. Measured (x) and predicted (-----) response (nematodes/100 cm^3 soil) of *P. penetrans* to growth of lettuce, leek, fallow and carrot.

2.5 Discussion

We promote the general applicability of a dynamic rotation model and the 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 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

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

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], $\tau(t) = t(\mathrm{mod})n$ describes the pattern of crop alternation and $g(x)$ may be a transformation of x such as $1/x$, $\log(x)$, or $\mathrm{logit}(x)$. 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).

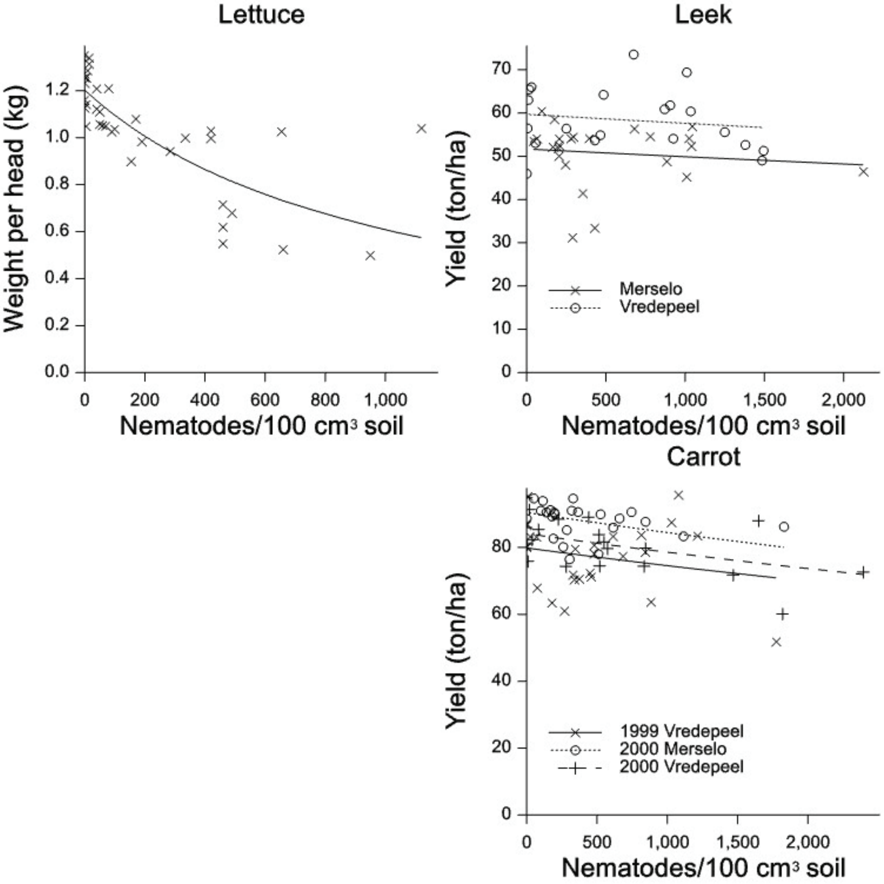

Fig. 3. Measured (x,o,+) and predicted (—) yield of carrot, leek and lettuce as function of initial nematode density (nematodes/100 cm^3 soil).

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 rotation with land-use types lettuce (LE), leek (LK), fallow (FW), and carrot (CT).

Crop Rotation	GM_R	$\frac{dGM_R}{d\alpha}$	$\frac{dGM_R}{d\beta}$	$\frac{dGM_R}{d\lambda}$
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

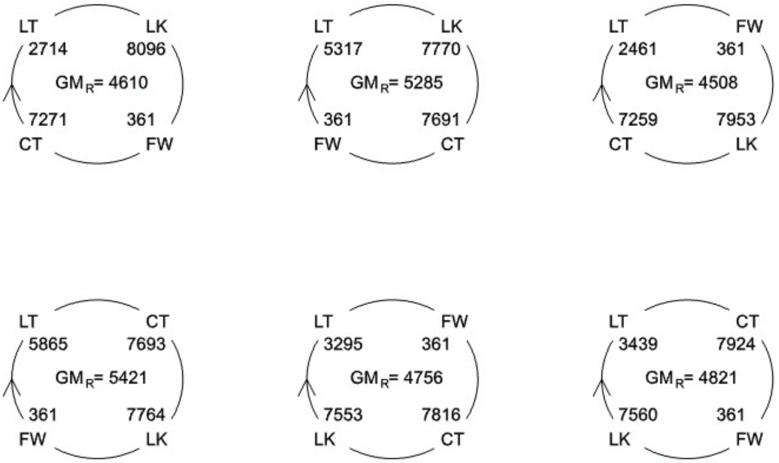

Figure 4. Gross margin per crop in each of the six crop rotations and mean Gross Margin of the rotation (GM_R) in euro ha^{-1}, $year^{-1}$. LT = Lettuce, LK = Leek, FW = Fallow and CT = Carrot.

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

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

By taking logarithms of both sides and replacing $\log(P_{t+1})$ and $\log(P_t)$ by L_{t+1} and L_t, and letting $\rho_0 = \log(\pi_0)$, Eq. [30] becomes

$$L_{t+1} = f(t, R_t) = \log\delta(\tau(t)) + \kappa(\tau(t))L_t, \qquad L_1 = \rho_0 \tag{31}$$

which is of the same form as Eq. [29]. A similar reasoning may be applied to the models where $\log(P_f)$ 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_f 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 a 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 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 will be 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 only be collated 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 of 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 semi-quantitative (Molendijk and Mulder, 1996). The approach presented in this paper represents a step towards 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 the Eq. [19], [20] and [21] can be written in matrix notation:

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

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

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

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

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

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

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

where

$$\overline{Y}_j = \frac{1}{1+\dfrac{\lambda(j)}{\overline{R}_j}}. \tag{A5}$$

Appendix B

Let

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

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

$$\frac{d\overline{R}_1}{d\alpha(1)} = \Psi \overline{R}_1 \prod_{k=2}^{n}\alpha(k), \tag{B2}$$

$$\frac{d\overline{R}_1}{d\alpha(j)} = \Psi\left(\sum_{k=1}^{j-1}\beta(k)\prod_{m=j+1}^{n}\alpha(m)\right) + \frac{\Psi \overline{R}_1 \prod_{s=1}^{n}\alpha(s)}{\alpha(j)} \quad j = 2,\ldots, n-1, \tag{B3}$$

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

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

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

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

Let

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

The derivative of *GM*($\bar{R}_j$) in Eq. [22] with respect to α(*j*), β(*j*) and λ(*j*) equals

$$\frac{dGM\left(\bar{R}_j\right)}{d\alpha(j)} = \Omega(j)FO(j)\frac{\lambda(j)}{\bar{R}_1^2}\frac{d\bar{R}_j}{d\alpha(j)} \ , \tag{B8}$$

$$\frac{dGM\left(\bar{R}_j\right)}{d\beta(j)} = \Omega(j)FO(j)\frac{\lambda(j)}{\bar{R}_1^2}\frac{d\bar{R}_j}{d\beta(j)} \ , \tag{B9}$$

$$\frac{dGM\left(\bar{R}_j\right)}{d\lambda(j)} = -\frac{\Omega(j)FO(j)}{\bar{R}_j} \ . \tag{B10}$$

Chapter 3: Contest and scramble competition and the carry-over effect in *Globodera* spp. in potato-based crop rotations using an extended Ricker model[2]

W. van den Berg, W.A.H. Rossing, and J. Grasman

Abstract

The Ricker model extended with a linear term was used to model the dynamics of a potato cyst nematode population on different potato cultivars over a wide range of population densities. The model accounts for contest and scramble competition and between-year carryover of unhatched eggs. Contest competition occurs due to the restricted amount of available root sites that are the feeding source of the female nematode. Nematodes not reaching such a feeding site turn into males and do not contribute to a new generation. Scramble competition results in a decrease of the number of eggs per cyst at high densities due to the decrease in the food supply per feeding site. At still higher densities, the size of the root system declines; then dynamics are mostly governed by carryover of cysts between subsequent years. The restricted number of three parameters in the proposed model made it possible to calculate the equilibrium densities and to obtain analytical expressions of the model's sensitivity to parameter change. The population dynamics model was combined with a yield-loss assessment model and, using empirical Baysian methods, was fitted to data from a 3-year experiment carried out in the Netherlands. The experiment was set up around the location of a primary infestation of *Globodera pallida* in reclaimed polder soil. Due to a wide range of population densities at short distances from the centre of the infestation, optimal conditions existed for studying population response and damage in different cultivars. By using the empirical Bayes methods it is possible to estimate all parameters of the dynamic system, in contrast to earlier studies with realistic biological models where convergence of parameter estimation algorithms was a problem. Applying the model to the outcome of the experiment, we calculated the minimum gross margin that a fourth crop needs to reach in order to be taken up in a 3-year rotation with potato. An equation was derived that accounted for both gross margin changes and nematode-related yield loss. The new model with its three parameters has the right level of complexity for the amount and type of collected data. Two other important models from the literature, containing 5 and 10 parameters respectively, may at this point turn out to be less appropriate. Consequences for research priorities are discussed and prediction schemes are taken in consideration.

Key words: carryover, contest competition, crop rotation, economic evaluation, gross margin, population dynamics, *Globodera* spp., Ricker model, scramble competition, sensitivity analysis, stability, steady state, yield loss assessment.

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3.1 Introduction

After the discovery of the Americas the potato was introduced into Spain from South America and from there the cultivation of potato spread across Europe. In the nineteenth century the potato-specific potato cyst nematode *Globodera rostochiensis* was imported from South America to Europe. In 1954, the first cultivars resistant to *G. rostochiensis* became available. Resistant cultivars cause potato cyst nematodes (PCN) occurring in the rooted fraction of the soil to hatch and penetrate the roots. However, multiplication is not observed, so the hatched PCN die and only the PCN present in the nonrooted fraction of the soil survive. Because resistance and tolerance, the ability to withstand yield loss after infection (Zadoks and Schein, 1979), have different genetic basis, resistant cultivars may incur loss. The *H1* and *H2* genes that make potato resistant to *G. rostochiensis* do not convey resistance to *G. pallida* (Stone, 1973). Therefore, infestations with *G. pallida* were initially controlled by use of nematicides. In the 1980s, cultivars partially resistant to *G. pallida* were introduced. With these cultivars the population density of the nematode can be kept at low levels. Environmental laws in The Netherlands currently allow fumigation once every 5 years. Control of PCN by deployment of resistant and tolerant potato cultivars is therefore an important strategic issue to enhance financial income for farmers and minimize environmental impacts.

During the twentieth century, extensive agricultural research programs were implemented to study soil sampling to estimate nematode population densities (Anscombe, 1950; Oostenbrink, 1950; Stelter and Raeuber, 1962; Seinhorst, 1982; Been and Schomaker, 2000). Moreover yield loss assessment (Seinhorst, 1965; Oostenbrink, 1966; Van Oijen et al., 1995; De Ruijter and Haverkort, 1999) and the population dynamics of nematodes (Oostenbrink, 1966; Seinhorst, 1970; Jones et al., 1978; Philips et al., 1991; Schomaker and Been, 1998) have been the subject of research. A mechanistic model for the dynamics of PCN and associated damage to potato was made by Schans (1993). In this paper we propose a model that is able to describe population dynamics of nematodes and their damage within a crop rotation scheme taking into account commonly measured quantities.

Nicholson (1954) recognised two extreme forms of competition which he called contest and scramble competition. In contest competition, each successful competitor obtains all resources it requires for survival or reproduction; the remaining competitor, being deprived of its resources, will not be able to function anymore. In scramble competition, the finite resource is shared equally amongst the competitors so that the quantity of food per individual declines with increasing population density (Varley et al., 1975). With potato cyst nematodes feeding on potato roots both forms of competition are present. There is a maximum number of feeding places per unit weight of roots of the potato to feed a female nematode (contest competition). In addition, feeding by nematodes is harmful for the potato plants, resulting in scramble competition (decline of the number of eggs formed per cyst with rise of density). Finally, at still higher nematode densities, there is a decline of the quantity of roots.

Jones et al. (1978) described the relation between population density of PCN after harvest (P_f) and before planting (P_i) as

$$P_f = \frac{fHP_i}{1+\dfrac{bHP_i}{h}}, \tag{1}$$

where, H is the proportion of the hatching juveniles that successfully settle in the roots of the potato plants, b is the constant of proportionality between the ratio of males to females and the density of juveniles in the roots, f is the average number of eggs laid per female, and h is the density of roots (cm root/g soil). This function (1) results in a type curve, with a horizontal asymptote (saturation). When the asymptote is approached, the maximum number of feeding places occupied by a female nematode is reached, each with ample food supply (contest competition). In their model (D), Philips et al. (1991) follow Elston at al. (1991) and assume root density, h, to be an inverse linear function of P_i

$$h(P_i) = \frac{h(0)}{1+cP_i}, \tag{2}$$

which is the product of h(0), the root density at $P_i = 0$, and the relative root density $1/(1+cP_i)$, being a function of P_i. Assuming that a fraction C_p of the nematodes does not hatch and is carried over to the following year, Philips et al. (1991) obtain:

$$P_f = \frac{fH(1-C_p)P_i}{1+\dfrac{bH(1-C_p)P_i(1+cP_i)}{h(0)}} + C_pP_i, \tag{3}$$

At low values of P_i the value of P_f increases according to Eq. (1), describing contest competition. At higher values of P_i, the value of P_f decreases as a result of scramble competition at still higher values the effect of carryover (C_p) dominates. Philips et al. (1991) found that estimates of C_p for the cultivars in their experiments ranged from 0.45 for the cultivar with lowest partial resistance to 0.74 for the most resistant cultivar. The latter value is higher than 0.67, the value of the surviving fraction usually found following a non-host crop. Because of the high estimates of C_p for resistant cultivars, Philips et al. (1991) propose C_p to be density-dependent in further studies, which is in agreement with the suggestion by Seinhorst (1986). When Philips et al. (1991) tried to fit Eq. (3) to data, they found their algorithm did not converge. To overcome this problem they estimated the parameter *c* fitting tuber yields to Eq. (2).

Seinhorst (1970) presented a model similar to Eq. (1). The corresponding curve of this model has a horizontal asymptote. The model is also based on contest competition as described by Nicholson (1954):

$$P_f = M\left(1 - e^{-\frac{a}{M}P_i}\right), \tag{4}$$

where *a* equals the slope of the curve in the origin and *M* is the horizontal asymptote. Seinhorst (1993) and Schomaker and Been (1998) extended Eq. (4) by two functions of P_i: one for relative decline of the number of eggs produced per cyst (y_e), and one for the relative decline of root growth, which is assumed to be proportional to haulm growth (y_h). The functions y_e and y_h are of the form (Seinhorst, 1965)

$$y_e(P_i) = m_e + (1 - m_e)z_e^{P_i - T_e}, \qquad P_i \geq T_e \tag{5a}$$

$$y_e(P_i) = 1, \qquad P_i < T_e \tag{5b}$$

$$y_h(P_i) = m_h + (1 - m_h)z_h^{P_i - T_h}, \qquad P_i \geq T_h \tag{5c}$$

$$y_h(P_i) = 1, \qquad P_i < T_h \tag{5d}$$

where T_e and T_h are threshold values above which density-dependent effects occur. Parameter m_e ($0<m_e<1$) and m_h ($0<m_h<1$) are asymptotes of y_e and y_h P_i tends to infinity. The parameters z_e ($0<z_e<1$) and z_h ($0<z_h<1$) are rate parameters. Furthermore, Seinhorst (1993) and Schomaker and Been (1998) added a term in Eq. (4) to describe density-dependent carryover of non-hatching nematodes to the next year. This resulted in an extended form of Eq. (4):

$$P_f = y_h y_e M\left(1 - e^{-\frac{a}{M}P_i}\right) + (1 - s y_h) b P_i, \tag{6}$$

where parameter *s* is the rooted fraction of the soil when P_i=0 and *b* is the non-hatching fraction of the nematodes that carry over to the next year in the non-rooted fraction of the soil. Note that equation (6) contains 10 parameters.

In this study, we will present an alternative model with fewer parameters that describes dynamics of potato cyst nematodes in potato crop rotations over the whole range of prevailing densities. It will be shown that the density approaches a stable steady state which can be expressed in an analytically form. We link the population dynamics model to a yield loss assessment model to facilitate ex ante economic evaluation of potato-based crop rotations in the presence of PCN. The performance of the model will be tested using results of a field experiment from The Netherlands.

3.2 Theory

The Ricker model extended with a linear term: In this section an extension of the Ricker model will be presented that replaces Eq. (3) and (6) and that also describes the dynamics of PCN in potato crop rotations at low as well at high population densities. The Ricker model is frequently used to describe scramble competition in fish populations where the offspring per female declines with increasing population density (Edelstein-Keshet, 1988). The model also applies to plant populations where the number of seeds formed per unit area declines with increasing number of plants per unit area (Silvertown and Charlesworth, 2001). To model scramble competition of PCN on potato, the carryover effect must be included. We therefore add a linear term to the Ricker model so that we have:

$$P_f = \beta_1 P_i e^{-\beta_2 P_i} + \beta_3 P_i . \tag{7}$$

At low densities multiplication is approximately equal to $\beta_1+\beta_3$ and at higher densities the parameter β_2 causes decline of the curve. Parameter β_3, the fraction of P_i which remains in the soil, represents the positive slope of the asymptote, for P_i tending to infinity (Figure 1).

In contrast to the Ricker model, Eq. (7) has no analytical solution for the value of P_i at which P_f is at its maximum. Similar to the point of inflection of the Ricker curve, the value of P_i at the point of inflection for Eq. (7) is $2/\beta_2$. At the point of inflection P_f equals

$$P_{f\text{-inflection}} = \frac{2\beta_1}{\beta_2 e^2} + \frac{2\beta_3}{\beta_2} . \tag{8}$$

The slope of the tangent to the curve in the point of infection is equal to $-\beta_1/e^2+\beta_3$.

Single year nematode dynamics: We will use Eq. (7) to model the dynamics of the PCN during growth of susceptible or partially resistant cultivars. When a resistant cultivar is grown in soil infested with a population of *G. rostochiensis*, the non-hatching fraction or carryover is described by:

$$P_f = \beta_3 P_i, \tag{9}$$

meaning that the parameters β_1 and β_2 are 0. When resistant cultivars are grown on soils infested with *G. rostochiensis,* the nematode population will become extinct. So

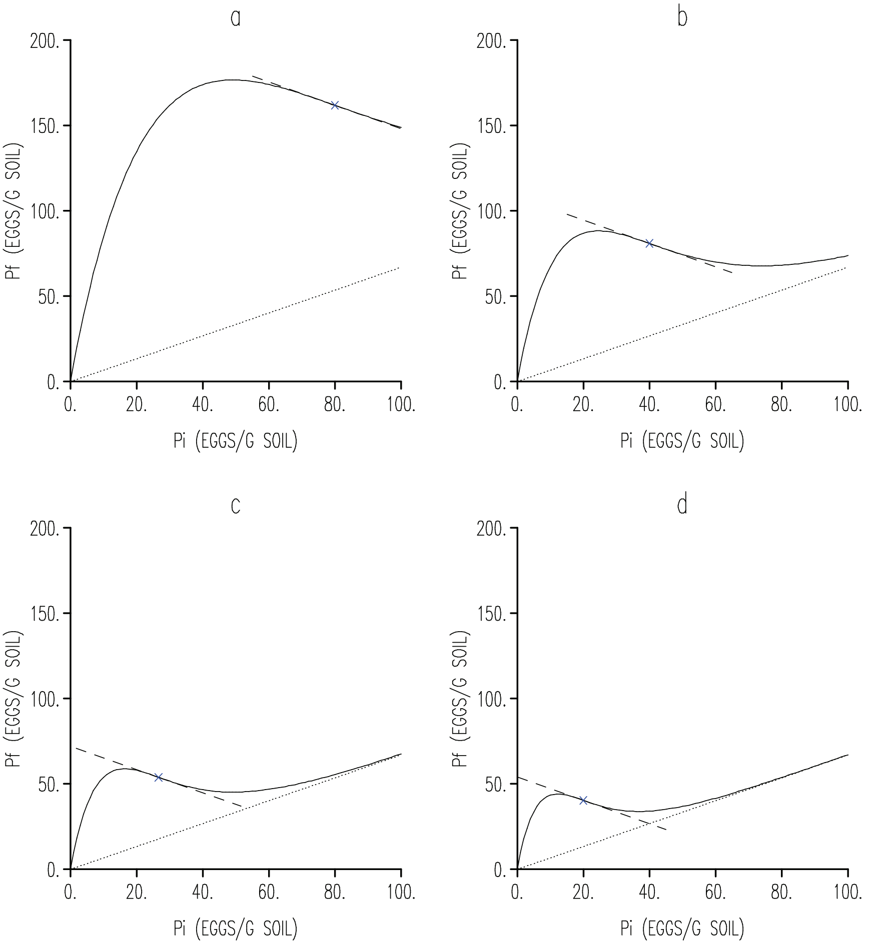

Figure 1. The Ricker model according to Eq. (7) for β_1 = 10 and β_2 = 0.025(a), 0.05(b), 0.075(c) or 0.10(d) and β_3 = 0.67. Also shown is the tangent to the curve in the point of inflection. The slope of the line from the origin equals β_3.

there is a stable, steady state equal to zero. When no potatoes are grown, a fraction 1-ρ of the nematodes will hatch in spring because of increasing temperature and subsequently die. Carryover in the absence of potato is described by parameter ρ, which often is assumed to be equal to 0.67 (Whitehead and Turner, 1998):

$$P_f = \rho P_i \,. \tag{10}$$

Yield loss assessment and financial result: In this study we use the following curve for yield loss assessment

$$Y = \frac{1}{1+\lambda P_i}, \tag{11}$$

where *Y* is the potato tuber yield relative to an uninfested control and λ is a rate parameter. The gross margin (*GM*) of a crop in absence of nematodes is equal to the financial output (*FO*) minus the specific costs (*SC*) of the crop

$$GM = FO - SC. \tag{12}$$

The expected values of these quantities are published regularly by Applied Plant Research for the major crops in arable farming and field production of vegetables in the most important agricultural regions of the Netherlands (Dekkers, 2001). Financial output is the product of the assumed yield of the crop (weight units/ha) and the assumed price of the yield (euros/weight unit). When nematodes are present we assume that the yield is a function of P_i, so *FO* in Eq. (12) is multiplied with relative yield from Eq. (11):

$$GM(P_i) = \frac{FO}{1+\lambda P_i} - SC \,. \tag{13}$$

Thus, the financial output, and consequently the gross margin only decline due to nematodes. The price per unit product is kept constant; product quality considerations are ignored.

Dynamics of potato cyst nematode in rotations: The Ricker model, extended with a linear term as in Eq. (7), fully captures the dynamics over the prevailing range of densities with fewer parameters than Eqs. (3) and (6). Now we will show how this equation can be used to map the dynamics of PCN in crop rotations over time. For potatoes grown in year *t*, the density P_{t+1} in spring of year *t*+1 is a function of the density P_t in spring of year t:

$$P_{t+1} = \beta_1 P_t e^{-\beta_2 P_t} + \beta_3 P_t , \qquad P_1 = \pi_0 . \tag{14}$$

For rotations in which n crops are grown in yearly succession, the period of the rotation is n years, and the number of passed rotations is p (p=0,…,∞). Assuming potatoes are grown in year $t=pn+1$, multiplication of nematodes during that year is described by Eq. (14). In each of the subsequent n-1 nonpotato years a fraction 1-ρ of the population will hatch and die from starvation. Population density in year $(p+1)n+1$ will be equal to:

$$P_{(p+1)n+1} = g\left(P_{pn+1}\right) = \beta_1 \rho^{n-1} P_{pn+1} e^{-\beta_2 P_{pn+1}} + \beta_3 \rho^{n-1} P_{pn+1} . \tag{15}$$

Steady state is reached when PCN densities at the start of subsequent potato crops are identical, $P_{(p+1)n+1} = P_{pn+1} = \overline{P_n}$. Substituting the steady state condition $\overline{P_n} = g\left(\overline{P_n}\right)$ into Equation (15) and solving the equation for $\overline{P_n}$ gives:

$$\overline{P_n} = \frac{-1}{\beta_2} \ln\left(\frac{1-\beta_3 \rho^{n-1}}{\beta_1 \rho^{n-1}} \right). \tag{16}$$

Equation (16) is valid for *G. pallida,* and for valid for *G. rostochiensis* when a susceptible cultivar is grown. Because $\overline{P}$ must be greater than or equal to zero, $\beta_1\rho^{n-1}$ has to be greater than $1-\beta_3\rho^{n-1}$, which holds when $(\beta_1+\beta_3)\rho^{n-1}>1$. When this is not true, the population will go extinct. When a resistant cultivar is grown on soil infested with *G. rostochiensis* parameters β_1 and β_2, as well as $\overline{P}$, the stable steady state, are all equal to zero. When a susceptible cultivar is grown on soil infested with *G. rostochiensis* or when a partially resistant cultivar is grown on soil infested with *G. pallida,* the parameters β_1 and β_2 are both greater than zero.

When comparing profitability of a 3-yr rotation and a 4-yr rotation in absence of harmful nematodes, the added fourth crop will increase the income of the farmer when the gross margin of the fourth crop is higher than the mean gross margin of the 3-yr rotation (GM_3). In a rotation with potato and in presence of PCN, the decision problem is as follows, The mean gross margin of a rotation (GM_R) with one potato crop and n-1 other crops is equal to

$$GM_{Rn} = \frac{\dfrac{FO_{potato}}{1+\lambda \overline{P_n}} - SC_{potato} + \sum_{r=2}^{n} GM(r)}{n} , \tag{17}$$

where GM_{Rn} is the mean gross margin of a rotation with n crops and $GM(r)$ is the gross margin of non-host crop r. In Eq. (17) and (18) potato is crop 1 and the nonhost crops are crop 2 to n. It is profitable to change from a rotation with n crops to a rotation with n+1 crops when $GM_{R(n+1)} > GM_{Rn,}$ which is true when

$$GM(n+1) > (n+1)GM_{Rn} - \frac{FO_{potato}}{1+\lambda \overline{P}_{n+1}} + SC_{potato} - \sum_{r=2}^{n} GM(r) \tag{18}$$

For example a farmer has to choose between a 3-yr and a 4-yr rotation with potato, so $n = 3$. In a 3-yr rotation, there is potato and two other crops. Addition of a fourth crop to the rotation is profitable when Eq. (18) holds .

The stability of the steady state in Eq. (15) is investigated as follows. The derivative of $g(P_n)$ at P_n is needed which equals

$$\left.\frac{dg}{dP_n}\right|_{P_n=\overline{P}_n} = \left(1-\beta_3\rho^{n-1}\right)\log\left(\frac{1-\beta_3\rho^{n-1}}{\beta_1\rho^{n-1}}\right)+1\,. \tag{19}$$

For stability, the absolute value of the derivative of $g(P_n)$ must be less than 1. For a sensitivity analysis, the derivatives of Eq. (16) and (17) to each of the parameters β_1, β_2, β_3, ρ and λ are necessary. These derivatives are given in Appendix A.

3.3 Materials and methods

Experimental design and analysis: During the years 1989 to 1991, an experiment was performed in a field infested with *G. pallida* pathotype Pa3. A focus of a young infestation was present, resulting in large density gradients (Schomaker and Been, 1999). In spring 1989, a grid of 132 experimental units of 3.8 x 1.5 m, 22 rows x 6 columns was superimposed on the focal infestation such that the highest density was at the intersection of rows 12 and 13 and columns 3 and 4 (Table 1). Each half column formed a block of 11 experimental units. In 1989, the cultivars Agria, Bintje, Santé and Van Gogh were randomized over the 12 available blocks. In 1990, the same four cultivars were grown, but the cultivars were assigned to the blocks in such a way that a susceptible cultivar was succeeded by a resistant cultivar and vice versa. In 1991, the cultivars Bintje, Darwina, Santé and Turbo were assigned to the 12 blocks. Cultivar

Table 1. Combinations of cultivar and initial density of *G. pallida* (number of eggs and larvae per g dry soil) per experimental unit of a field experiment in 1989. Cultivar codes: A = Agria, B = Bintje, S = Santé, VG = van Gogh. Size of the experimental unit was 3.8 x 4.5 m. Initial density is not mentioned when lower than 0.5. Rows 1, 2, 3, 20, 21 and 22 contained very low densities and are not shown.

Column	1	2	3	4	5	6
Row						
4	A	VG	B 1	A	S	A
5	A	VG 1	B 1	A	S	A
6	A	VG	B 1	A	S	A
7	A	VG	B 1	A	S	A
8	A 1	VG	B 3	A 1	S	A
9	A 2	VG 2	B 4	A 1	S	A
10	A 3	VG 2	B 8	A 3	S 1	A 1
11	A 3	VG 3	B 6	A 4	S 2	A 3
12	B 5	A 5	S 15	VG 2	B 6	S 3
13	B 2	A 4	S 6	VG 4	B 1	S 4
14	B 1	A 2	S 13	VG 2	B	S 1
15	B	A 1	S 7	VG	B	S
16	B	A	S 4	VG	B	S
17	B	A	S 2	VG	B	S
18	B	A	S 3	VG	B	S
19	B	A	S 1	VG	B	S

Bintje is susceptible for all pathotypes of *Globodera*, cultivars Agria, Turbo and Van Gogh are resistant to pathotype Ro1 of *Globodera*, cultivar Santé is resistant to Ro1 and Pa2, and cultivar Darwina is resistand to R1, Pa2 and Pa3.

On each experimental unit, nematode density was measured before potatoes were planted (P_i) and also after potatoes were harvested (P_f). Density defined as number of eggs and larvae per gram dry soil was measured six times: in spring and autumn of the years 1989, 1990 and 1991. Tuber yield was measured on the two central rows of each experimental unit and expressed per unit area. Parameter λ of the tuber yield loss, as function of initial density in spring, Eq. (11), was estimated with nonlinear regression.

Parameter estimation using Bayesian methods: There were 168 parameters to be estimated: 12 estimates of β_1, β_2 and β_3 because there were 12 combinations of year and cultivar. Further, an estimate of parameter π_0 had to be made for each experimental unit. The experimental design allowed estimation of these parameters of the model describing the dynamics of the nematode. Eq. (7) was formulated in a dynamic fashion and fitted to data of the six measurements in time with the Metropolis algorithm and empirical Bayesian methods (Carlin and Louis, 2000, chapter 5). For such an analysis the likelihood of the data and the prior distribution of the parameters must be specified (Appendix B). The likelihood was calculated by assuming the data are Poisson distributed with an expectation equal to the prediction of the dynamic fashion of Eq. (7). Pearson's X^2 was calculated to estimate dispersion of the data

$$X^2 = \sum_{i=1}^{n} \frac{(y_i - \hat{y}_i)^2}{\hat{y}_i}, \tag{20}$$

where y_i is the observation, $\hat{y}_i$ is the prediction, and n the number of observations. The dispersion is equal to X^2 over the number of observations minus the number of parameters. The natural logarithm of the 12 estimates of parameters β_1, β_2 and β_3 and the 132 estimates of parameter π_0 were each assumed to have a normal prior distribution. Thus β_1, β_2 and β_3 and π_0 are assumed to have prior distributions $N(\mu_{\beta1}, \sigma_{\beta1}^2)$, $N(\mu_{\beta2}, \sigma_{\beta2}^2)$, $N(\mu_{\beta3}, \sigma_{\beta3}^2)$, $N(\mu_{\pi0}, \sigma_{\pi0}^2)$. The means and variances of these four normal distributions were estimated in a Bayesian analysis. For stability of the analysis, the logarithms of all parameters were estimated. Back-transformed medians are presented, and with a Taylor expansion the corresponding standard errors were calculated. In the Metropolis algorithm, new candidate parameters sets for each iteration step was generated by adding a sample from the normal distribution $N(0, 0.0002)$ to the logarithm of the current value of each parameter. It was assumed that population density did not change during winter months.

Scenario study: Using the estimated parameters of Eq. (7), economic consequences of less potato-intensive crop rotations were explored. The Dutch classical intensive 3-yr rotation (*R3*) potato - sugar beet - winter wheat acted as a reference. The mean gross margin of this rotation when PCN is not present is equal to (3490+2867+1330)/3 = 2562 €/ha. As an illustration, the gross margin of several arable crops are shown in Table 2 (Dekkers, 2001). *FO* and *SC* are mentioned for potato only; roots of the other crops are not harmed by potato cyst nematode, so for economic evaluation of these crops only the gross margin is necessary. When PCN is present, a susceptible nontolerant potato cultivar will have a higher yield in a 4-yr rotation than in a 3-yr rotation. It is assumed that in nonpotato years, 33% of the eggs hatch and die from starvation because they cannot feed or reproduce on potato roots.

For each combination of cultivar and year the parameters β_1, β_2, β_3 and λ of the extended Ricker model and the yield loss assessment model were estimated and used to calculate steady states for the 3- yr ($\overline{P_3}$) and 4- yr ($\overline{P_4}$) rotations, respectively.

Table 2. Financial output (*FO*), specific costs (*SC*) and gross margin (*GM*) of crops in evaluated rotations (€ /ha).

Crops	*FO*	*SC*	*GM*
Ware Potato (average of all cultivars)	5413	1923	3490
Sugar-beet			2867
Winter-wheat			1330
Onions			3279
Chicory			1611
Flax			983

Stability of the steady states was investigated. Sensitivity of the result to uncertainty in each of the parameters was analyzed. To conclude whether a candidate fourth crop is profitable for including in rotation *R*3, the necessary gross margin *GM*(4) was calculated wit Eq. (18).

3.4 Results

The density of PCN, averaged over all plots, increased each year between spring and autumn during cultivation of potato. The size of the increase depended on initial density and susceptibility of the cultivars grown (Table 3). For example, in 1991 multiplication was low (26.8/20), due to higher initial density than in 1989 and 1990 and growth of two resistant cultivars, Darwina, and Santé. Density in winter 1989-1990 increased from 5.9 to 8.7, due to removal of 32 experimental units with low population density from the experiments in spring 1990. The density of the remaining 106 experimental units was 7.2 eggs and larvae/g soil in autumn 1989. In winter 1990-1991, density decreased from 23.3 to 20.0, so on average density was rather stable during winter (Table 3). Removal of the 32 experimental units from the experiment after 1989 did not influence the analysis and resulted in 662 measurements in the analysis.

At the start of the experiment in spring 1989 the nematode density was low even in the centre of the infestation (Table 1, Fig. 1). In the course of the 3-yr experiment, nematode density reached a level of about 80 eggs/g soil. Estimates of parameter β_1 describing the fractional multiplication in the presence of a potato crop ranged from 6.9 to 22.1 for the susceptible cultivars Agria, Bintje, Van Gogh and Turbo. For the resistant cultivars Santé and Darwina values between 0.6 and 2.6 were found (Table 4, Fig 2). Cultivar Turbo, resistant only to pathotype Ro1, multiplied less in 1991 than Bintje and so showed partial resistance to *Globodera pallida*.

Estimates of parameter β_2 describing the scramble effect varied between 0.05 and 0.60. Parameter β_3 varied between 0.39 (Darwina in 1991) and 0.88 (Turbo in 1991). The cultivar Agria appeared to be more tolerant than the other three cultivars in1990, but differences in parameter λ were not significant (Table 4). In 1989 with low initial densities, the rate parameter, λ, was estimated with high standard errors, especially for Bintje, Santé, and Van Gogh (Table 4, Fig. 3). In 1991 the estimate of λ for Darwina was higher (P=0.05) than for cultivars Santé and Turbo. No correlation between the parameters β_2 describing scramble competition and the parameter λ, the rate parameter for yield loss per unit nematode infection, was detected. Because 3 and 4-yr rotations prevail in practice, we will discuss $\overline{P_3}$ and $\overline{P_4}$ from Eq. (16) for the 12 combinations of year and cultivar in this case study. For the susceptible cultivars

Table 3. Density of potato cyst nematode in spring and autumn of 1989, 1990 and 1991.

Year	Spring	Autumn
1989	1.4	5.9
1990	8.7	23.3
1991	20.0	26.8

Table 4. Estimates of parameters β_1, β_2, β_3 and λ with standard deviation between brackets for each combination of year and cultivar. Estimates without a common letter are significantly different (P=0.05).

Year/Cultivar	β_1	β_2	β_3	λ
1989 Agria	7.3(0.5)c	0.12(0.02)bc	0.78(0.09)d	0.027(0.010)a
1989 Bintje	6.9(0.4)c	0.08(0.01)ab	0.61(0.05)cd	0.025(0.123)a
1989 Santé	0.8(0.2)a	0.32(0.02)ef	0.47(0.03)ab	0.039(0.013)ab
1989 v Gogh	12.3(0.6)e	0.05(0.01)a	0.77(0.07)d	0.080(0.024)ab
1990 Agria	9.8(0.6)d	0.08(0.00)ab	0.58(0.06)bcd	0.042(0.005)ab
1990 Bintje	16.2(2.2)e	0.22(0.03)d	0.79(0.09)d	0.079(0.009)ab
1990 Santé	0.6(0.1)a	0.23(0.04)de	0.65(0.04)cd	0.076(0.014)ab
1990 v Gogh	16.2(1.4)e	0.09(0.01)b	0.71(0.06)d	0.068(0.011)ab
1991 Bintje	22.1(1.5)f	0.10(0.00)b	0.65(0.05)cd	0.049(0.005)ab
1991Darwina	2.6(0.4)b	0.60(0.19)f	0.39(0.02)a	0.083(0.016)b
1991 Santé	3.4(0.4)b	0.15(0.01)c	0.57(0.03)bc	0.033(0.005)a
1991 Turbo	14.0(1.0)e	0.12(0.00)b	0.88(0.06)e	0.026(0.004)a

Agria, Bintje, Turbo and Van Gogh, $\overline{P_3}$ and $\overline{P_4}$ were high while these densities were low for the resistant cultivars Santé and Darwina (Table 5).
Steady state states $\overline{P_3}$ and $\overline{P_4}$ were negative for Santé in 1989 and 1990 and $\overline{P_4}$ was negative for Darwina in 1991 (Table 5) because values of $(\beta_1+\beta_3)\rho^2$ and $(\beta_1+\beta_3)\rho^3$ were less than 1. Based on these parameter estimates, the population would become extinct. The positive steady states were stable for all objects even when potatoes were grown continuously. In 1989 and 1990 the mean gross margin of the 3-yr rotation, GM_{R3}, was highest for Santé, in 1991 for Darwina. The gross margin needed for a fourth crop to be profitable as extension of a 3-yr rotation to a 4-yr rotation, G*M*(4), was above 2,000 euro for the resistant cultivars Darwina and Santé (Table 5). However, *GM*(4) was lower than 2,000 euro for all susceptible cultivars. According to the gross margins in Table 2 from Dekker (2001), flax will never be profitable as a fourth crop because its gross margin is lower than GM(4) for every combination of year and cultivar in Table 5. Onion will be always profitable as a fourth crop because the gross margin of onion is higher than *GM*(4) for every combination of year and cultivar in Table (5). Chicory, with a gross margin of 1,611 euro/ha/yr is higher than *GM*(4) of some of the combinations of susceptible and year in Table 5.

Table 5. Average of $\overline{P_3}$, $\overline{P_4}$, GM_{R3} and $GM(4)$ for each combination of year and cultivar. For $\overline{P_3}$ and $\overline{P_4}$ means without a common letter are significantly different (P=0.05).

Year/Cultivar	$\overline{P_3}$	$\overline{P_4}$	GM_{R3}	$GM(4)$
1989 Agria	13.9(1.5)de		1796	1748
1989 Bintje	18.3(2.5)ef	11.8(1.5)de	2128	1914
1989 Santé	-2.1(0.6)a	-3.6(0.7)a	2629	2336
1989 van Gogh	41.1(8.7)f	30.3(6.4)g	1344	1331
1990 Agria	22.2(0.6)f	15.8(0.6)f	1752	1663
1990 Bintje	10.9(0.6)d	8.3(0.4)c	1687	1608
1990 Santé	-4.2(0.9)a	-6.6(1.3)a	2540	2264
1990 van Gogh	25.5(1.0)f	19.6(0.6)g	1440	1393
1991 Bintje	26.2(0.7)f	21.0(0.6)g	1555	1475
1991 Darwina	0.6(0.3)b	-0.2(0.4)b	2380	2093
1991 Santé	4.9(0.7)c	1.4(0.8)b	2345	2108
1991 Turbo	20.3(0.6)f	15.1(0.5)ef	1922	1761

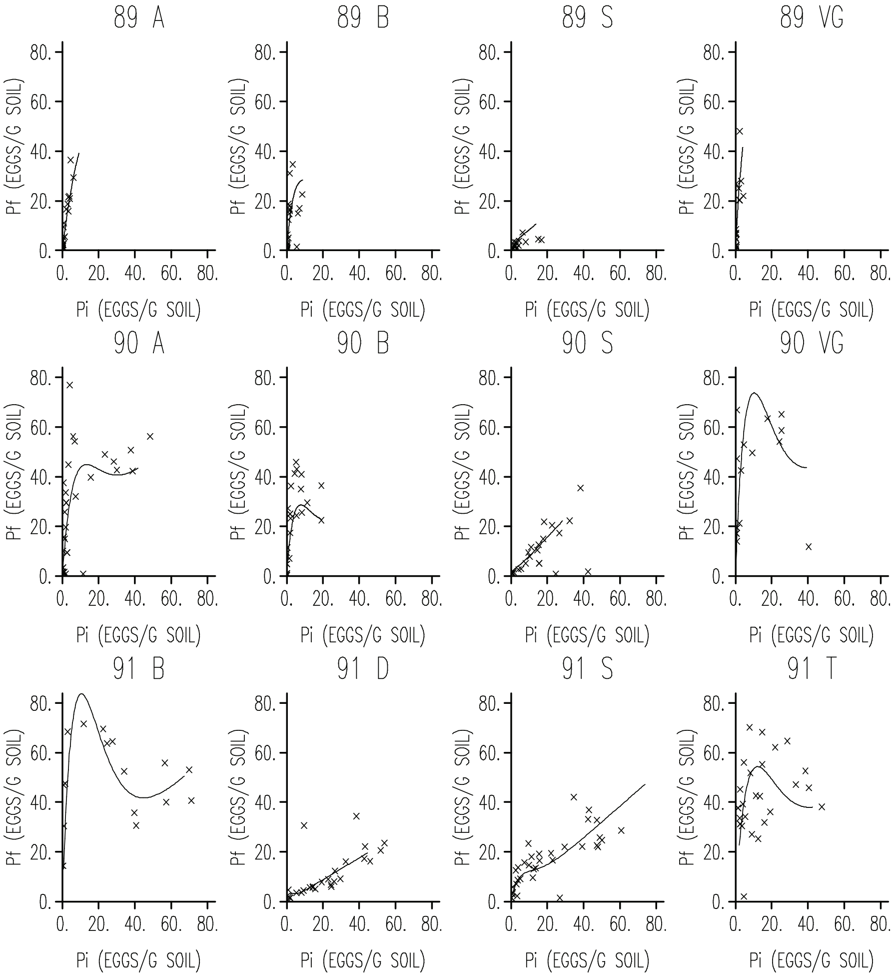

Figure 2. Relation between final density (P_f) and initial density (P_i) of *G. pallida* as observed (x) and estimated by regression (drawn line) for combinations of year and cultivar. Cultivar codes: A = Agria, B = Bintje, S = Santé, VG = van Gogh.

In contrast to parameters β_1 and β_3, sensitivity of the mean gross margin to parameter β_2 was high, but not as high as for parameter λ from the yield loss assessment model. The Pearson X^2 statistic was equal to 1,203. The dispersion was equal to 1,203/(662-176) = 2.47 and significantly greater than 1 (Quasi Likelihood). However, the residuals plotted against the expected values showed that assuming the variance to be proportional to the expected values was reasonable.

3.5 Discussion

The Ricker model extended with a linear term, Eq. (7), has only three parameters. Nevertheless it is capable of describing dynamics similar to that of more complex models, see Eq. (3) and (6), which have 5 and 10 parameters respectively. The curve that corresponds with the function of P_i, given at the right hand side of Eq. (7), rises from the origin with declining slope until a maximum is reached (contest competition). Beyond the maximum the curve declines. The crop resource is negatively affected by the high nematode densities. At very high values of P_i, the curve tends to a line through the origin with slope equal to the fraction nonhatching nematodes carried over to the following year. In our case study, empirical Bayesian methods allowed estimation of the three parameters of the model for all combinations of year and cultivar. The extended Ricker model allows the computation of analytical expressions for steady states, which were found to be stable. Moreover, because its robustness, the extended Ricker model may be used for modeling interacting dynamics of more than one nematode species and offers the opportunity to fit such a model to data.

Due to the relative simplicity of the Ricker model with an additional linear term, an analytical expression for the steady state could be derived. Furthermore, an analysis of the sensitivity of the model to parameter change could be carried out. We found the steady states to be stable even when potato was grown each year. This phenomenon was also found in the dynamics of annual plants and ascribed to carryover of dormant seeds (Silvertown and Charlesworth, 2001). The reason for the lack of chaotic behaviour in our case lies in the fact that a fraction of the nematodes is carried over to the next year, which stabilizes the dynamics (Jones et al., 1978). In reality, more than one nematode species occurs and soil fungi also will be present so that consequences for stability in practice, are more complex than we may conclude for our model. Sensitivity analysis demonstrated that the mean gross margin of the evaluated rotations is most sensitive to the parameter λ from the yield loss assessment model. This is in agreement with findings of Van den Berg and Rossing (2005) for a different dynamical system describing crop damage of nematode species. A second source of sensitivity was the parameter β_2 from the exponent of the Ricker model. The conclusion is that research aimed at better understanding of yield response of cultivars must have priority; more precise estimates of λ and β_2 will result in a greater increase in accuracy of prediction of the gross margin of a future rotation than more precise estimates of parameters β_1 and β_3. This conclusion holds for the levels of nematode infestation of the present case study experiment.

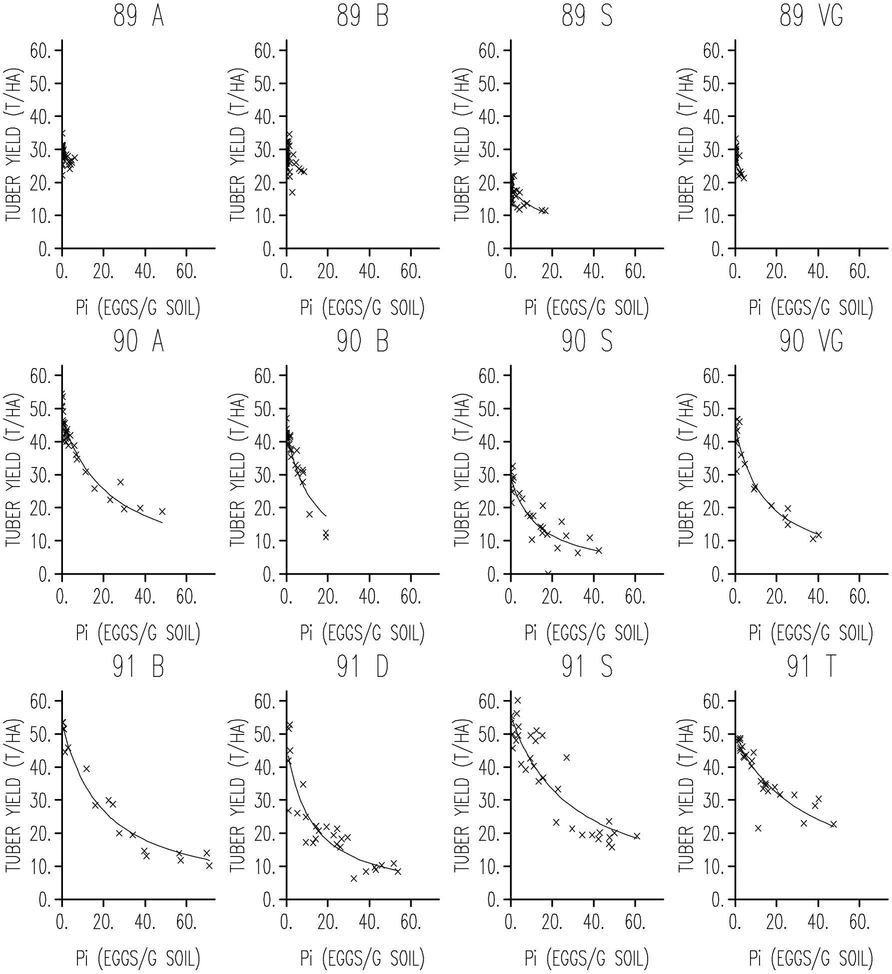

Figure 3. Relation between tuber yield and initial density of *G. pallida* (P_i) as observed (x) and estimated by regression (drawn line) for combinations of year and cultivar. Cultivar codes: A = Agria, B = Bintje, S = Santé, VG = van Gogh.

There was no correlation between the parameter β_2 of the Ricker model, which represents the sensitivity of the roots as feeding place for the nematode, and the rate parameter, λ, from the tuber yield-loss assessment model. For example estimates of β_2 and λ both were very high for cultivar Darwina in 1991(Table 4), whereas the high estimate of λ for Agria 1990 was associated with a low estimate of parameter β_2. Also correlation between estimates of β_3 and λ was not significant. These findings confirm the lack of a common causal basis for resistance and tolerance (Whitehead and Turner, 1998). Philips et al. (1991) reported higher carry over for resistant cultivars, but in our case study there was no significant negative correlation between estimates of parameter β_1 and β_3.

Each year of the experiment resulted in different estimates of model parameters. Different authors have found parameter values that vary drastically from year to year. They used these values to build stochastic population models (McSorley, 1992). In addition to philosophical implications for the way one views the system, i.e. deterministic or stochastic, such a choice also determines the type of method for generating predictions.

Experiments in nematology are time consuming due to the relatively slow changes in the system. Initial densities of nematodes are hard to manipulate and usually relatively few traits of the system are measured. As a consequence, statistical analysis is faced with limited possibilities for estimating parameters in models with much biological detail. For instance, Philips et al. (1991) started with a rather detailed biological model, but had to combine parameters during estimation for statistical reasons. At the same time, a statistical analysis should not ignore the complex dynamics outside the range of densities found in a single experiment. Using a linear relation to describe the relation between initial and final nematode densities may suffice for certain experiments, but can not be used for extrapolation. The approach we present here aims to find middle ground, by proposing a model with only a few parameters and evaluating parameters with Markov chain Monte Carlo that uses prior knowledge. The Bayesian approach provides the opportunity to use information between experiments that pertains to sufficiently similar conditions, to obtain better parameter estimates over a wider range of system conditions. Experience with use of prior information in this way is still in its infancy, and theoretical and practical insights are needed. The theoretical opportunities, however, are exciting and warrant further investigation in times of decreasing expenditure in large-scale multi-year field experiments (Coleman and Block, 2006).

Calibration of parameters in parameter-rich models such as Eq. (3) and Eq. (6) would benefit from use of the Markov chain Monte Carlo approach employed in this study. Biological prior knowledge about the parameters from literature or former experiments may be included as prior distributions of the parameters. Calibration thus serves to assess to which extent the current dataset alters the historical likelihood of parameters. Sensitivity analysis may be incorporated into the estimation procedure by monitoring change of parameter estimates in posterior distribution by a change of the parameter value in the prior distribution.

The extended Ricker model was shown to have descriptive power in a complex field experiment with potato and PCN. Further testing on experimental data will enhance confidence in the model, as well as the relatively novel parameter assessment procedures. We have shown how crop and cultivar choice have an impact on nematode population dynamics and rotation gross margin. As an illustration, we demonstrated the economic consequence of ‘diluting’ a potato-based rotation with non-potato crops taking both economic effects and nematode-mediated yield effects into account. The illustration showed that it is difficult but not impossible to find crops that constitute an economically interesting alternative for potato under Dutch production conditions. For true practical applications, a more extensive analysis of cropping system scenarios than presented here is desirable. In such analyses, considerations such as differences in economic performance between cultivars (e.g. Dekker, 2001) can be combined with their differential response to nematode infestation. This provides a basis for an integrated analysis of cropping systems in which response to nematode dynamics is only one component of cropping systems design and improvement (Kropff and Struik, 2002).

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Appendix A

The derivative of $\overline{P}_n$ in Eq. (16) with respect to β_1, β_2, β_3 and ρ is equal to

$$\frac{d\overline{P}_n}{d\beta_1} = \frac{1}{\beta_1\beta_2}, \tag{A1}$$

$$\frac{d\overline{P_n}}{d\beta_2} = \frac{-\overline{P_n}}{\beta_2}, \tag{A2}$$

$$\frac{d\overline{P_n}}{d\beta_3} = \frac{\rho^{n-1}}{\beta_2\left(1-\beta_3\rho^{n-1}\right)}, \tag{A3}$$

$$\frac{d\overline{P_n}}{d\rho} = \frac{(n-1)}{\beta_2\rho}\frac{1}{1-\beta_3\rho^{n-1}} \tag{A4}$$

and the derivative of $\overline{Y}_n$ to parameter p ($p = \beta_1$, β_2, β_3, ρ) is equal to

$$\frac{d\overline{Y_n}}{dp} = \frac{-\lambda\frac{d\overline{P_n}}{dp}}{\left(1+\lambda\overline{P_n}\right)^2}. \tag{A5}$$

The derivative of $\overline{Y}$ to parameter λ is equal to

$$\frac{d\overline{Y_n}}{d\lambda} = \frac{-\overline{P_n}}{\left(1+\lambda\overline{P_n}\right)^2}. \tag{A6}$$

The derivative of GM_R to parameter p ($p = \beta_1$, β_2, β_3, ρ) is equal to

$$\frac{dGM_R}{dp} = \frac{d\overline{Y_n}}{dp}FO_{potato}. \tag{A7}$$

Appendix B

The expression for the posterior distribution (p) is equal to the Poisson likelihood for the 662 counts times the four normal prior distribution functions of π_0, β_1, β_2 and β_3:

$$p = \prod_{i=1}^{662} \frac{\mu_i^{y_i} e^{-\mu_i}}{y_i!} \prod_{f=1}^{132} N\left(\pi_{0f}, \mu_{\pi_0}, \sigma_{\pi_0}^2\right) \prod_{j=1}^{12} N\left(\beta_{1j}, \mu_{\beta_1}, \sigma_{\beta_1}^2\right)$$

$$\prod_{k=1}^{12} N\left(\beta_{2k}, \mu_{\beta_2}, \sigma_{\beta_2}^2\right) \prod_{m=1}^{12} N\left(\beta_{3m}, \mu_{\beta_3}, \sigma_{\beta_3}^2\right) \sigma_{\pi_0} \sigma_{\beta_1} \sigma_{\beta_2} \sigma_{\beta_3}, \qquad \text{(B1)}$$

where $N(a, b, c)$ is the normal distribution function of a, with mean b and variance c. The final four terms in Eq. (B1), σ_{π_0}, σ_{β_1}, σ_{β_2}, σ_{β_3} are the priors for $\sigma_{\pi_0}^2$, $\sigma_{\beta_1}^2$, $\sigma_{\beta_2}^2$, $\sigma_{\beta_3}^2$ (Gelman et al., 2004, paragraph 11.7).

Chapter 4: Multimodel inference for the prediction of disease symptoms and yield loss of potato in a two-year crop rotation experiment[1]

W. van den Berg, J. Vos and J. Grasman

Abstract

Arable soils contain different species of pathogens that may reduce the crop yield. Interactions among pathogen species may increase crop damage even further. For analyzing such phenomena, this study deals with multimodel inference based on information theoretical methods. In the statistical analysis of a two year crop rotation experiment, the second order Akaike information criterion was used for the assessment of potential models for three responses of potato test crops: (a) incidence of *Spongospora subterranea* on the harvested tubers, (b) percentage haulms infected with *Verticillium dahliae* and (c) tuber yield. Four variables that are likely related to the response variables were taken into consideration: soil infestations of the fungus *Verticillium dahliae* and infestations of three nematode species (*Globodera pallida, Trichodoridae* and *Meloidogyne* spp.). In addition the factors soil pH and water soluble phosphor (P) as well as interactions between *V. dahliae* and the three nematode species were included. Only those models were considered for which both predictors were included in case their interaction was required in the model. It resulted in 139 models that were fitted to the data using Generalized Linear Modelling. The outcome showed that tubers suffered more from *S. subterranea* for higher soil pH values. Moreover, tuber yield and the percentage of infected haulms were mainly determined by the presence of microsclerotia of *V. dahliae* in the soil and by the soil pH. Finally, yield reduction from the presence of *V. dahliae* was enhanced by the presence of higher densities of *G. pallida*. Multimodel inference yielded improved estimates of model parameters as it takes in consideration all plausible models and gives them a weight based on the Akaike information criterion. This approach reduces the risk of loosing essential information. Using the bootstrap technique a confidence set of models was constructed. Furthermore, based on multimodelling, predictors are given a weight from which one may decide about the need to include them in a prediction of crop yield. In the present study it was concluded that from the six predictors the most important ones were soil infestation levels of *V. dahliae* and *G. pallida* and the soil pH.

Keywords: nematodes, potato crop, multimodel inference, Generalized Linear Models

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4.1 Introduction

To answer research questions in agronomy, statistical hypotheses are formulated and an analysis of variance on experimental results is performed in order to detect the effect of different treatments (Fisher, 1949). In data obtained from common types of experiments, effects of treatments are causal because of randomization of the treatment levels over the experimental units. In crop rotation experiments, a wider approach is needed in the sense that not only controlled treatments are considered, but also other predictors such as weather and soil characteristics. Ultimately, such procedures should lead to a statistical model giving the best crop prediction. In crop rotation experiments on soil borne pathogens, different pathogen species may be present and various regression models can be formulated about the harm caused by these species in combination with the effect of abiotic predictors for crop growth. The aim of this study is to select from a set of plausible predictors for tuber yield the ones that definitely should be included in a model. We will use the multimodel inference approach in which a model is constructed as a weighted combination of all models under consideration. The advantage of this approach is that one uses information from all models instead of choosing the best model. This can be attractive when a number of models are doing about equally well. To calculate the weights, the Akaike Information criterion is used. In the generalized linear models, used in this study, the multimodel method also leads to improved estimates of parameters based on the weights of the different models. Furthermore, with bootstrapping, a confidence set of plausible models can be constructed. This indicates which of the predictors are essential for the assessment of crop damage from soil-borne pathogens. The study uses data of an experiment by Scholte (2000) on the application of trap crops to reduce the damage from potato cyst nematodes.

Farmers grow potatoes as a component in a crop rotation system. Short intervals between successive potato crops may result in a build up of harmful soil-borne pathogens, including several fungi and nematode species (Vos and Van Loon, 1989). Above a threshold level of infestation, tuber yield will suffer from the presence of potato cyst nematodes (Jones and Kempton, 1988; Schans, 1993).

If more than one soil-borne pathogen is present, interaction effects are expected resulting in a further increase of crop damage (Back et al., 2002). Apart from Scholte (2000), there is a wealth of other studies reporting on the relation between inoculum density of interacting pathogens and crop response. Evans (1987), for instance, showed in a pot experiment with several potato cultivars, higher infection rates of the fungus *Verticillium dahliae* in the presence of cyst nematode species (*Globodera rostochiensis* or *G. pallida*). Potato early dying (Mulder, 1994) is caused by *V. dahliae* and *V. albo-atrum*, but severity aggravates when soil is also infested by *Pratylenchus penetrans*.

Many results have been published on the harming effects of soil-borne pathogens in combination with environmental factors such as temperature, soil pH and soil texture. The index of powdery scab (*Spongospora subterranea*) tended to take lower levels when the pH of the soil increased by adding lime (Harrison et al., 1997). Yield loss of potato by *G. pallida* is more severe at high than at low pH values of the soil due to a lower availability of phosphate at higher pH values (De Ruiter and Haverkort, 1999). On sandy soils damage from *Meloidogyne* spp., *Pratylenchus* spp. and *Trichodoridae* is larger than on clay soils. Temperature affects growth and development of nematodes as well as the agricultural crops themselves. Moreover, the number of generations of *Meloidogyne* may be one or two in cool summers while at higher temperature three generations are possible (Dropkin, 1988).

In the past, mathematical models have been introduced to quantify the damage from pathogens and their interactions using multiple linear regression (Dobson, 1988; Scholte and s'Jacob, 1990). Wheeler et al. (1992) modeled the simultaneous effect of *P. penetrans* and *V. dahliae* on tuber yield of potato with nonlinear regression, while Jacobsen et al. (1979) modelled tuber yield as a function of the density of both *M. hapla* (x_1) and *V. albo-atrum* (x_2) as predictors on the natural log scale, resulting in an additive model plus an interaction term:

$$y = \alpha + \beta \log(x_1) + \gamma \log(x_2) + \delta \log(x_1) \log(x_2), \tag{1}$$

where y is the yield of potato tubers and α, β, γ and δ are regression coefficients. Here and elsewhere "log" means the natural logarithm.

This paper presents a new statistical analysis of a case study dealing with four factorial treatments applied in a two year crop rotation experiment (Scholte, 2000). Results of such an experiment can be used to formulate models for the prediction of pathogen dynamics and yield loss based on measured values of predictor variables. Parameters in expressions of this type are estimated by means of Generalized Linear Models (GLMs) using a logarithmic link function. In this study we took an information-theoretical approach for model selection and multimodel inference (Burnham and Anderson, 2002). In Garret et al. (2004) this approach has already been placed in the context of phytopathological research problems. First we select a biologically plausible subset of predictors from the available set including their interactions. The second order Akaike information criterion (Akaike, 1973), is used to select the best models. Using a bootstrap approach, a confidence set containing the best-fitting models is determined. The approach is applied to the prediction of three responses: (a) the incidence of *S. subterranea* at tuber skin, (b) percentage of haulm infection by *V. dahliae*, and (c) tuber yield. This statistical analysis results in the selection of the predictors and interaction terms that provide a reliable forecast under conditions comparable with those of the experiment of the case study.

4.2 Materials and methods

Experimental design. The data used in this study arose out of a field trial with a two year crop rotation (Fig. 1) as presented in Scholte (2000). The experiment consisted of two so-called ‘sets’: preparations for Set 1 started in 1994 and for Set 2 in 1995. In both sets the same treatments were applied in the same sequence. The advantage of having two sets is that observations on main potato crops could be done each year. Set 1 consisted of two two-year cycles of the crop rotation and Set 2 of 1.5 cycles of the crop rotation. The first year of the crop rotation cycle is divided into the spring period and the period of summer taken together with autumn. In the spring period two trap cropping treatments were applied: (i) cropping with potato cultivar Kartel acting as a trap crop for potato cyst nematode (PCN), which resulted in a decline of the infestation

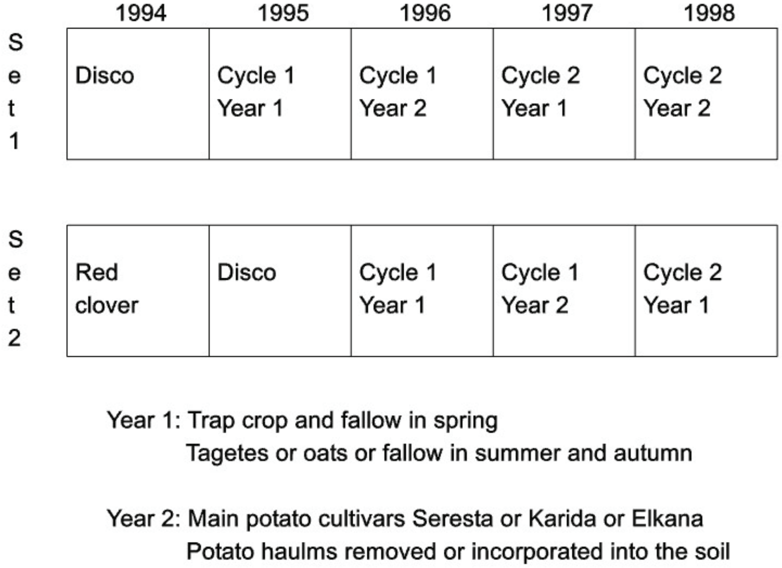

Fig. 1. The two years crop rotation scheme, representing the sequence of crops and treatments for one of three blocks. Each block was split into two ‘sets’: the experimental cycles in Set 1 started with the potato cultivar Disco in 1994. The experimental cycles of Set 2 started with the same potato cultivar in 1995, and red clover was grown in 1994. A cycle consisted of a sequence of crops and treatments, see Scholte (2000) for more details.

(see the paragraph “justification of the treatments” for details) and (ii) a fallow control. In summer and autumn (after destroying the potato trap crop) three green manure cropping treatments were applied: (i) growing of *Tagetes*, (ii) growing of oats (*Avena sativa)* and (iii) fallow control. In year two of the crop rotation cycle potatoes were grown; the choice of cultivar is a treatment (Seresta, Karida and Elkana). In addition to the cultivar factor, another treatment factor was applied: immediately after the harvest potato haulms were either incorporated into the soil or removed from the plot.

The two trap cropping treatments, the three green manure cropping treatments and the two haulm removal treatments were combined in a factorial design. The 12 treatment combinations of trap crop x green manure crop x haulm removal were randomized over 12 main plots. The potato cultivars split the main plots into three plots meaning that one replicate of one set consisted of 36 plots. Thus, the design consisted of three blocks each being split into the two sets as mentioned before. Set 1 of the experiment was terminated in November 1998 after growing potato in that year. Set 2 was terminated in March 1999 after sampling the plots for determination of soil infestation with pathogens. The experiment was located in Achterberg (51° 59′ N, 5 ° 35′ E), The Netherlands, on a sandy soil.

Justification of the treatments. The treatments were designed to differentially affect the infestation level of the soil-borne pests and diseases. In the first year potato itself was used as a trap crop against PCN; the other half of the plots remained fallow. Potato can be used as a trap crop for PCN, provided the crop is killed by glyphosate by the end of June, i.e. before PCN complete their life cycle and multiply (Scholte, 2000). The green manure *Tagetes* was used to reduce the density of *P. penetrans.* Oats was expected to enhance antagonists of *Rhizoctonia solani* (Scholte et al., 1996; Struik and Bonciarelli, 1997)*,* while fallow was used to reduce the density of all soil-borne pathogens. In the second year the three potato cultivars were grown: Seresta, Karida and Elkana. They are respectively highly resistant, moderately resistant and susceptible to *G. pallida* and all three are highly resistant to the pathotypes of *G. rostochiensis*. Potato haulms are the most important source of *V. dahliae* microsclerotia. Hence, the soil inoculum level of *V. dahliae* can be influenced by incorporating or removing haulms (Mol et al., 1995).

Inoculation. In 1994 and 1995 inoculations were made to uniformly infest the plots with the organisms under study. *R. solani,* anastomosis group 3 (AG3) and *Pratylenchus crenatus* were already present in the soil at high densities as a result of previously grown crops. Inoculations were made with *G. pallida, M. hapla, M. chitwoodi* and *P. penetrans* and *V. dahliae* (details in Scholte, 2000).

Soil sampling. Before planting main crop potatoes, 60 soil cores were taken at random from each plot with a 2.0 cm diameter auger to a depth of 20 cm early March. Each sample was gently but thoroughly mixed and then separated into four parts: 300 ml soil was used for a biotest for the presence of root-knot nematodes, 2000 ml to analyze the populations of other nematodes, 250 ml to determine soil infestation with *V. dahliae*, and the remaining soil was used to measure pH and analyze N, P and K levels. In spring soil pH was measured as well as the soil concentrations of nitrate, ammonium, and water soluble P and K on the plots to be planted with the potato main crop.

Data acquisition of nematode densities. Cysts of nematodes were extracted from a subsample of moist soil using the method described by Oostenbrink (1960). After crushing the cysts, numbers of viable juveniles were counted using a stereo dissecting microscope. In 1999 Set 2 was treated differently: air-dried soil samples were used from which cysts were separated using the method described by Van Bezooijen et al. (1999). Populations of *Pratylenchus* spp. and *Meloidogyne* spp. were counted after extracting them using the method described by Oostenbrink (1960).

Haulm infections with *V. dahliae* and *R. solani.* Each year, in the second week of August, 20 randomly chosen plants of the potato test crop were harvested, five from each of the inner four rows of each plot. A transverse section of 1-2 mm thickness was cut from the middle of each haulm piece and eight sections per dish were placed on a selective medium in Petri dishes and incubated for two weeks (Mol et al., 1995). Colonies of *V. dahliae* were counted using a stereo dissecting microscope. *Rhizoctonia* haulm canker was recorded at the underground part of each haulm using five classes of disease severity.

Inoculum density of *V. dahliae* in the soil. Microsclerotia are the surviving structures of *V. dahliae* in soil quantified by a colony forming unit (cfu). To that end soil samples were dried and sieved, and were dispersed on a selective agar plate. The plates were incubated and after three weeks the number of cfu's of *V. dahliae* was determined using a stereo dissecting microscope; the number of cfu's was expressed per g soil (details: Scholte, 2000).

Incidence of S. subterranea on tubers. For each plot the amount of *S. subterranea* was assessed using five severity classes: 0, 0-25%, 25-50%, 50-75% or 75-100 % of tuber skin covered with powdery scab.

Specification of plausible predictors. In the case study, a large number of variables were measured for monitoring soil fertility, density of pathogens in soil and growth of the potato crop. To save time and effort in the selection process and to obtain parsimony using multimodel inference, we only retained predictors in the model that are meaningful as possible predictors of tuber yield: some disease symptoms were measured in the field during crop growth or afterwards on harvested tubers. These quantities have no predictive value and were discarded from the analysis. Potatoes are host to the fungus *V. dahliae* and to the nematodes *G. pallida*, *Trichodoridae* and *Meloidogyne* spp. Densities of these pathogens were measured in the soil before planting. *Trichodoridae* stands for all nematodes belonging to the genera *Trichodorus* and *Paratrichodorus*. Also soil fertility measurements were made before planting the crop. Only pH and water soluble P were assumed to be relevant (De Ruiter and Haverkort, 1999) and retained, while total N and water soluble K were discarded from the analysis as these nutrients are too mobile and variable in the soil to have predictive value.

Following the literature (Evans, 1987; Dropkin, 1988) the interaction between *V. dahliae* and the three nematode species were added to the predictor set. We did not include the interaction between pH and nematode density in spring as Mulder (1994) did, because there the range of pH values was much larger than in our case study. Three of the nine predictors are interactions. From all 2^9 models, we only considered those in which both predictors were included when their interaction was in the model (Lee et al., 2006). Therefore, for each of the three responses (i.e. incidence of *S. subterranea* on harvested tubers, percentage of haulms infected with *V. dahliae* and dry tuber yield) only 139 predictive models were selected to which multimodel inference was applied. The model with all nine predictors is called the global model.

Regression models. A simple nonlinear model for yield loss caused by nematodes of one species is formulated as

$$\mu = \mu_0 \rho^x , \qquad (2)$$

where μ is the expected tuber yield and x the initial density of the pathogen at the moment potatoes are planted. Parameter μ_0 is the maximum yield when the pathogen is absent, and the parameter ρ represents the intact fraction of the roots after attack due to one unit of pathogen (Schomaker and Been, 2006). Eq.(2) has also been used by Mol et al. (1996) for the assessment of yield loss by *V. dahliae*, where x was the initial density of cfu g^{-1} soil. Here, we assume that parameter ρ is identical for all three cultivars we consider. This means that the relative damage per unit of pathogen is assumed to be the same for all cultivars. However, we use the parameter μ_{0c} to express the differences in yield of the three cultivars (c = 1, 2, 3). In this way we capture the effect of more than one soil-borne pathogen species in a multiplicative yield loss model with a restricted number of parameters

$$\mu = \mu_{0c}\rho_1^{x_1}\rho_2^{x_2}...\rho_n^{x_n}\ , \tag{3}$$

where x_1, x_2 … x_n are the initial densities of the n soil-borne pathogens (Zadoks and Schein, 1979). It is noted that the parameter ρ varies with the pathogen type. Yield decrease due to two pathogens e.g. *V. dahliae,* x_1, and *G. pallida,* x_2, is modeled as

$$\mu = \mu_{0c}\rho_1^{x_1}\rho_2^{x_2}\rho_{12}^{x_1 x_2}\ . \tag{4}$$

The parameters of Eq.(4) were estimated with a Generalized Linear Model (GLM) with a logarithmic link function and with the response having a normal distribution (McCullagh and Nelder, 1989). The product of x_1 and x_2 can be written as x_3, so that Eq.(4) transforms into

$$g(\mu) = \log(\mu) = \beta_{0c} + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3\ , \tag{5}$$

where $\beta_{0c} = \log(\mu_{0c})$, $\beta_i = \log(\rho_i)$, $i = 1, 2$ and $\beta_3 = \log(\rho_{12})$. For an analysis based on a reciprocal link function we refer to France and Thornley (1984) and Elston et al. (1991).

The environmental predictors, pH and water soluble P content of the soil, can be added in the same way to Eq.(5). We have p predictors for which the regression coefficients are identical for the three cultivars. Furthermore, the intercept is assumed to depend on the choice of the cultivar, so that there are $p + 3$ regression parameters. Including the error term, the GLM with a logarithmic link function takes the form

$$g(\mu) = \log(\mu) = \beta_{0c} + \sum_{j=1}^{p}\beta_j x_j \tag{6}$$

Besides the tuber yield we have the two other response variables. Firstly, the percentage of haulms infested with *V. dahliae* for which a logit link function is used with the infested number as response and the total number of haulms as binomial total. Secondly, the distribution of tubers over the five severity classes of coverage with *S. subterranea* is analyzed with ordinal regression (McCullagh and Nelder, 1989).

Second Order Akaike Information Criterion (AIC^c). In our case study nine predictors are available for prediction of the tuber yield μ. We assume the tuber yield to be normally distributed, so we have to maximize the normal likelihood, *L*, as function of the regression parameter vector, β, and the standard deviation, σ, of the error term given the data, *y,* (Lee et al., 2006):

$$L(\beta,\sigma\mid y)=\left(\frac{1}{\sqrt{2\pi\sigma^2}}\right)^n \exp\left(-\frac{\sum_{i=1}^{n}\left(y_i-\mu_i(\beta)\right)^2}{2\sigma^2}\right) \quad \text{with} \quad \log\left(\mu_i(\beta)\right)=\beta_{0c}+\sum_{j=1}^{p}\beta_j x_{ij}\ , \tag{7}$$

where *i* is the observation index. Replacing σ^2 by its estimate, being the residual sum of squares divided by *n*, we are left with a likelihood function of β only, that has to be maximized. For model selection and multimodel inference we use the second order Akaike Information Criterion (AIC^c):

$$\mathrm{AIC}^c = -2\log L\left(\beta,\sigma\mid y\right)+2K+\frac{2K(K+1)}{(n-K-1)}, \tag{8}$$

where *n* is the number of observations and $K = p + 4$ the number of parameters (*p* regression coefficients, 3 intercepts for the cultivars and σ^2 for the error term). It can be seen as a goodness of fit function. Burnham and Anderson (2002) demonstrated that AIC^c should be preferred above the standard AIC if $n/K < 40$. In our case study n/K is indeed below this value for most of the candidate models and so we use Eq.(8). In the following we take for the parameters in the model those values that minimize the AIC^c.

Kullback-Leibler distance and bootstrapping. Let *R* candidate models be selected in advance. For each model $r = 1,\ldots, R$ the AIC_r^c with the best choice of parameters is calculated. Following Burnham and Anderson (2002) the model with the lowest AIC^c is denoted by AIC_{r*}^c. The Kullback-Leibler distance Δ_r between AIC_r^c and AIC_{r*}^c is used to compute an appropriate weight w_r for each of the $r = 1,\ldots, R$ models:

$$w_r = \frac{e^{-\Delta_r/2}}{\sum_{r=1}^{R} e^{-\Delta_r/2}} \qquad \text{with} \qquad \Delta_r = \mathrm{AIC}_r^c - \mathrm{AIC}_{r*}^c\,. \tag{9}$$

Using w_r we can order the models: $r_1 = r*$ and so on. The summed weight of the first *k* models

$$P(k)=\sum_{j=1}^{k} w_{r_j} \tag{10}$$

denotes the probability that from all R models the best approximation to truth is among these k models.

The above way of ordering models still depends on the data from the experiment as it has been carried out. Using bootstrap we can make our result less dependent on this given circumstance. As an illustration, we construct the 95% confidence set of models, see Burnham and Anderson (2002). Using the data from the experiment, a large number of samples are simulated. Such a resample, b, having the same size as the original data set, is composed by drawing, with replacement, n cases from the original data set. Let $\mathrm{AIC}^{c}_{b,r_b^*}$ be the minimum value over all models for this resample, then we consider the Kullback-Leibler difference, w_r given by Eq. (9), where now AIC^{c}_{b,r^*} is the value for model r^* in resample b. Carrying out this procedure $B = 1000$ times gives us the set $\{\Delta_1, \dots, \Delta_{1000}\}$ ordered by (increasing) size. A 95% confidence set of candidate models consists of those models r, for which Δ_r of Eq. (9), is lower than Δ_{950} of the ordered set.

Multimodel inference. Now, based on the weights w_r, we compose the (multi)model having estimated regression coefficients

$$\hat{\beta}_j = \sum_{r=1}^{R} w_r \hat{\beta}_{rj}\,, \quad j = 1, \dots, p, \tag{11}$$

meaning that in a model without predictor j the coefficient, β_{rj}, is given the value zero. Furthermore each predictor can be given a weight

$$v_j = \sum_{r=1}^{R} w_r I_j(r)\,, \quad j = 1, \dots, p\ , \tag{12}$$

where $I_j(r) = 1$ if predictor j is in model r, otherwise $I_j(r) = 0$. The weight v_j takes values in the interval [0, 1] and is an indication for the importance of this predictor in the process of constructing the best regression model. Following Lukacs et al. (2010) the variance of the regression coefficient j takes the form

$$\mathrm{var}\left(\hat{\beta}_j\right) = \sum_{r=1}^{R} w_r \left\{\mathrm{var}\left(\hat{\beta}_{rj}\right) + \left(\hat{\beta}_{rj} - \hat{\beta}_j\right)^2\right\}, \quad j = 1, \dots, p. \tag{13}$$

Statistical package. All statistical analyses are carried out using GenStat (Genstat Committee, 2008).

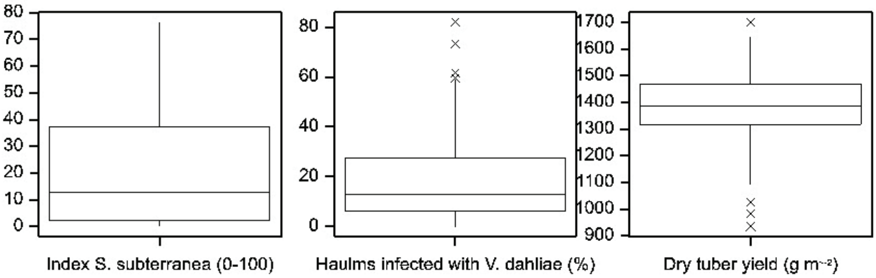

Figure 2. Boxplot diagrams of the three response variables in 1998. Observations (marked x) are at a distance between 1.5 and 3 times the quartile range from the box.

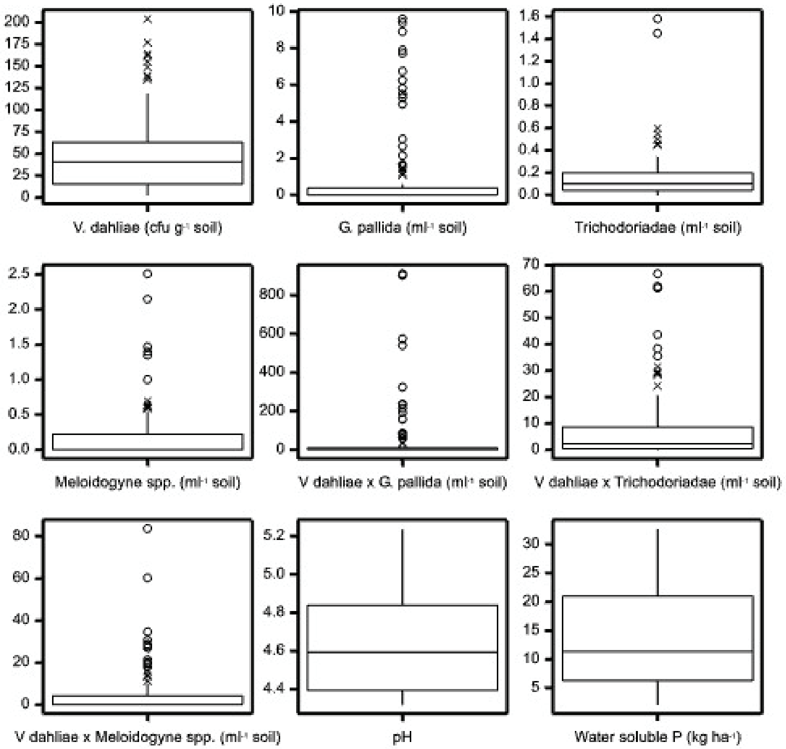

Figure 3. Boxplot diagrams of the nine predictors in 1998. Observations (marked x) are at a distance between 1.5 and 3 times the quartile range from the box. Observations (marked o) are more than 3 times the quartile range beyond the box.

4.3 Results

Statistics. Using boxplots we present in Figure 2 descriptive data on medians and ranges of values of the three response variables for the year 1998. The index (0-100) for *S. subterranea* varied from 0 to 78.4 with median equal to 12.7. Percentage of haulms infected with *V. dahliae* varied from 0 to 86.4 with median value 12.8. Tuber dry yield ranged from 910 to 1729 g m^{-2}. Figure 3 gives similar statistics for the nine predictors (interactions included) for the year 1998. Densities of *V. dahliae*, *G. pallida*, *Trichodoridae* and *Meloidogyne* spp. had medians equal or near 0. Water soluble P varied from 5.5 to 34.0 kg/ha. A similar range of values was found for these predictors in 1996 and 1997.

In multiple regression analysis, high correlations between two or more predictors, also called multicollinearity (Montgomery and Peck, 1982), may complicate the analysis and the interpretation of the outcomes. In the first place, multicollinearity may increase the standard errors of the parameters in a model ("inflation"). Secondly, multicollinearity increases model uncertainty by inducing different estimates across different models, which enlarges the second term between accolades in Eq. (13). Table 1 gives the correlation matrix for the nine predictors in 1998. As expected a positive correlation between interaction terms and their corresponding two predictors was found. All correlation coefficients were below 0.7, so multicollinearity was not deemed a problem.

The goodness of fit of the global model Eq. (6) was quantified by the coefficient of multiple determination R^2 (Table 2). In the analyses over the three years

Table 1. Correlation matrix for the nine predictors in the year 1998. There are 108 pairs in each correlation.

Nr	Predictor	1	2	3	4	5	6	7	8	9
1	*V. dahliae*	1.00								
2	*G. pallida*	0.00	1.00							
3	*Trichodoridae*	-0.02	-0.09	1.00						
4	*Meloidogyne* spp.	-0.20	-0.17	-0.11	1.00					
5	*V.dahliae* x *G. pallida*	0.40	0.60	-0.09	-0.13	1.00				
6	*V.dahliae* x*Trichoridae.*	0.51	-0.09	0.67	-0.12	0.08	1.00			
7	*V.dahliae* x *Meloidogyne* spp.	-0.01	-0.17	-0.05	0.69	-0.13	0.00	1.00		
8	pH	0.39	-0.08	0.21	-0.12	0.15	0.43	-0.06	1.00	
9	Water soluble P	-0.19	0.01	-0.06	0.06	-0.07	-0.13	0.15	-0.33	1.00

Table 2. The coefficient of multiple determination, R^2, of the global model for the three responses over the three years. In the global model the nine predictors are present as well as the cultivar term. Between brackets R^2 is given for the model with only the cultivar term.

Year	Index *S. subterranea* (0-100)	Haulms infected with *V. dahliae* (%)	Dry tuber yield (g m^{-2})
1996	0.44 (0.05)	0.55 (0.12)	0.44 (0.16)
1997	0.38 (0.16)	0.41 (0.05)	0.52 (0.37)
1998	0.50 (0.09)	0.66 (0.29)	0.46 (0.22)

R^2 ranged from 0.38 for *S. subterranea* in 1997 to 0.66 for the percentage of haulms infected with *V. dahliae* in 1998. The R^2 for the model with only the cultivar term varied from 0.05 for *S. subterranea* in 1996 to 0.37 for tuber yield in 1997. The part of R^2 representing the variance explained by the nine predictors ranged from 0.15 (= 0.52 – 0.37) for dry tuber yield in 1997 to 0.43 (= 0.55 – 0.12) for the percentage of haulms infected with *V. dahliae* in 1996. The coefficients of multiple determination in Table 2 are rather low. This may be caused by predictors not taken into consideration and/or measurement errors. Wider ranges in the predictors would have resulted in a wider range of the response, increasing R^2. The question whether all nine predictors substantially contributed to the size of R^2 was answered in the multimodel approach.

Akaike Information Criterion AIC^c. For each year and for each of the three response variables, the 139 candidate models were fitted to the data. The regression coefficients, with corresponding standard errors, were saved for each model and the AIC^c was calculated using Eq. (8). For each response variable the models were sorted according to ascending AIC^c. As an illustration, the 10 models with the lowest AIC^c values from the analysis of tuber yield in 1998 are presented in Table 3. The predictors *V. dahliae* and *G. pallida* and their interaction were present in each of these 10 models, while in the best model pH was also present. The weight w_r calculated using Eq. (9) was 0.24 for the best model, 0.10 for the second best model, and so on. The sum of the weights for the 10 models of Table 3 was 0.75, which can be interpreted as the probability that the truly best model is among these 10 models. For the first 23 models the summed weight reached 0.90 and for the first 66 models the summed weight reached 0.95. The regression coefficients of the best model for prediction of tuber yield in 1998 are presented in Table 4. This model is not much better than the ones ranking 2 and 3 in Table 3, with, respectively, water soluble P and *Trichodoridae* added. In Tables 4, 6, 7 and 8 density for *V. dahlia* is cfu (0.01 g)$^{-1}$ soil and for the nematodes ml^{-1} soil.

Table 3. The 10 best-fitting models from the 139 models for the 1998 tuber yield. The numbers 1 to 9 in column Model correspond to the predictor numbers in the other tables. K is the number of parameters in the model. Δ and w are defined by Eq.(9).

Rank	Model[a]	K	AIC^{c}	Δ	w
1	12—5—8–	8	1308.3	0.0	0.24
2	12—5—89	9	1310.0	1.7	0.10
3	123–5—8–	9	1310.3	2.0	0.09
4	12–45—8–	9	1310.4	2.2	0.08
5	12—5——	7	1310.9	2.6	0.07
6	123–5——	8	1311.9	3.7	0.04
7	123–5—89	10	1312.1	3.8	0.04
8	12–45—89	10	1312.2	3.9	0.03
9	12345—8–	10	1312.4	4.1	0.03
10	123–56–8–	10	1312.7	4.4	0.03

[a] hyphen (–) at the j^{th} position means predictor j is not in the model, an j (values 1 to 9) at the j^{th} position means predictor j is in the model.

Table 4. Estimated regression coefficients, $\hat{\beta}_j$, and their standard error in the best dry tuber yield model in 1998.

Predictor	$\hat{\beta}_j$	se $\hat{\beta}_j$
cv. Seresta	6.887	0.168
cv. Karida	6.952	0.168
cv. Elkana	6.865	0.169
V. dahliae	-0.073	0.020
G. pallida	0.001	0.005
V.dahliae x *G. pallida*	-0.025	0.009
pH	0.074	0.034

Table 5. The size of the 90% and 95 % confidence sets of models for the three response variables. Given is the number of models, from the total of 139 models, that are included in the sets. The results are based on the bootstrap method explained in the text.

Confidence set	Index *S. subterranean*			Haulms infected with *V. dahliae*			Dry tuber yield		
	1996	1997	1998	1996	1997	1998	1996	1997	1998
90%	50	27	3	13	46	78	8	81	24
95%	54	28	7	20	56	95	20	97	67

Confidence sets of models. 90 % and 95 % confidence sets were calculated using bootstrapping. The size of the 90% confidence set for *S. subterranea* consisted of only three models (Table 5). For dry tuber yield, the 90 % confidence set contained 81 models in the year 1997.

Multimodel inference. Multimodel inference results are presented from analyses for the three response variables. The summed weights, v_j, for predictor j, $j = 1,\ldots,9$, are given by Eq. (12) and lie between 0 and 1, see in Tables 6, 7 and 8 for their values in the analysis of the three responses. A value close to 1 for a predictor indicates that it has a high predictive value. Next we comment on the outcome of the multimodel inference for each of the response variables:
(a) For *S. subterranean*, the summed weights v_1, v_8 and v_9 of the predictors *V. dahliae*, pH and water soluble P have the value 1 in each of the three years. The severity of *S. subterranea* on the tubers increased with the density of *V. dahliae* and with the pH. It only increased with the water soluble P concentration in 1997 (Set 2) and decreased for higher concentration in the other years. The summed weights v_2 and v_4 for *G. pallida* and *Meloidogyne* spp. were 0.99 for both of them in 1998. Also in 1998, the summed weight v_5 and v_6 of the interactions between *V. dahliae* and *G. pallida* and between *V. dahliae* and *Trichodoridae* were high: they were, respectively, 0.93 and 1.00.
(b) As expected the number of cfu's of *V. dahliae* $(0.01\text{g})^{-1}$ soil measured in soil in spring was the most important predictor for the percentage of haulm infections. In 1998 *V. dahliae* was the only predictor with a high summed weight. Water soluble P and pH in 1996, and pH in 1997, also showed high summed weights.
(c) For tuber yield loss, *V. dahliae* (cfu $(0.01\text{g})^{-1}$ soil) in spring was the most important predictor. The summed weight v_1 took the values 1.00, 0.91 and 1.00 in the three consecutive years. The summed weights v_3 and v_9, for *Trichodoridae*, and water soluble P were high in 1996; for *Trichodoridae* and pH, the summed weight v_3 and v_8 were high in 1997. In 1998 the summed weights v_2 and v_5 for *G. pallida* and for the interaction between *V. dahliae* and *G. pallida* were high (0.94).

4.4 Discussion and conclusions

We dealt with the prediction of crop damage from soil-borne pathogens in potato using predictors that are at hand at the start of the growing season. Only predictors such as initial densities of nematode species for which potato is a host, and soil properties, such as pH level, were considered. In this way we ended up with only predictors that are biologically relevant and were only weakly correlated, see Table 1. This resulted in six candidate predictors and three interactions. Instead of considering all possible combinations of these nine predictors, we discarded the models with interactions for which at least one of the predictors forming the interaction was absent (Lee et al., 2006). This reduced the number of models from $2^9 = 512$ to only 139. According to the information-theoretical approach (Burnham and Anderson, 2002; Anderson, 2008), these models represent multiple working hypotheses about the research problem. For each model (or hypothesis) r, a weight w_r, is calculated using the Akaike information criterion corrected for small datasets. The weight w_r, denotes the probability that model r provides the closest approximation to the true model out of all the models considered. The quotient w_i/w_j yields evidence about the superiority of model i over model j or vice versa (Royall, 1997). Averaging of parameter estimates based on multimodelling is carried out with the use of these model weights. This approach utilizes the information from all models and requires less computational effort than e.g. a Bayesian alternative (Hoeting et al.,1999).

The use of common stepwise multiple regression methods, does not necessarily lead to the best model based on Akaike's criterion. Therefore, statistical packages supply searching algorithms that select the best model from all models satisfying the requirements. Evaluation of these models is made possible by the increasing power of computers and by restriction of the number of models in the selection process by only retaining the plausible ones (Burnham and Anderson, 2002).

Differences in the levels of pathogens were created in four orthogonal treatments. For example, removal of potato haulms from the field in autumn on half of the plots considerably reduced the cfu g^{-1} soil of *V. dahliae* compared to plots where haulms were incorporated into the soil (Scholte, 2000). Density of *G. pallida* was higher on fields where no trap crop was grown in the second year of each cycle. So the design of the experiment has been successful, given that the experimenter aimed at analyzing separately the effects of several soil-borne pathogens in rotations by varying (via factorial treatments) the soil infestation levels of the target organisms. If continued after 1998, for further years, the experiment would probably have given more insight to possible interactions between the pathogens that were present. The summed weights, as given in Table 6, 7 and 8 for the years 1996, 1997 and 1998, already showed this trend in crop damage from these predictors. In 1998, for the first time the summed weight for the interaction of *V. dahliae* and *G. pallida* was high. If the time series would have covered more years, the modelling results probably could show a rise of the summed weights for *Trichodoriadae*, *Meloidogyne* spp. and their interaction with *V. dahliae* in the years after 1998.

By using data from only one experimental field, results are strongly influenced by the local soil characteristics. Differences in the pH levels as well as in the levels of

Table 6. Summed weight, $v_j = \Sigma w_r I_j(r)$, weighted regression coefficients, $\hat{\beta}_j$, and standard errors of $\hat{\beta}_j$, calculated with Eqs. (11)-(13) for *S. subterranea* in the years 1996, 1997 and 1998.

	Year	1996			1997			1998		
j	Predictor	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$
1	*V. dahliae*	1.00	0.46	0.35	1.00	1.13	0.65	1.00	0.90	0.45
2	*G. pallida*	0.31	0.02	0.21	0.29	0.00	0.12	0.99	-0.21	0.26
3	*Trichodoridae*	0.54	0.36	0.62	0.94	0.23	0.50	1.00	1.65	0.62
4	*Meloidogyne* spp.	0.84	3.42	1.57	0.50	-0.18	0.40	0.99	-0.68	0.48
5	*V. d* x *G.pal*	0.13	-0.01	0.11	0.08	-0.02	0.15	0.93	0.16	0.24
6	*V. d* x *Trichod.*	0.41	-0.35	0.51	0.44	0.48	0.63	1.00	-5.33	0.90
7	*V. d* x *Meloid.* spp.	0.80	-13.51	2.33	0.17	0.23	0.53	0.20	-0.01	0.42
8	pH	1.00	2.52	0.56	1.00	1.10	0.48	1.00	3.80	0.57
9	Water soluble P	1.00	-0.04	0.10	1.00	0.08	0.10	0.99	-0.03	0.09

Table 7. Summed weights, $v_j = \Sigma w_r I_j(r)$, weighted regression coefficients, $\hat{\beta}_j$, and standard errors of $\hat{\beta}_j$, calculated with Eqs. (11)-(13) for percentage haulms infected with *V. dahliae* in the years 1996, 1997 and 1998.

	Year	1996			1997			1998		
j	Predictor	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$
1	*V. dahliae*	1.00	0.35	0.30	0.99	1.19	0.73	1.00	1.27	0.42
2	*G.pallida*	0.41	-0.02	0.24	0.83	0.00	0.28	0.41	0.02	0.14
3	*Trichodoridae*	0.30	-0.07	0.40	0.45	0.09	0.38	0.36	0.03	0.34
4	*Meloidogyne* spp.	0.84	-5.54	1.84	0.40	-0.08	0.38	0.66	-0.38	0.50
5	*V.d* x *G.pallida*	0.11	-0.01	0.10	0.53	0.31	0.47	0.14	-0.02	0.13
6	*V. d* x *Trichod.*	0.08	-0.01	0.20	0.21	-0.26	0.53	0.09	-0.02	0.26
7	*V. d* x *Meloid.* spp.	0.23	1.12	1.37	0.21	0.52	0.72	0.23	0.26	0.57
8	pH	0.98	1.11	0.59	1.00	1.03	0.54	0.27	0.06	0.33
9	Water soluble P	1.00	-0.03	0.11	0.24	0.00	0.07	0.47	-0.02	0.09

Table 8. Summed weights, $v_j = \Sigma w_r I_j(r)$, weighted regression coefficients, $\hat{\beta}_j$, and standard errors of $\hat{\beta}_j$, calculated with Eqs. (11)-(13) for tuber dry yield in the years 1996, 1997 and 1998.

	Year	1996			1997			1998		
j	Predictor	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$	v_j	$\hat{\beta}_j$	se $\hat{\beta}_j$
1	*V. dahliae*	1.00	-0.044	0.146	0.91	-0.105	0.233	1.00	-0.071	0.150
2	*G.pallida*	0.29	0.001	0.069	0.47	0.004	0.060	0.97	0.001	0.070
3	*Trichodoridae*	1.00	0.075	0.306	0.99	0.005	0.172	0.36	0.008	0.120
4	*Meloidogyne* spp.	0.30	-0.041	0.329	0.73	-0.038	0.171	0.30	0.003	0.079
5	*V. d* x *G.pallida*	0.07	0.000	0.029	0.10	-0.001	0.061	0.94	-0.023	0.091
6	*V. d* x *Trichodoridae*	0.65	0.077	0.221	0.21	-0.000	0.160	0.08	0.003	0.101
7	*V. d* x *Meloid.* spp.	0.07	0.023	0.263	0.21	-0.037	0.224	0.07	0.000	0.076
8	pH	0.23	0.000	0.108	0.91	-0.093	0.191	0.76	0.057	0.173
9	water soluble P	1.00	0.005	0.035	0.37	0.001	0.028	0.28	0.000	0.017

infestation with *S. subterranea* were already present at the start of the experiment. As the incidence of *S. subterranea* is positively correlated with the value of soil pH, the statistical results should be interpreted with care because other factors in the soil are correlated to the pH, such as antagonists of *S. subterranea*. Furthermore, inoculation of *P. penetrans* was not successful, maybe because *P. crenatus* was already present in the soil. The presence of antagonists of soil-borne pathogens varies between locations and has a strong influence on observed treatment effects (Postma et al., 2008).

Our statistical analysis on factors that affected the response variables leads to the following conclusions.

(a) For the incidence of *S. subterranea*, the predictors *V. dahliae*, pH and water soluble P had the largest effect on the distribution of tubers over the five severity classes (Table 6). No hierarchy within this set of three predictors could be discerned.

(b) The percentage of haulms infected with *V. dahliae* is mainly determined by the number of cfu $(0.01\ \text{g})^{-1}$ soil measured in spring (Table 7).

(c) *V. dahliae* is the most important predictor of potato yield loss. According to the regression coefficients for *V. dahliae* (Table 8), yield loss was most severe in 1997 when the measured density of cfu was low (Scholte, 2000).

The approach we presented is worth to be considered in other applications, such as the design of new crop experiments and the planning of potato crops based on expert systems. With multimodel inference, predictors are given a weight which can be employed in a farmers' decision support system (e.g. Nemadecide.com). Identification of influential predictors plays a role in various other disciplines, such as in conservation biology where the persistence of a species depends on the interaction with other species and on the habitat with its different abiotic components. Since no specific model choice has to be made, multimodel inference guarantees that no information gets lost in an early stage of the analysis.

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Chapter 5: Optimal design of experiments dealing with nematode dynamics and crop yield

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Abstract

The continuous optimum design approach is used to construct designs for experiments dealing with yield loss in potato crops caused by the presence of nematodes on these crops. The results of such experiments are used for the estimation of parameters in dynamical nematode models and in yield loss functions. We consider two response variables: the nematode density at the end of the season and the size of the crop. Both variables depend on the same predictor, the initial nematode density. Continuous optimum design theory applies to linear regression models. It provides preferred levels of the predictor in planned experiments and assigns a certain weight to each of them. Models that are nonlinear in the parameters, as it is the case in this study, are linearized at a given point in parameter plane. The two response variables are functions of the predictor containing each two parameters. Continuous design results can still be applied when the computed weights of the chosen predictor levels cannot be expressed in a suitable number of replications at each of the preferred levels of the initial nematode density: one may choose the best design close to the continuous optimum. Moreover, when only a restricted number of levels without replication are possible one may select from all combinations the design with the highest efficiency for the problem under consideration.

Key words (not in the title): continuous design, exact design, nonlinear models

5.1 Introduction

The occurrence of soil-borne plant pathogens causes considerable economic losses in agriculture. To reduce these losses, a lot of effort is spent in monitoring these pathogens and estimating the damage they may bring about. In a next step, this knowledge can be employed in management strategies maximizing crop yield; different rotation schemes can be taken in consideration for that purpose (Van den Berg et al., 2006). The aim of this study is designing optimal experiments that maximize information on parameters in the pathogen dynamics and yield loss functions.

Crop management and soil-borne pathogens

Farmers analyse soil samples to obtain data about the presence of pathogen populations. Together with information about crop yield, optimal crop sequences and control strategies can be developed using a decision support system, see e.g. www.nemadecide.com. Quantitative biological knowledge of the dynamics of pathogens and the tolerance of crops/cultivars for these pathogens given certain crops/cultivars combinations may lead to adequate recommendations on crop management under various conditions. To obtain appropriate estimates of crop damage from nematodes, pot and field experiments are carried out (Schomaker and Been, 2006). These experiments are expensive because a lot of soil samples must be gathered and processed in the laboratory to measure densities of soil borne-pathogens. Often, experiments cannot be laid out on an experimental station, but must be carried out on farmer fields, where the organisms appear. When the pathogen is a quarantine organism care must be taken to prevent its dispersal during the experiment.

Regression models and the design of experiments

In order to predict yield loss given the density of a nematode population in the field, a biologically sound regression model has to be formulated. The model parameters are estimated by fitting the model to data from experiments. For that purpose different initial nematode density levels are taken and the resulting crop damage is measured. In addition, the nematode density at the end of the season can be derived yielding also information about the soil condition at the start of the next season. In order to predict the response variables “crop yield” and “final density of nematodes” estimates for the regression parameters are needed. These are obtained from experiments which should be designed such that these parameters are computed as accurate as possible. These are called *D*-optimum designs. For that purpose initial nematode levels (support points) have to be chosen optimally within the given constraints of the range of initial densities and the maximum allowable number of trials. This study deals with *continuous optimum designs* which assign to the advised levels of the predictor (initial nematode density) also certain weights. These weights represent the fraction of experimental units to be assigned to each computed level of the predictor. The method applies to systems that are linear in the parameters. Nonlinear systems need to be linearized at some value of the parameter vector (Parker and Gennings, 2008). This requires information in advance: a good guess of this parameter vector is needed. Such a preliminary estimate can be obtained from earlier experiments or from literature where possible response curves as well as prevailing ranges of parameter values can be found. In many situations, it is not possible to apportion the experimental units to the predictor levels according to the assigned weights of the continuous design. Then, given the number of experimental units and the prescribed levels, a design is chosen with the fraction of units assigned to each level as near as possible to the weights in the continuous design. This design is the best possible to realize and is called an *exact design*. Exact designs also arise in situations where a set of possible support points are given in advance. From this set a subset of given size has to be selected from all possible permutations that yields the most efficient design. *D*-optimal continuous designs have the property that they also minimize the variance of the response variables which is called G-optimality. For exact designs this property does not hold in generality.

Designing experiments in agriculture

Optimum experimental design theory has been mainly applied in response surface methodology in industry, where the response is a rather elementary function of the predictor, levels of this predictor are easily set and the range of predictor values is small (Atkinson et al., 2007). Then linear polynomial models suffice to obtain the predictor levels for a design that yields an optimal production scheme. In biological and agricultural research, one mostly deals with a nonlinear response over a wide range of values of a predictor. In addition the response variable may be a count which is not normally distributed (Atkinson and Bailey, 2001). More specifically, in agricultural research, predictor levels such as doses of fertilizers (Sparrow, 1979) and crop protection agents can be easily and accurately installed. However, the amount of fertilizer or crop protection agents taken up by the crops is variable (Carrol et al., 1995). For soil-borne pathogens, installation of initial levels of pathogens is more difficult to realize. When inoculating the soil with pathogens in a pot experiment, a range of densities can be installed, but in field experiments such a procedure does not apply. Evans (1987) inoculated the soil with cysts of *Globodera rostochiensis* or *Globodera pallida* to give population densities up to 1250 eggs per g of soil. Since numbers of eggs per cyst vary between cysts, the applied amount of eggs/g soil per pot will also vary. Scholte (2000) inoculated soil in a field experiment with *V. dahliae*, *G. pallida*, *Meloidogyne* spp. and *P. pratylenchus* with only one initial density for each of these pathogens. A different strategy is to accept the prevailing densities in the soil of the experimental field (Philips et al., 1998) or to create plots with a range of densities by growing resistant and non-resistant potato genotypes in a preliminary year (Elston et al., 1991).

Measurement errors

The density of a soil-borne pathogen in the field is measured with errors (Ferris, 1984). Firstly, a soil sample is taken that represents the density of the whole plot with error. Secondly, extracting the pathogens from the soil into a suspension and counting their number in 1 ml from this suspension is another source of error. These measurement errors inflate the standard errors in the parameters (Snedecor & Cochran, 1987). Even when initial densities are deliberately installed the fraction of inoculated pathogens, that invade the roots of the test crop will vary between crops (Carroll et al., 1995). Measurement error can be taken in consideration when constructing optimum designs (Fedorov, 1972). In this respect it is noted that an increase of the predictor range may result in a decrease of the influence of the measurement error especially when the response variable changes strongly with the value of the predictor. Therefore, in this study on optimum designs we assume that the range of the support points is sufficiently wide so that measurement errors in the predictor can be neglected.

Overview

In the next section we introduce a 2-parameter model for nematode dynamics in the presence of a host and a model for yield loss having also two parameters. In Section 3 we specify the parameter values as estimated from an experiment and give the corresponding covariance matrix. In that section we also shortly introduce the topic of nonlinear regression and show how to linearize models. In Section 4 a summary of the method of *D*-optimum designs is presented, including the use of additional weights. It is also indicated how the optimum design can be computed. In Section 5 the results for the 2-parameter models of Section 2 are given for the case of two predictor levels (support points). Then the additional weights are specified and the efficiency of a design is defined. Furthermore, it is worked out what the best design choice is given the limitation of a budget or a required accuracy in the response variable. In Section 6, we consider the same problems as in Section 5 allowing three or more support points. Finally, in Section 7, we discuss the results emphasizing the practical use of optimum designs in agricultural applications. All calculations were performed using GenStat (Genstat Committee, 2009).

5.2 Modelling nematode dynamics and yield loss

In the statistical analysis of processes a function is chosen that represents the response as it depends on the predictors. Brown (1969) used a simple linear model for yield loss caused by nematodes. A yield curve that, as a function of the nematode density, decreases exponentially above a threshold value was introduced by Seinhorst (1965). For a review of the subject of yield loss caused by plant epidemics we refer to Madden et al. (2008). In this section we will choose biological plausible functions for the final nematode population density at the end of the season and for crop yield as they both depend on the initial density. We fit these functions to the data and give estimates of the parameters.

Single-year nematode dynamics in the presence of a host

To describe population dynamics in a one year trial we will use a model presented earlier in Van den Berg and Rossing (2005). In experiments nematode density is usually measured in spring before a crop is sown or planted to estimate the initial density P_{ini} (number of nematodes g^{-1} soil). In autumn when the crop is harvested the final density P_f is determined. The following equation will be used to describe the relation between P_f and P_{ini}:

$$P_f = \eta_1(P_{ini};\alpha,\beta) + \varepsilon_1 \qquad \text{with} \qquad \eta_1(P_{ini};\alpha,\beta) = \frac{P_{ini}}{\alpha + \beta P_{ini}} \;, \tag{1}$$

where $\varepsilon_1 \sim N(0,\sigma_1^2)$ is a normally distributed error term with expected value zero and variance σ_1^2. The slope at the origin of the function $\eta_1(P_{ini};\alpha,\beta)$ equals $1/\alpha$ and for $P_{ini} \to \infty$ the graph of the function approaches the horizontal asymptote with value $1/\beta$. The model equation ignores population decrease at high initial population levels, a finding well known for *e.g.* potato cyst nematode (Seinhorst, 1970). Thus, the model should be applied only where rotations keep the density of nematodes at relatively low levels, as may be expected in economically exploited cropping systems.

Yield loss

We will use the inverse linear model to study yield as function of initial density of soil-borne pathogens, see Elston et al. (1991) and Van den Berg et al. (2006):

$$Y = \eta_2(P_{ini}; Y_0, \lambda) + \varepsilon_2 \qquad \text{with} \qquad \eta_2(P_{ini}; Y_0, \lambda) = \frac{Y_0}{1 + \lambda P_{ini}}, \tag{2}$$

where parameter Y_0 is the maximum yield ($P_{ini} = 0$), λ a rate parameter and $\varepsilon_2 \sim N(0, \sigma_2^2)$.

5.3 Nonlinear regression

Regression analysis deals with the estimation of model parameters using data of processes to which these models apply. In nonlinear regression, this procedure is applied to a linearization of the model equations at a suitable starting estimate of the parameter vector (first guess). Using linear regression a better estimate is found and in an iterative way this estimate can be improved.

Linear regression

For an experiment consisting of N observations, the linear regression model (Montgomery et al., 2001) takes the form of a set of equations of the type

$$y_i = \theta_0 + \theta_1 x_{1i} + \theta_2 x_{2i} + \ldots + \theta_k x_{ki} + \varepsilon_i, \qquad i = 1,\ldots,N, \tag{3}$$

where x_{ji} denotes the value the j-th predictor in case i, and y_i is the value of the response. It is possible to analyze models that are nonlinear in the predictor variable by taking e.g. $x_2 = x_1^2$. The *residual*, also called the *error*, ε_i is assumed to have a normal distribution $N(0, \sigma^2)$. In vector notation we have

$$y = X\theta + \varepsilon,$$

with X the *design matrix* with N rows and $k + 1$ columns. The parameter vector $\hat{\theta}$ is selected that minimizes the *residual sum of squares* $\varepsilon^T\varepsilon$ yielding the normal equations being of the type

$$X^T y = X^T X \hat{\theta}, \qquad \text{giving} \qquad \hat{\theta} = \left(X^T X\right)^{-1} X^T y. \tag{4}$$

The covariance matrix of $\hat{\theta}$ is given by

$$\mathrm{Cov}\left(\hat{\theta}\right) = \sigma^2\left(X^T X\right)^{-1}. \tag{5}$$

The variance σ^2 of the error ε can be estimated from the sample variance, so that (5) may yield an estimate of the covariance matrix.

Nonlinear regression

Although models (1) and (2) can be transformed so that they take the form of expressions that are linear in the parameters, we still continue with the nonlinear approach for these problems. The main reason for this is that the response P_f of model (1) is Poisson distributed. After such a linearizing transformation the variance of the error would not have the same constant value over all cases. For model (2) the linearizing transformation, being the reciprocal of the tuber yield is gamma distributed and would also lead to a non-constant variance of the error. Moreover, GenStat provides a regression procedure that exactly fits model (2).

Nonlinear regression models with a single predictor, such as (1) and (2), take the general form (Schabenberger and Pierce, 2002):

$$y_i = \eta\left(x_i, \theta\right) + \varepsilon_i, \qquad i = 1,\ldots,N, \tag{6}$$

where η is a nonlinear function of the parameter vector $\theta = (\theta_1,\ldots, \theta_p)$. Estimation of the vector value θ that minimizes $\varepsilon^T\varepsilon$ is done in an iterative way. It starts with an initial guess $\hat{\theta}^{(0)}$. Then linear regression is applied to the model

$$\eta(x,\theta) = \eta(x,\hat{\theta}^{(0)}) + \left[\frac{\partial\eta(x,\theta)}{\partial\theta}\right]_{\theta=\hat{\theta}^{(0)}} (\theta - \hat{\theta}^{(0)}), \tag{7}$$

being the linearization of (6) at $\theta = \hat{\theta}^{(0)}$. In (7) the term within the brackets [.] indicates a row vector with components being the value of the derivative of η with respect to θ_j, $j = 0, 1, 2,\ldots, p$ at $\hat{\theta}^{(0)}$. Next we introduce the matrix F with rows identical to this row vector with in row i the value x_i. The normal equations then become

$$F^T(y - y^{(0)}) = F^T F\ (\theta - \hat{\theta}^{(0)}), \tag{8}$$

where the column vector $y^{(0)}$ contains at position i the estimate $\eta(x_i, \hat{\theta}^{(0)})$. A solution of the type (4) for $(\theta - \theta^{(0)})$ yields the estimate $\hat{\theta}^{(1)}$ replacing the first guess $\hat{\theta}^{(0)}$. In this way an iteration process is started leading to more accurate estimates of the parameters. The covariance matrix for the estimate of $\hat{\theta}$ is given by

$$\mathrm{Cov}(\hat{\theta}) = \sigma^2\left(F^T F\right)^{-1}. \qquad (9)$$

Parameter estimates from historical data for models (1) and (2)

From a previous experiment the parameters of (1) and (2) are estimated (Van den Berg et al., 2006) using the nonlinear regression facilities of GenStat (Genstat Committee, 2009). Initial nematode population density P_{ini}, final nematode population density P_f and tuber yield Y were obtained from three rows of experimental plots stretching from the focus of an infestation to its periphery. In this way 34 plots with a wide range of initial population densities were obtained. Fitting model (1) to the 34 observations of P_f and P_{ini} , the following estimates were obtained

$$\hat{\sigma}_1^2 = 2.67, \qquad \hat{\alpha} = 0.2734 \quad \text{and} \quad \hat{\beta} = 0.03366 \qquad (10)$$

with an estimated covariance matrix

$$\mathrm{Cov}(\hat{\alpha},\hat{\beta}) = \begin{pmatrix} 0.00492448 & -0.00020044 \\ -0.00020044 & 0.00001853 \end{pmatrix}, \qquad (11)$$

see Figure1a. For model (2) the parameters were estimated with the GenStat directive FITCURVE applying exactly to this model, see Figure 1b. Fitting model (2) to the 34 observations of tuber yield and P_{ini} , the following estimates were obtained

$$\hat{\sigma}_2^2 = 38.75 \qquad \hat{Y}_0 = 55.57 \qquad \hat{\lambda} = 0.03337 \qquad (12)$$

with estimated covariance matrix

$$\mathrm{Cov}(\hat{Y}_0,\hat{\lambda}) = \begin{pmatrix} 4.92534468 & 0.00808384 \\ 0.00808384 & 0.00002460 \end{pmatrix}. \qquad (13)$$

5.4 *D*-optimum designs

When constructing an optimum design of a nonlinear model, use is made of estimates of the parameters obtained from previous experiments or from the literature. For

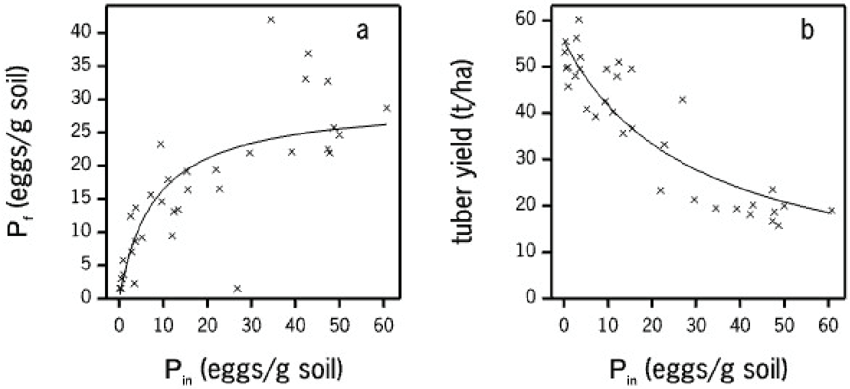

Fig. 1. Fitting the two models to data of previous experiments: (a) Model (1) yielding parameter estimates (10) using Poisson regression; (b) Model (2) with estimates (12).

designing a new experiment we can select levels of the predictor that minimize the determinant of the covariance matrix, being equivalent to minimizing the volume of the confidence ellipsoid for the given estimate θ of the parameter vector. This procedure is referred to as a *D*-optimum design. Its primary goal is to design the experiment such that model parameters are estimated as accurate as possible. Mathematically it can be phrased as finding levels that maximize the determinant of the so-called *information matrix* X^TX/σ^2 being the inverse of the covariance matrix.

For the nematode dynamics model as well as for the yield loss model we construct *D*-optimum continuous designs that maximize the determinant of the information matrix. *D*-optimality is the most often used criterion because optimality in this sense will also mean a good score for other optimum criteria (Atkinson et al., 2007). For example, *D*-optimality means that also the maximum of the standardized variance of the response over the full range of predictor values is minimized (*G*-optimality).

Both (1) and (2) are nonlinear regression models of the form

$$y_i = \eta(x_i, \theta) + \varepsilon_i, \qquad i = 1, \ldots, N,$$

for which we consider a linearization of the type (7) at a value of the parameter vector θ being an estimate we obtained in advance, see Section 3.

Choosing a design

Let the given parameter vector θ have dimension *p*. We choose continuous optimum experimental designs with one quantitative predictor *x* for which, with appropriate weights ω_i, n different levels $x_i^{(s)}$ (support points) are chosen. Thus, a design is characterized by two vectors $x^{(s)}$ and ω:

$$\xi = \begin{Bmatrix} x_1^{(s)}, x_2^{(s)}, \dots, x_n^{(s)} \\ \omega_1 \,, \omega_2 \,, \dots, \omega_n \end{Bmatrix} \quad \text{with} \quad \sum_{i=1}^{n} \omega_i = 1 \qquad \text{and}\, p \le n \le p(p+1)/2\,, \tag{14}$$

see Atkinson et al. (2007) for a more detailed description. The superscript (s) will be used from here on, to indicate whether x is a support point. From the weights, the required number of trials r_i at each support point can be determined. If N is the total number of trials, then the weights relate to the number of trials as follows

$$\omega_i = r_i / N\,, \qquad i = 1, \dots, n. \tag{15}$$

If the weights ω_i of the optimum design are such that (15) cannot be realized, then rational numbers r_i / N near ω_i have to be found satisfying the constraints in the most profitable way.

A measure for the precision of a design

The criterion will be D-optimality which is based on minimizing the determinant of the covariance matrix as a function of ξ. Its inverse, the information matrix, can be formulated as (Atkinson and Bailey, 2001)

$$M\left(\omega, x^{(s)}; \theta\right) = \sum_{i=1}^{n} \omega_i \frac{\partial \eta\left(x_i^{(s)}; \theta\right)}{\partial \theta} \left(\frac{\partial \eta\left(x_i^{(s)}; \theta\right)}{\partial \theta} \right)^T = F^T(x^{(s)}; \theta)\, \Omega\, F(x^{(s)}; \theta)\,, \tag{16}$$

where the n x p matrix F is the same as in (9) and Ω is a n x n diagonal matrix containing the weights ω_i ($\Sigma\omega_i = 1$). For θ a given value based on available knowledge is chosen. The variance of the predicted response at x equals

$$\mathrm{Var}(\hat{y}(x)) = \frac{1}{N} \sigma^2 d(x, \xi, \theta) \tag{17}$$

with

$$d(x, \xi, \theta) = f^T(x) M^{-1}\left(\omega, x^{(s)}\right) f(x) \qquad \text{and} \qquad f(x) = \frac{\partial \eta(x; \theta)}{\partial \theta}.$$

In a continuous optimum design the upper bound of the *standardized variance* $d(x, \xi, \theta)$ over the x-interval equals the number of parameters p. It takes this value at the support points $x_i^{(s)}$. *D*-optimality is reached if the *general measure of imprecision*

$$\Psi(M(\xi)) = \ln(\det(M^{-1}(\xi))) \tag{18}$$

is minimized.

The continuous optimum design
The minimum with respect to ξ of this function $\Psi(M(\xi))$ is obtained by considering the directional derivative function $\phi(x,\xi)$. In a minimum ξ^* this derivative is non-negative in all directions. The optimum design ξ^* satisfies

$$\phi(x,\xi^*,\hat{\theta}) = p - d(x,\xi^*,\hat{\theta}) \geq 0\,. \tag{19}$$

It is noted that a *D*-optimal design is also *G*-optimal, because the standardized variance satisfies

$$\max_x[d(x,\xi^*,\hat{\theta})] = \min_\xi[\max_x[d(x,\xi,\hat{\theta})]] = p. \tag{20}$$

Additional weights
In addition to the weight ω in the continuous optimum design we may consider an extra weight. E.g. we may take in consideration that an observation error depends on the size of the response variable. For observation *i* this weight must take the form $w(x_i)$, so it is indeed allowed that this weight is a function of the expected response because $w[\eta(x_i)] = w(x_i)$. Consequently, then (17) changes into

$$d(x,\xi,\hat{\theta}) = f^T(x)M^{-1}\left(u,x^{(s)}\right)f(x) \quad \text{with} \quad u_i = \omega_i w(x_i^{(s)}),\ i = 1,\ldots,p\,. \tag{21}$$

Methods of computation
The simplex method of Nelder & Mead (1965) is used to search for the values of $x_i^{(s)}$ and ω_i minimizing $\Psi(M(\xi))$ given by (18). The sum of ω_i's is forced to the value 1 by the use of sine and cosine functions (Atkinson and Donev, 1996) and the $x_i^{(s)}$ are forced to lie in the interval $[0, x_{\max}]$ by setting $x_i^{(s)} = x_{\max}\, e^{xsi}/(1+e^{xsi})$ with *xsi* replacing $x_i^{(s)}$ in the algorithm. It is noted that ξ has dimension $2p - 1$. The algorithm requires a set of starting values ξ. The size of this set needs to be one higher than the dimension of ξ, so in our case $2p$ starting values are needed. In each iteration step, one element of the set is replaced: the one with the highest value of the object function (18) is removed and a point is added for which the object function is below the values found before, see Thompson (1999) for the scheme that is used.

For models defined by analytical functions the optimum analytical design with a small number of support points can be computed using a formula handling software package. Note that for $\xi = \xi^*$ the expression Det($M(\xi)$) takes its maximum value. Thus, ξ^* is found by setting the partial derivatives with respect to ξ equal to zero.

5.5 Optimum design with the minimum of two support points for 2-parameter models

As outlined in the previous section, we construct the continuous optimum designs for the two models of Section 2.

The nematode dynamics

For model (1) with parameter values (10) we restricted the allowable values of the support points to the interval [0, 100]. An upper limit is chosen because otherwise the upper support point would take a physically unfeasible value: higher values would further improve statistically the estimate of the upper asymptote $1/\beta$ of the dynamic model (Parker and Gennings, 2008). The value 100 lies well above the largest value (60.76) found in the experiment of Section 3. The information matrix M given by (16) takes the form

$$M\left(\omega, x^{(s)}\right) = \sum_{i=1}^{2} \omega_i \, q\left(x_i^{(s)}\right) q^T\left(x_i^{(s)}\right)$$

with

$$q^T\left(x_i^{(s)}\right) = \left(\frac{-x_i^{(s)}}{\left(\hat{\alpha} + \hat{\beta} x_i^{(s)}\right)^2} \quad \frac{-(x_i^{(s)})^2}{\left(\hat{\alpha} + \hat{\beta} x_i^{(s)}\right)^2} \right), \tag{22}$$

so that

$$\mathrm{Det}(M(\xi)) = \omega_1 \omega_2 \left(x_2^{(s)} - x_1^{(s)}\right)^2 \prod_{i=1}^{2} \left(\frac{x_i^{(s)}}{(\hat{\alpha} + \hat{\beta} x_i^{(s)})^2} \right)^2 .$$

From this last expression existing of two factors of which one depends only on the weights and the other on the support points, we right away conclude that for the optimum design the weights satisfy $\omega_1 = \omega_2 = ½$. Maximizing the other factor of the determinant we obtain the D-optimum design

$$\xi^* = \begin{pmatrix} 6.99 & 100 \\ 1/2 & 1/2 \end{pmatrix}. \tag{23}$$

A computation based on the simplex method confirms the result (23). Note that the variance (17) takes its maximum value over the interval at the support points with the standardized variance $d(x,\xi^*)$ equal to the number of support points as it can be expected for a continuous optimum design with $n = p = 2$.

Using an additional weight

The way the measurements for model (1) were obtained makes it advisable to consider an appropriate additional weight function $w(x)$. The residual plot for the case $w(x) = 1$, see Figure 2a, also indicates the need of it: at low values of the response the residual is also systematically smaller. The values of P_{ini} and P_f were determined by extracting the eggs of potato cyst nematode from the soil. Their numbers in 1 ml of a suspension were counted with two or three replications. With these counts the density per gram soil was calculated. Since P_f is derived from a count ranging from 0 to over 40 (Figure 1a), it is not realistic to assume that it has a normal distribution with a fixed variance. Choosing a Poisson distribution would be more appropriate. For a stochastic variable having a Poisson distribution the variance equals the mean, so the residuals are well balanced if we choose as additional weight

$$w(x) = 1/\eta_1(x,\hat{\theta}), \tag{24}$$

see (1) and (21). In Figure 2b we observe that indeed the residuals for smaller x-values have become of the same order as the ones for the larger x-values.

The P_{ini}-range is again restricted to the interval [0, 100] and the optimum design is estimated by minimizing the maximum over x of the standardized variance, $d(x,\xi,\widehat{\theta})$, of (21) for all ξ and with the constraint $\omega_1 + \omega_2 = 1$. The information matrix is of the same form as (16) with ω_i replaced by $\omega_i w(x_i)$, see (24). We find as D-optimum design:

$$\xi^* = \begin{pmatrix} 3.62 & 100 \\ 1/2 & 1/2 \end{pmatrix}, \tag{25}$$

giving for the general imprecision measure (18) as minimum

$$\Psi(\xi^*) = \ln[\det(M^{-1}(\xi^*))] = -12.55. \tag{26}$$

For the optimum design of model (1) with the additional weight (24) the lower point is positioned closer to the origin compared with the design without an additional weight ($w(x) = 1$). This due to the fact that with (24) smaller P_{ini}-values get now a larger weight. Using (17) and (21) we obtain for the variance of a prediction of P_f at $P_{ini} = x$ in the D-optimal design

$$\mathrm{Var}\left(\hat{P}_f(x)\right) = \frac{\hat{\sigma}_1^2}{N} q^T(x^{(s)})\, M^{-1}\left(\omega w(x^{(s)}), x^{(s)}\right) q(x^{(s)}) \,, \quad N = r_1 + r_2$$

with an equal number of trials at the two support points: $r_1 = r_2$ ($\omega_1 = \omega_2 = ½$), see Figure 3.

The yield loss model

For model (2) with (12) we perform the same calculations as for model (1). It suffices to take here $w(x) = 1$. We find as D-optimum design

$$\xi^* = \begin{pmatrix} 0 & 29.97 \\ 1/2 & 1/2 \end{pmatrix} \tag{27}$$

with for the matrix M given by (16) the expression

$$M\left(\omega, x_i^{(s)}\right) = \sum_{i=1}^{2} \omega_i q\left(x_i^{(s)}\right) q^T\left(x_i^{(s)}\right) \text{ with } q^T\left(x_i^{(s)}\right) = \left(\frac{1}{1+\lambda x_i^{(s)}} \quad \frac{-Y_0 x_i^{(s)}}{\left(1+\lambda x_i^{(s)}\right)^2} \right).$$

For the minimum of the imprecision measure we get

$$\Psi(\xi^*) = \ln(\det(M^{-1})) = -10.68. \tag{28}$$

Formula (17) for the variance of a prediction of the yield at $P_{ini} = x$ for the D-optimal design equals

$$\mathrm{Var}\left(\hat{Y}(x)\right) = \frac{\hat{\sigma}_2^2}{N} q^T\left(x^{(s)}\right) M^{-1}\left(\omega(x^{(s)}), x^{(s)}\right) q\left(x^{(s)}\right), \quad N = r_1 + r_2 \ (r_1 = r_2), \tag{29}$$

see Figure 4.

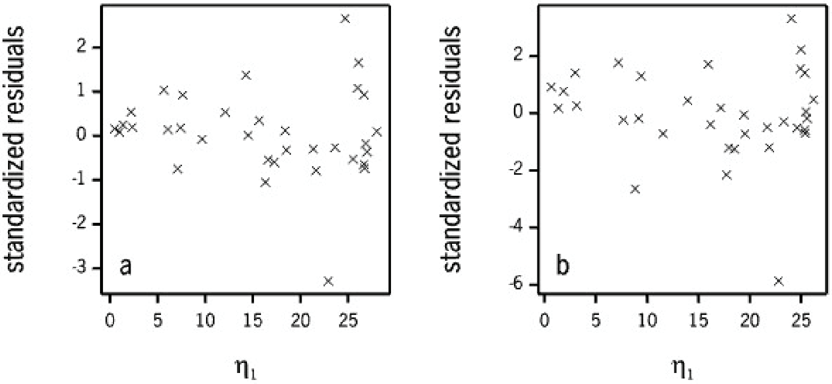

Fig. 2. Residual plot of fitting model (1) to data from the case study described in Section 2 with an additional weight (a) $w(x) = 1$ (no weight); (b) $w(x) = 1/\eta_1(x,\hat{\theta})$.

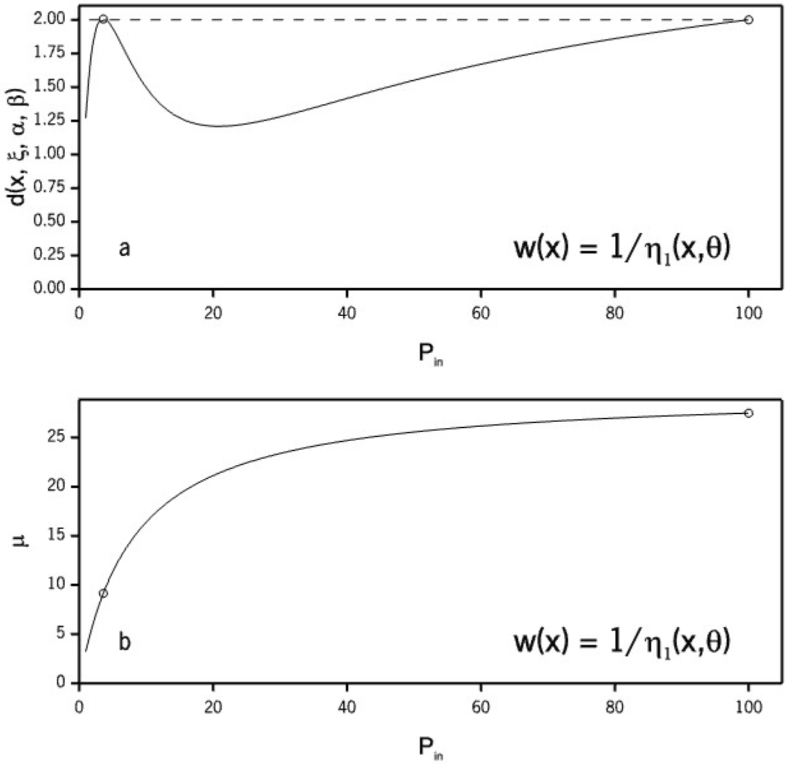

Fig. 3. A continuous optimum design with two support points for the nematode dynamics model (1): (a) The (standardized) prediction variance $d(x,\xi;\widehat{\alpha},\widehat{\beta})$ given by (17) for the final density P_f of nematodes. (b) The prediction $\mu = \hat{P}_f = \eta_1(P_{ini};\hat{\alpha},\hat{\beta})$ itself as a function of the initial density P_{ini}, see (1) and (10).

The lower support point of the optimum design of model (2) is 0, as this is an efficient choice for estimating parameter Y_0. The higher support point is at $x = 29.97$. This value is understood from the composition of the denominator of (2): near that value the term λP_{in} comes along the value 1 in the denominator.

Relative efficiency of a design

For any experiment, for which a model of type (14) can be formulated and parameter estimates are available at forehand, the efficiency of its design ξ relative to that of a continuous optimum design ξ^* with $n = p$ support points can be defined. Let, as in the case study described in Section 3, such an experiment have a design (Rasch et al., 1997):

$$\xi = \begin{pmatrix} x_1^{(s)} & \cdots & x_N^{(s)} \\ \dfrac{1}{N} & \cdots & \dfrac{1}{N} \end{pmatrix}, \tag{30}$$

then $M(\xi)$ follows from (16) and the relative efficiency is defined by

$$E_{rel} = \left(\frac{\det(M(\xi))}{\det(M(\xi^*))} \right)^{1/p}, \tag{31}$$

see Atkinson et al. (2007). The $(1/p)^{\mathrm{th}}$ power results in an efficiency proportional to the design size: if $E_{rel} = 0.5$, then two trials are needed to achieve the same reduction of variance in the response as with one trial from the optimum design.

Now that we have obtained optimum designs for model (1) and (2) we can compute the relative efficiency of the design of the case study of Section 3 with parameter values and covariance matrices given by (10)-(13). From these covariance matrices we derive that

$$M^{(1)}(\xi) = \frac{\hat{\sigma}_1^2}{N}\left(\mathrm{Cov}(\hat{\alpha},\hat{\beta})\right)^{-1} \qquad \text{and} \qquad M^{(2)}(\xi) = \frac{\hat{\sigma}_2^2}{N}\left(\mathrm{Cov}(\hat{Y}_0,\lambda)\right)^{-1}, \tag{32}$$

so that with the use of (26) and (29) we obtain

$$E_{rel}^{(1)} = \left(\frac{\det\left(M^{(1)}(\xi)\right)}{\det\left(M^{(1)}(\xi^*)\right)} \right)^{1/p} = 0.652 \quad \text{and} \quad E_{rel}^{(2)} = \left(\frac{\det\left(M^{(2)}(\xi)\right)}{\det\left(M^{(2)}(\xi^*)\right)} \right)^{1/p} = 0.733\,. \tag{33}$$

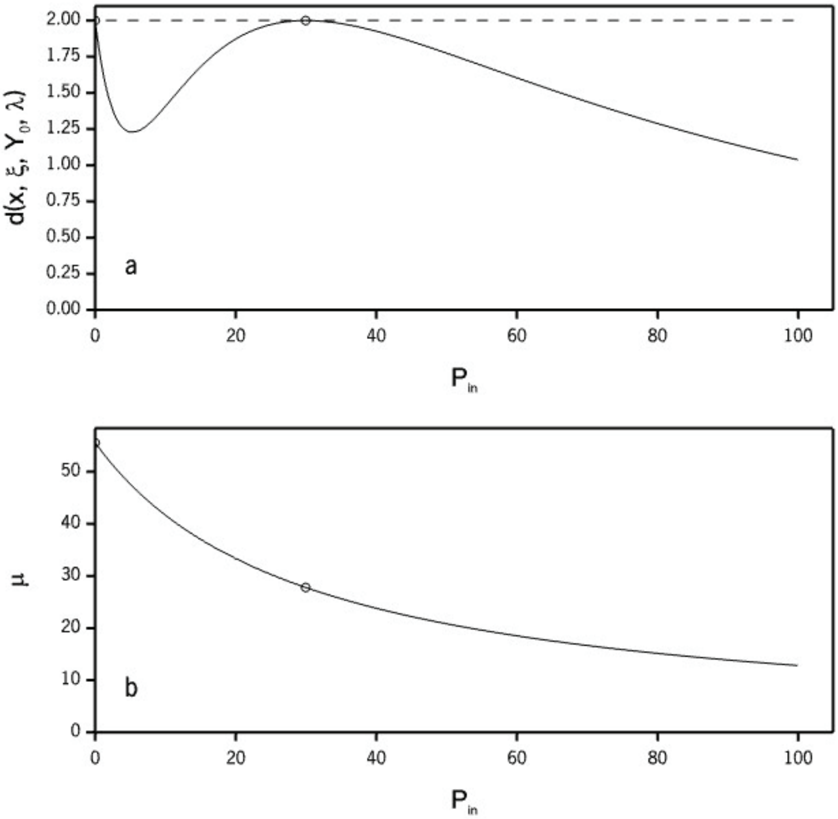

Fig. 4. A continuous optimum design with two support points for the yield model (2). (a) The (standardized) prediction variance $d(x,\xi;\widehat{Y}_0,\widehat{\lambda})$ given by (17) for the yield Y. (b) The prediction $\mu = \hat{Y} = \eta_2(P_{ini};\hat{Y}_0,\hat{\lambda})$ itself as a function of the initial density P_{ini}, see (2) and (12).

Planning a feasible optimum design

The objective of analyzing possible designs is to select, within the available budget, the one that performs the best in the sense that it has the lowest variance in the response variable. The total number of trials N is then given. For two support points with $\omega_1 = \omega_2$ as in this study two cases can be discerned. When N is even $N/2$ experimental units can be assigned to each of the two support points. Here the continuous and the exact design coincide. When N is odd $(N - 1)/2$ experimental units can be assigned to each of the two support points and the N^{th} experimental unit can freely be assigned to one of the support points, both alternatives will have the same efficiency. For large odd N this efficiency will be slightly below the continuous optimum design.

If at forehand the required performance is specified, then the minimum number of trials $N_{\min}$, that is needed to achieve this result, should be found. A continuous optimum design with two support points for the 2-parameter model has the property that the maximum of the standardized variance at the x-interval takes the value 2 so that the maximum variance of the response variable itself depends on N as

$$\mathrm{Var}\{\hat{y}(x)\}_{\max} = 2\hat{\sigma}^2 / N, \tag{34}$$

see (17). Then $N_{\min}$ is the smallest value of N for which this maximum variance is below the required value. From the two designs at the line $r_1 + r_2 = N_{\min}$ nearest to the intersection with $r_2 = (\omega_2^* / \omega_1^*)\, r_1$ the best exact design is selected using the formula for the relative efficiency, see Figure 5.

More couples of support points

The quality of the optimum design with two support points as derived above strongly depends on the choice of the parameter values (10) and (12) of the two models. In the present case they are based on the results from one season. If we have more information from other seasons or from the literature, we may produce extra couples of optimum support points. In this way a better spread over the range of feasible predictor levels is obtained. If we are concerned about measurement errors corrupting the choice for α and β as given by (10) we may draw parameter values from a bivariate normal distribution with expected values (10) and covariance matrix (11). A same argument applies to the parameters Y_0 and λ of model (2).

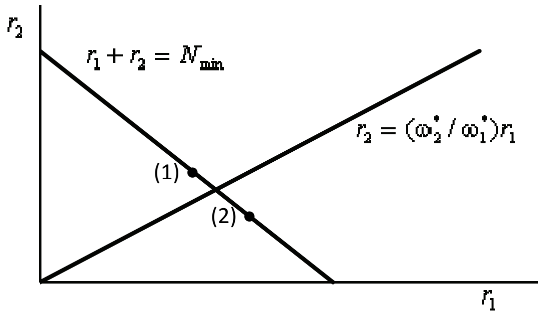

Fig. 5. Finding the best design given the maximum allowed variance (34) in the response using the continuous optimum design approach. The exact design is chosen from the two indicated by (1) and (2) in the figure; they are nearest to the point of intersection.

5.6 Designs with three or more support points for the 2-parameter models

In the previous section the number of support points n was taken equal to the number of parameters p. The optimum design then has the property that the standardized variance of the response takes the same maximum value p on the chosen x-interval. For $p > n$ two different cases should be discerned. First for $n \le p(p+1)/2$ an optimization over the number of design points will give the same support points as in (25) as will be shown in the next paragraph. For $n > p(p+1)/2$ a continuous optimum design cannot be found anymore.

Three support points

Since our models (1) and (2) contain 2 parameters, three support points is the maximum number for which we can reach optimality as stated in (14), see also Silvey (1980). For model (1) with previously obtained parameter estimates (10) we compute the continuous D-optimum design with three support points for the x-interval [0, 100] and with the additional weight function (24):

$$\xi^* = \begin{pmatrix} 3.62 & 3.62 & 100 \\ 0.48 & 0.02 & 0.5 \end{pmatrix}. \qquad (35)$$

This result is identical to (25).

Four or more support points and a replication free design

Before laying out an experiment in the field, one can sample the soil of each experimental unit that is at hand and determine its pathogen density. Next one can select a subset of the experimental units resulting in a design with maximum relative efficiency. As an example we take the 34 experimental units of the case study on models (1) and (2) with parameter specifications (10)-(13) and assume that in the next season the same initial pathogen densities can be taken. We examine designs with n = 4, 5, or 6 predictor levels which are chosen from the 34 experimental plots with given initial levels x_j of pathogens, $j = 1,\ldots,34$. Since this a replication free design (Rasch et al., 1979) we have

$$\omega_i = 1/n, \qquad i = 1,\ldots,n. \qquad (36)$$

The optimum design for n support points is found by considering all possible choices of n experimental units out of the 34 available ones, see Table 1. From each of them it is determined for which value of the n-dimensional vector $x^{(s)}$ the determinant of the information matrix (16) takes its maximum value. For these values the relative efficiency (31) is computed and the best scoring combination is selected, see Tables 2 and 3 for both models (1) and (2). The value of the relative efficiency makes it possible to make comparisons within the groups of the table and do not have a meaning by themselves. This procedure leads to a choice of experimental units with nematode densities as close as possible to the optimum designs (25) and (27): for model (1) and n = 4, 6 half the points are near 3.62 and the other are at the upper end. Comparing the designs with n = 4 and n = 5 we see that they only differ in the additional fifth point of the case n = 5. It turns out that it is more efficient to choose it near 3.62 than at the upper end. The relative efficiency for n = 5 is somewhat below the one for n = 4 (and n = 6), because it is at larger distance from the optimum continuous design. For the yield loss model (2) with n = 5 three points are chosen close to 29.97 and two close to 0.

Table 1. The 34 initial levels of pathogen density to choose from in experimental designs dealing with the presence of soil-borne pathogens and associated crop damage.

x:	0.19	0.39	0.54	0.91	0.96	2.60
2.84	3.44	3.63	3.77	5.17	7.20	9.42
9.70	11.13	12.03	12.43	13.43	15.34	15.58
21.98	22.78	26.89	29.62	34.49	39.20	42.30
42.91	47.35	47.37	47.77	48.76	50.00	60.76

Table 2. Replication free designs for a final pathogen density estimate based on (1).

n	$x_1^{(s)}$	$x_2^{(s)}$	$x_3^{(s)}$	$x_4^{(s)}$	$x_5^{(s)}$	$x_6^{(s)}$	$E_{rel}^{(n)}$
4	3.44	3.63	50.00	60.76			0.8711
5	3.44	3.63	3.77	50.00	60.76		0.8532
6	3.44	3.63	3.77	48.76	50.00	60.76	0.8613

Table 3. Replication free designs for a yield loss estimate based on (2).

n	$x_1^{(s)}$	$x_2^{(s)}$	$x_3^{(s)}$	$x_4^{(s)}$	$x_5^{(s)}$	$x_6^{(s)}$	$E_{rel}^{(n)}$
4	0.19	0.39	29.62	34.49			0.9681
5	0.19	0.39	26.89	29.62	34.49		0.9488
6	0.19	0.39	0.54	26.89	29.62	34.49	0.9597

5.7 Discussion

Putting much effort in finding the best design for an experiment will almost certainly pay off. Restrictions on the availability and range of meaningful predictors as well as constraints of budgetary type will bound the set of possible designs. Within this set one has to look for a design that is optimal in achieving some goal. In our study we wish to estimate model parameters with the highest accuracy in order to make the best possible prediction of response variables.

In our case we have to deal with pathogen densities and associated crop damage. It is important that all available information influencing the choice of the ultimate design is used. Additional weight functions may be employed for that purpose as we demonstrated for the nematode dynamics model. In continuous optimum design not only levels of a predictor are computed, their effect is also given a weight. If such weights are rational numbers, the optimum design can be realized by using an appropriate number of replications at each level of the predictor. A larger number of replications results in a higher accuracy of the parameter estimates. If no replications are made, the weights can be applied directly in the computation of the design.

The range and controllability of the predictor levels play a decisive role in the process of finding the most suitable design. For research purposes one year pot experiments on the dynamics of soil-borne pathogens can very well be carried out because initial densities can be installed at wish by inoculation. In field experiments one has to accept the density in the available experimental units. In the latter case it has no use to compute an optimum continuous design. In Section 6 we dealt with this situation in which an exact design is constructed under the constraints that a limited number of initial pathogen density levels as well as a limited number of experimental units are available. As remarked already, including replications is in many cases not an option, e.g. in case of an experiment on farmland near a focus with spatially variable nematode densities.

Extensions of the designs we presented can be made. When for example tolerance for potato cyst nematode has to be tested on different cultivars the optimisation problem is to divide the experimental units over the available experimental units such that the relative efficiencies per cultivar are maximized. This is an extension of the design we constructed in Section 6. Another problem one may wish to deal with is that of estimating simultaneously for a cultivar the tolerance for a pathogen and the presence of a pathogen. Clearly the optimal designs for tolerance and pathogen densities do not coincide. If the budget allows, all experimental units of both optimal designs can be used. Besides the higher accuracy of the estimates this approach also has as advantage that the design is more robust against local perturbations. Such deviations are inevitable in field crop research where environmental conditions may strongly vary in space and time. A systematic method to choose a design that is optimal in relation with two criteria is to minimize the sum of the relative efficiencies of both criteria (Atkinson et al., 2007).

An extension directly related with the present case study deals with crop rotation as a method to reduce economic damage from soil-borne pathogens. Potato cultivars grown in a rotation and potato cyst nematode living on this crop can be analysed as a coupled dynamical system (Van den Berg et al., 2005). If this rotation is continued indefinitely, the system will reach a steady state with nematode densities and crop yield expressed in the model parameters (α, β, λ and Y_0). After performing a multivariate regression analysis (Gelman et al., 1995) the variance of e.g. the yield level at steady state can be minimized using a *C*-optimum design (Atkinson et al., 2007). Not only the support points and their weights can be varied also the composition and the period of the rotation can be chosen within the constraints imposed by the farmers' management of crops. The relative efficiency of different solutions can then be compared.

Local *D*-optimum designs for nonlinear functions require given parameter values obtained from literature or from former experiments. Clearly, the optimum design depends on these supplied parameter values. However, in a future experiment the parameter estimates will not be equal to the preliminary supplied estimates because of changing environmental conditions. Deviating properties of pathogens and crops may also result in parameter values that differ from previous years. We may think of changing virulence of the pathogen or the tolerance of the grown crop or cultivar. In the design process we may handle this by gathering as much information from literature as possible. This information is next used to construct a prior probability density function for each of the parameters. This prior distribution can be combined with *D*-optimality.

Another way to anticipate uncertain conditions is to use Bayesian methods (Chaloner and Verdinelli, 1995) by using more support points; their number is allowed to exceed the maximum that holds for the continuous optimum design. In the Bayesian approach one uses the above mentioned prior distribution of the parameter vector instead of a fixed value. An alternative is to use utility functions with a penalty for coinciding support points (Parker and Gennings, 2008).

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Chapter 6: General discussion

This thesis aims at increasing the capacity for predicting crop yields in cropping sequences in the presence of soil borne pathogens, thus contributing to better informed management decisions. In Chapters 2 and 3, we followed a theoretical approach to describe population dynamics of soil-borne pathogens in crop rotations. The emphasis was on schemes leading to high crop yields while taking into account the risk of damage from soil-borne pathogens. Using a statistical approach, in Chapter 4 incidence of powdery scab (*Spongospera subterranea*), *Verticillium dahlia* and potato yield were predicted based on soil biological and soil chemical predictors. The prediction was based on a weighted average of the predictions of all possible models using information as the weighing factor. In Chapter 5 we concentrated on the efficiency of experimental designs for predicting the dynamics of soil-borne pathogens and their yield loss. In this concluding General Discussion we will dwell on the choices made and evaluate their possible effect on our results.

Agricultural systems and crop rotations

Crop rotation experiments are mainly performed to estimate long term effects of crop sequences or treatments on physical, chemical and biological soil fertility. Statistical theory was developed for design and analysis of such experiments (Patterson, 1954, Yates, 1954). Because the sequences and treatments were tested under optimal management conditions, these experiment were seen as a way to integrate the available agricultural knowledge. Also system theory was developed for studying parts of reality having interrelated elements (Von Bertalanffy, 1969). This theory is applied nowadays in disciplines such as biology, economics, psychology and demography. In agriculture crop systems can be represented by relations between plant parts and the environment using mathematical equations. Also the notion of farming systems was introduced comprising the husbandry and economics of a variety of crops and animals, and their interaction (Rabbinge and De Wit, 1989). Within farming systems, management based on ecophysiological analysis of processes was more important than dosage-effect relations as studied in factorial experiments (Zadoks, 1989). Farming systems are part of agroecosystems being ecosystems modified for agricultural production (Rabbinge and De Wit, 1989). The systems approach facilitated the optimization of the input of nutrients and pesticides and the development of strategies for ecological control of pests and diseases (De Wit, 1992). Farmers became acquainted with these strategies and reduced the use of chemicals in crop protection and fertilization. An important success factor was that in addition to a reduced emission of chemicals also production costs for the farmers were reduced. Crop rotation and selection of resistant cultivars are other factors contributing to a sustainable crop production (Zadoks and Schein, 1979). Vereijken (1997) discusses the design of multifunctional crop rotation. In such rotations, next to the choice of the crop sequence, the management strategies within the agricultural systems are important e.g., fertilization regime, disease control and soil tillage regime. However, to reconcile ecological principles with economic interests of the agricultural sector remains a challenge (Spiertz and Kropff, 2011). An interesting way out is presented in Pollan (2006), where the choice of crop rotation is presented as a way to enhance sustainability of agriculture.

Use of dynamic models in crop rotations

Each crop that is grown and each treatment that is applied to a crop or to the soil has a residual effect on growth and production of crops in subsequent years (De Kantzow and Sutton, 2006). For example a control strategy for weeds in one year changes the number of weed seeds in the seed bank and so the number of emerging weed plants. In order to study such processes multi-year crop experiments are needed. Since these are very costly, predictions are often based on short-term studies, assuming that a beneficial effect of a treatment in a single year will also be beneficial in the long term. In Chapters 2 and 3, we use short-term data to model the influence of soil-borne pathogens and estimate the density of the pathogens in the steady state that is reached, if a given rotation scheme is continued indefinitely. Similar approaches were used by Wolf et al. (1987) and Verloop et al. (2010) to describe the soil phosphate dynamics and its effect on crop yield; Pekrun et al. (2004) considered the effect of weeds in seed banks. Along similar lines Yang and Janssen (1997) developed a model for the decay of crop residues and manure supplied to the soil and the consecutive decay of organic matter already in the soil.

Crops growing on fertile soils are more tolerant to pests. Soil with higher organic matter content better retains water, reducing dependence on irrigation. Thus, wise management strategies will diminish the density of harmful soil-borne pathogens and enlarge soil fertility and will consequently reduce the risk of crop failure (Bardgett, et al., 2005; De Ruiter et al., 2005). It can be seen as a challenge to combine the above models with their different steady states for finding the optimal crop rotation scheme.

In practice, rotation schemes are maintained for only a restricted number of cycles and never reach equilibrium. Farmers anticipate fluctuation of product prices and therefore adapt the crop rotation. Especially in intensive farming systems tactical measures will be taken to control soil pathogens enabling a rotation with a high frequency of the most profitable crops. For the management of soil-borne pathogens with only one host crop the frequency of a profitable crop within the rotation scheme can be optimized quite well, by choosing cultivars resistant to the pathogen. This method is restricted to areas, such as the North-East part of The Netherlands, where starch potato is grown once per two years. However, also here, farmers may choose cultivars not included in the original scheme and differing in resistance to potato cyst nematode, so that a steady state will never be reached. Most advisory systems do not consider steady states; they sketch possible scenarios as a result of decisions taken by the farmer over a time horizon of a number of years (Ehwaeti et al., 2000). To address such problems Taylor and Rodriguez-Kabana (1999) used stochastic dynamic programming to maximize the expected present profit of future sequences of peanut and cotton.

To predict yield loss in a dynamic system approach, the initial state of the system should be known as accurate as possible. However, soil-borne pathogens spread from foci of infestation resulting in samples with a high variability. Moreover, the measurement method itself may produce additional uncertainty especially at low pathogen densities. Soil-borne pathogens are measured by counting the numbers present in a quantity of soil. When no pathogen is found, the pathogen may be absent in the soil or just absent in the sample. Usually soil sampling for measuring the density of new pest species is only done from the moment crops show symptoms indicating their presence, in contrast to the usually yearly measurement of chemical soil properties. In The Netherlands some pathogens have a quarantine status. This holds for instance for potato cyst nematodes when seed potatoes are grown. Then it is necessary to sample the soil with a prescribed intensity prior to sowing. Only when no cysts are found, it is allowed to grow seed potatoes.

Next to the definition of the initial state of a system, we have to formulate the way the state changes in time. For the growth of the crop we keep it simple and postulate a certain yield under optimal conditions. However, if pathogens are present, the situation changes drastically. Not only do we have to augment the yield with a loss term, we also have to include the dynamics of the reproducing pathogen population as it fluctuates in time. Putting this together with the crop growth we arrive at an interacting system for which it is not easy to make long term predictions.

Dynamic models of crop rotation and crop yield

In Chapter 2 the dynamics of a population of *P. penetrans* and the yield of the various host crops were analysed for a trial with 25 different crops and fallow. For each crop the parameters of both the nematode population model and the yield loss model were estimated; for fallow and two nematicidal crops, the parameter describing the surviving fraction of the population was estimated. From this result the financial yield of any rotation scheme that includes combinations of the 25 crops or fallow could be calculated. As an example, for all six possible rotations containing leek, carrot, lettuce and fallow, the financial yield was calculated. A sensitivity analysis was performed showing that the financial result of the rotations was most sensitive to the parameter determining the tolerance of the crop for yield loss in presence of the pathogen.

In Chapter 3 the dynamics of a population of *G. pallida* was considered as a case where resources become limiting at high nematode densities and the growth rate of the nematode population declines. This phenomenon is called scramble competition and was modelled by a Ricker function extended with a linear term, meaning that at very high initial densities only survival of potato cyst nematodes of the previous season is relevant. The same yield loss model was used as in Chapter 2. Model parameters were estimated with the empirical Bayes method based on a three year experiment with six different potato cultivars. The parameter estimates of the nematode population model and the yield loss model for each cultivar were used to evaluate gross margin for each cultivar grown once every three or four years. Again, sensitivity analysis showed that the financial result was most sensitive to the parameter of the yield loss model representing tolerance to the pathogen.

The evaluation of crop rotations as made in Chapters 2 and 3 does not necessarily require long-term crop rotation experiments because the regression equations describing the dynamics of nematodes and the associated yield loss can be fitted to data from one-year experiments. A prerequisite is that the population density of the nematodes is measured before planting. Next, yield has to be estimated and final population density of the nematode. In this way, parameters of the yield loss and the dynamic model can be estimated. Parameters can be estimated with a high precision in one year experiments in case a wide range of initial nematode densities is available. This situation can be created in a rotation experiment only after continuing the experiment for many years and with a wide range of frequencies of the host crops.

Nematode advisory systems

Nematode advisory systems, e.g. NemaDecide, support potato growers in controlling the presence of potato cyst nematodes, root-knot nematodes, and root-lesion nematodes. For these three nematode species a user can supply potato cyst nematode density measured within a field and choose different crops and control strategies for e.g. the next five years. For the various crop combinations and control strategies NemaDecide shows the financial result. Also the density of nematodes from the three groups in the course of these five years is forecasted (Been and Schomaker, 2004). NemaDecide accounts for spatial heterogeneity: for that purpose the field is split up into sections and for each section nematode density measurements are made. Subsequently, for each section individually an optimum crop sequence for the next years can be computed. NemaDecide allows for stochastic input caused e.g. by weather conditions or differences in virulence of local populations by constructing a probability distribution for the related parameters. This is similar to our dynamic approach of Chapters 2 and 3 where in the Bayesian estimation process parameters have a given statistical distribution resulting in a distribution for the yield in the steady state.

Selecting predictors of disease symptoms and crop yield using multi-model inference

The yield level of crops depends on physical and chemical soil characteristics. Next to this soil-borne pathogens may reduce yield levels. Crop damage by a pathogen may depend on the presence of other pathogens and on characteristics of the soil. In Chapter 4, a set of measurements of soil characteristics and soil-borne pathogen densities was used to predict the incidence of *Spongospora subterranea* on the tubers. Also a forecast of the percentage haulms infected with *V. dahliae* and of the yield of the potato test crop was made. From the set of predictors, six biologically plausible ones were selected: densities of *V. dahliae*, *G. pallida*, *Meloidogyne* spp. and *Trichodoridae* before planting potato and pH and P content of the soil. Next to these predictors, the interaction of *V. dahliae* density with the density of the three nematode species were added. The Akaike information criterion corrected for small datasets (AIC^c) was estimated for all possible models. Next the parameter estimates of the different models were averaged using the AIC^c values as weights. This method is known as multimodel inference and results in a better prediction compared to the model with the lowest AIC^c, because information obtained from all models is used. In case the best model has only a slightly lower AIC^c value than some of the other models, using multimodel inference, it is not necessary to choose between models with small differences in AIC^c value.

Optimal design of new experiments

In order to obtain a range of pathogen densities for an experiment the frequency of host crops should be varied within a rotation scheme. Prior information on parameter values in models of crop growth and nematode dynamics can be used to set up such schemes. Next to this, in Chapter 5 optimum designs were obtained for one year experiments yielding new estimates for the parameters in the models presented in

Chapter 2. The levels of pathogen density to be installed in a new experiment are known as the so-called support points. Using the D-optimality criterion the support points are selected by maximizing the determinant of the information matrix. The number of support points should equal the number of parameters. The method applies to linear models. Nonlinear models have to be linearized at a point in the parameter space. The models under consideration were nonlinear and therefore a point estimate of the parameter vector was needed to construct the optimum design. In a case study (Chapter 3) such an estimate was obtained for a potato cultivar grown on plots with soil infested with potato cyst nematode (*G. pallida*). Different optimum designs were found for the nematode response and the yield response, respectively. Since the models had two parameters the optimum design consists of two support points. Although, a design in which the number of support points is larger than the number of parameters is not optimal, it is worth to consider this option as a larger number of support points decreases the variance in the response. One may find the best combination of support points from a given set by taking in account all permutations. This is called an exact design. In Chapter 5 this is elaborated in some examples. An important factor in the construction of a design is the available budget for an experiment. The cost of different designs can be computed by comparing the efficiency of one plot with that of an optimum design. The method can be applied when a field experiment is laid out and the density of soil-borne pathogens of each plot is measured beforehand. Using the prior information on the model parameters per treatment, the plots can be assigned to the treatments in a way it maximizes the relative efficiency.

Statistical considerations

As already stated, the aim of this thesis is to increase the capacity for predicting crop yields in cropping sequences in the presence of soil borne pathogens, thus contributing to better informed management decisions. By using statistical methods, estimates of model parameters are obtained by combining information from different sources. One could follow an approach of giving high precision estimates by taking large samples. To reduce the residuals of the response one may also strive for more complex models. However, such approaches do not automatically lead to greater predictive power. This property is more likely found in robust models with a restricted number of parameters. In practice, when data are scarce, this parsimony is a valuable guideline. In statistics one uses the adjusted R^2 to account for the number of parameters used, while in information sciences the Akaike criterion and other, comparable indicators are used. In Chapter 2 we modelled the dynamics of *Pratylenchus penetrans* with a non-linear function with only two parameters with a clear biological meaning. Also the yield loss model contained only two parameters. In Chapter 3 the Ricker function had only three parameters. Compared to other studies in the field of soil borne pathogen research we kept the number of parameters low. For example Seinhorst (1993) formulated a model on crop damage by soil-borne pathogens with ten parameters. Another advantage of a low number of parameters is that fewer experimental units are needed to obtain the same level of precision (Gurney and Nisbet, 1998). Furthermore, in dynamic models data are processed more efficiently because per plot the information concerning the sequence of monitored years is integrated. In Chapter 4 parsimony was realised by choosing a set of plausible predictors from the set of all available predictors. This reduced the number of possible models in our multimodel approach, and decreased the risk of aliased or nearly aliased predictors. In Chapter 5 the parsimony aim resulted in the selection of treatment levels with a high relative efficiency.

Bayesian methods for model parameter estimation require a probability distribution of the parameters at the start of the estimation procedure. These so-called prior distributions may come from previous experiments. Also data obtained from advisory systems can be a useful source of initial information. When the model with the prior distributions is confronted with the data a new (posterior) distribution of the parameters will be the result. In our study we met difficulties in applying the Bayesian method. Correlation between parameters may delay convergence of the Bayesian estimation process. In the dynamic population model of Chapter 2 the two parameters became strongly correlated when the range of initial pathogen densities is narrow. In that case the Bayesian algorithm for estimation of the model parameters will not converge. More research is needed to find the range of initial densities that guarantees convergence.

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Summary

Agricultural entrepreneurs prefer to grow those crops that generate the highest financial yield. In Dutch arable farming, potato is the most profitable crop. However, this crop is host to several nematode species and soil-fungi. When potato is grown at a high frequency these pathogens strongly multiply and cause damage to the roots reducing in this way the tuber yield. For the potato cyst nematode (*Globodera* spp.) potato is the only host crop. Females of this species turn into cysts containing eggs that remain viable for several years. Also the root knot nematode (*Meloidogyne* spp.) lives in potato roots and forms galls on the roots. The root-lesion nematode (*Pratylenchus penetrans*) feeds on the roots causing lesions. This root damage from nematodes facilitates the entry of fungi such as *Verticillium dahliae*, which in turn blocks the vascular bundles in the stems causing wilt.

To control the spread of harmful soil-borne pathogens, crop rotation can be an important means. Chapter 1 outlines the role of crop rotation in the development of agricultural practice and in the design of crop experiments in which the plants are exposed to harmful soil organisms.

Chapter 2 provides an analysis of a multi-year trial where vegetables are grown in a field infested with *P. penetrans.* Each spring, the initial nematode density in the soil of each experimental plot is measured before the crops are planted or sown. From this value also the final nematode density of the previous year is derived. In the dynamical model of *P. penetrans*, the final density is a nonlinear function of the initial density of the preceding spring. Next the model is expanded to cover the population dynamics of *P. penetrans* in vegetable crop rotations over several years. It is shown that in a fixed rotation, the solution of the model equation tends to a stable steady state. The parameters of the model are estimated with Bayesian methods. In this way estimates of the nematode densities at a stable steady state can be obtained. In the yield loss model, tuber yield is a decreasing nonlinear function of the initial nematode density. The parameters of the yield loss model are computed with nonlinear regression. Hence, the gross margin for each crop and for the rotation as a whole can be estimated using economic indicators. As an application, for each of the six possible rotations with lettuce, leeks, carrots and fallow, and in presence of *P. penetrans,* the gross margin is calculated.

In Chapter 3 a data-analysis is carried out for a three year-trial. In total six potato cultivars were grown, four each year. The density of the potato cyst nematode in the soil is measured in spring as well as in autumn. The final nematode density as a function of the initial density is described by the Ricker curve, extended with a linear term. This functional relation takes the following form. An increase of the initial

density starting from zero results in a final density that first rises to a maximum. Next after a decrease of the final density, caused by high crop damage from scramble competition, the function rises again while approaching a line. The slope of this line through the origin equals the surviving fraction of nematode eggs of the previous year. The yield loss model is identical to the one used in Chapter 2. The nematode population model is iterated so that the dynamics of the potato cyst nematodes over several years can be described. Also in this model, being more complicated than the one of Chapter 2, the density in a fixed rotation tends to a stable steady state. After estimation of the parameters, similar to the computations of Chapter 2, the gross margin of the rotation is calculated at different frequencies of potato in the rotation.

In Chapter 4, a statistical analysis of the following crop rotation experiment is made. In advance potato cyst nematode (*Globodera* spp.), root lesion nematode (*P. penetrans*), root knot nematode (*Meloidogyne* spp.) and the soil-fungus *Verticillium dahliae* were inoculated into the soil. Every two years, three potato crops are grown and harvested with and without removing the foliage from the field. In the intervening years biological control measures are tested. In spring next to fallow, potato is grown until the longest day. Then, the potato crop is killed, and the cyst nematodes, gathered in the crop root system, also die. In autumn there is again a fallow treatment: beside the cultivation of *Tagetes,* nematicidal against *P. penetrans*, oats is grown to promote the natural enemies of soil-fungi. Before planting the potato main crop, the density of the inoculated organisms in the soil is measured. By the orthogonal combination of treatments in the experiment, densities of soil pathogens vary independently, which facilitates the prediction of plant injury.

The yield of the crop may fall from the presence of soil-borne pathogens, but also soil properties play a role. Besides the density of the inoculated organisms, phosphate content and pH of the soil are relevant as well as the interaction processes between the three inoculated nematodes and the fungus *V. dahliae*. With model selection, the predictive value of these interaction terms in the regression model is investigated.

With respect to damage from soil fungi it is remarked that *Spongospora subterranean* causes powdery scab on the harvested tubers of the potato main crop. The severity is higher at higher pH levels. Furthermore, the percentage of stems in August, infested with the wilt fungus *V. dahliae*, increases with the density of the fungus in the soil measured in spring prior to cultivation. The tuber yield of the potato crop is mainly determined by *V. dahliae*, *G. pallida* and the pH. At the end of the survey years, more damage is caused by *V. dahliae* on plots with high density of *G. pallida.* After three survey years the experiment was ended. A further continuation of the trial, would likely have produced more information about the interaction between the three nematodes and soil fungi *V. dahliae*.

Chapter 5 describes how optimal nematological crop growth experiments can be designed. This type of experiments may heavily weigh down the research budget in this field. Soil sampling and measuring pathogen densities in soil samples at the laboratory is labor intensive. For the population dynamics model as well as for the yield loss model, studied in Chapter 2, optimum designs are constructed. According to the mathematical theory the required number of levels of a predictor (support points) in an optimum design equals the number of parameters being two for both models of Chapter 2. The two support points for the yield loss function appeared to be lower than the ones for the nematode population model. However, because the parameters of both curves are estimated in one trial, a compromise has to be found. Beside this point, there is the problem that an optimum design only applies to models that are linear in the parameters. Therefore, a linearization has to be made valid near some point in the parameter space. Next to an optimum design an exact design is taken in consideration. Then, if a given number of support points have to be chosen from an available set of predictor levels, all possible permutations can be considered. For each permutation the efficiency can be computed, so that the best one can be selected.

The general conclusion of this thesis is formulated as follows. Crop rotation experiments extend over large time intervals. Due to the variability of environmental factors, it is not feasible to plan with exact precision future rotation schedules at the basis of the outcomes of past experiments. Statistical methods in combination with dynamical models of biological populations provide the tools to deal with uncertain data obtained from those experiments. To estimate the yield of a given design, additional assumptions must be made. In Chapters 2 and 3, it is supposed that a rotation is stationary in the sense that the cycle is repeated infinitely often. Then an estimate of total crop yield over the cycle can be made. In Chapter 4, we analyze statistically an existing experiment and estimate the parameters in a model predicting crop yield and diseases symptoms accompanying crop damage. A crop experiment consisting of a more efficient trial also yields more information given a certain financial budget. In Chapter 5, it is described how such a design can be derived in the sense that the levels of a treatment are chosen such that the design as a whole can be performed in an experiment at the lowest cost.

Kwantificeren van de dynamica van bodempathogenen en de consequenties voor de opbrengst in gewasrotaties

Samenvatting

Agrarische ondernemers telen bij voorkeur de gewassen, die de hoogste financiële opbrengst leveren. In de Nederlandse akkerbouw is de teelt van het gewas aardappel het meest profijtelijk. Echter, dit gewas is gastheer voor diverse soorten nematoden en bodemschimmels. Wordt het gewas aardappel in hoge frequentie geteeld, dan vermeerderen zich deze aaltjes (nematoden) en schimmels, beschadigen de wortels van het gewas en verlagen zo de knolopbrengst. Voor het aardappelcysteaaltje (*Globodera* spp.) is aardappel de enige gastheer. Vrouwelijke exemplaren vormen in de wortels cysten, gevuld met eieren die in de bodem jarenlang levensvatbaar blijven. Ook het wortelknobbelaaltje (*Meloidogyne* spp.) leeft in de wortel van de aardappelplant en vormt knobbels eveneens gevuld met eieren. Het wortellesieaaltje (*Pratylenchus penetrans*) leeft zowel in de wortels als in de grond en vormt lesies op de wortels. Deze beschadiging van de wortels vergemakkelijkt het binnendringen van de schimmel *Verticillium dahliae,* die de vaatbundels in de stengels blokkeert waardoor het gewas verwelkt.

Voor het beheersen van schadelijke nematoden en schimmels is gewasrotatie een belangrijk hulpmiddel. In Hoofdstuk 1 wordt uiteengezet welke rol gewasrotatie speelt binnen de ontwikkeling van de landbouw en wat de betekenis is van rotatie experimenten waarin het gewas blootgesteld wordt aan schadelijke bodemorganismen.

Hoofdstuk 2 geeft een analyse van een meerjarige proef op een veld besmet met *P. penetrans* waarop diverse groentegewassen worden geteeld. Ieder voorjaar wordt de dichtheid van het aaltje in de bodem gemeten, waarna de gewassen worden geplant of gezaaid. De meting van het volgend voorjaar geldt als einddichtheid voor ieder gewas geteeld in voorgaand jaar. In het dynamisch model van *P. penetrans* is de einddichtheid een niet-lineaire functie van de begindichtheid in het voorafgaand voorjaar. Vervolgens is het model zodanig uitgebreid dat de vermeerdering van *P. penetrans* beschreven kan worden binnen een rotatie van groentegewassen, over meerdere jaren. Aangetoond wordt dat bij het gekozen model de dichtheid bij vaste rotatie naar een stabiel evenwicht gaat. De parameters van het dynamisch model worden geschat met Bayesiaanse methoden. Op deze manier kan de dichtheid van de nematoden bij een stabiel evenwicht worden geschat. In het schademodel is de knolopbrengst een niet-lineaire dalende functie van de nematodendichtheid bij het poten. De parameters van het schademodel worden geschat met niet-lineaire regressie analyse. Met de verkregen parameterschattingen kan bij het stabiele evenwicht de financiële opbrengst van de gewassen worden berekend met behulp van economische

kengetallen. Als toepassing is voor een rotatie met sla, prei, peen en een braakjaar, bepaald welke volgorde van deze gewassen in aanwezigheid van *P. penetrans* de hoogste financiële opbrengst geeft.

In Hoofdstuk 3 is een data-analyse uitgevoerd voor een driejarige proef. In totaal werden 6 verschillende aardappelrassen verbouwd: vier verschillende rassen per afzonderlijk jaar. De dichtheid van het in de bodem aanwezige aardappelcysteaaltje werd zowel in het voorjaar als in het najaar gemeten. De einddichtheid als functie van de begindichtheid is beschreven met de Ricker curve, uitgebreid met een lineaire term. Bij toename van de begindichtheid gaat deze functie vanaf nul naar een maximum en nadert na een daling, door schade aan het gewas vanwege een hoge nematode concentratie, tot een rechte lijn door de oorsprong met helling gelijk aan de fractie overlevende nematode cysten van het voorgaande jaar. Het schademodel is hetzelfde als gebruikt in Hoofdstuk 2. Het dynamisch model is weer uitgebreid naar meerdere jaren. Ook bij dit model, dat gecompliceerder is dan dat van Hoofdstuk 2, gaat bij vaste rotatie de dichtheid naar een stabiel evenwicht. Na schatting van de parameters, analoog aan Hoofdstuk 2, wordt de financiële opbrengst van de rotaties berekend bij uiteenlopende frequenties van de diverse aardappelrassen in de rotatie.

In Hoofdstuk 4 zijn data geanalyseerd van een vruchtwisselingsproef met de volgende opzet. Bij aanleg van het experiment werden aardappelcysteaaltje (*Globodera* spp.), wortellesieaaltje (*P. penetrans*), wortelknobbelaaltje (*Meloidogyne* spp.) en de schimmel *Verticillium dahliae* in de bodem geïnoculeerd. Om het jaar worden drie aardappelrassen geteeld en geoogst met en zonder dat het loof van het veld wordt verwijderd. In het tussenliggende jaar worden biologische bestrijdingmethoden getest. In het voorjaar wordt naast het aanhouden van braak, het gewas aardappel geteeld tot de langste dag. Door het aardappelgewas dan te doden gaan ook de cysteaaltjes die zich verzameld hebben in het wortelstelsel van het gewas dood. In het najaar werd weer braak aangehouden: naast de teelt van Afrikaantjes ter bestrijding van *P. penetrans,* wordt ook haver geteeld om natuurlijke vijanden van bodemschimmels te vermeerderen. Voor iedere aardappelteelt wordt steeds de dichtheid van de geïnoculeerde organismen gemeten. Door de orthogonale combinatie van de behandelingen in de proef, variëren de dichtheden van de bodempathogenen onafhankelijk van elkaar, hetgeen een voorspelling van de schade vergemakkelijkt.

De opbrengst van het gewas kan dalen door aanwezigheid van nematoden en schimmels maar ook bodemeigenschappen spelen een rol. Naast de dichtheid van de geïnoculeerde organismen wordt het fosfaatgehalte en de pH van de grond relevant geacht, evenals de interacties tussen de 3 geïnoculeerde nematoden en de schimmel *V dahliae*. Vervolgens wordt met modelselectie nagegaan welke van deze relevant geachte invloedsfactoren ook daadwerkelijk van invloed zijn.

Naast de geïnoculeerde organismen treedt ook de schimmel *Spongospora* *subterranea* op. Deze schimmel veroorzaakt in deze proef poederschurft op de knollen en wel meer naarmate de pH van de grond hoger is. Het percentage stengels in augustus, waarin de verwelkingsschimmel *V. dahliae* werd aangetroffen, nam toe met de dichtheid van de schimmel in de bodem, gemeten voorafgaand aan de teelt. De knolopbrengst van het gewas aardappel wordt vooral bepaald door de predictoren *V. dahliae*, *G. pallida* en de pH, en in het laatste van de drie onderzoeksjaren wordt de schade door *V. dahliae* meer naarmate de dichtheid van *G. pallida* hoger was. Een verdere voortzetting van de proef dan nu het geval was had zeer waarschijnlijk meer informatie kunnen geven over de interactie tussen de drie nematoden en de bodemschimmel *V. dahliae*.

Hoofdstuk 5 beschrijft hoe optimale nematologische experimenten kunnen worden opgezet. Toepassing van deze proefopzetten kan de kosten van het onderzoek aanzienlijk verlagen. Bemonstering van de grond en de laboratorium bepaling van de pathogeendichtheden in de grondmonsters is arbeidsintensief. Voor het populatie-dynamica model en voor het schademodel uit Hoofdstuk 2 werden optimale proefopzetten ontworpen. Voor een optimaal ontwerp is volgens de wiskundige theorie het aantal instellingen gelijk aan het aantal parameters, dus gelijk aan 2 voor beide modellen. Voor de schade curve blijken deze twee instellingen lager te liggen dan voor de nematoden dynamica curve. Omdat de parameters van beide curven in één proef geschat worden, moet een compromis worden gevonden. Daarnaast zijn optimale opzetten alleen mogelijk voor lineaire modellen. Daarom moet het model worden gelineariseerd voor een omgeving van een te kiezen waarde van de parametervector. Naast een optimale opzet werd ook een exacte opzet in beschouwing genomen. Wanneer een aantal instellingswaarden gekozen moet worden uit een beschikbaar aantal voorspellingsniveaus, kunnen alle permutaties worden nagelopen. Voor iedere permutatie kan de efficiency worden berekend, zodat de beste kan worden uitgekozen.

De algemene conclusies die uit de onderzoekingen van dit proefschrift getrokken kunnen worden, laten zich als volgt omschrijven. Proeven om gewasrotaties te vergelijken beslaan een lange tijdsperiode. Door de variabiliteit van de omgevingsfactoren is het niet mogelijk om exact toekomstige rotatie schema’s te plannen op basis van historische data. Statistische methoden in combinatie met dynamische modellen van biologische populaties leveren het gereedschap om met onzekere gegevens om te gaan. Om de opbrengst van een gegeven ontwerp te schatten dienen extra aannames te worden gemaakt. Zo wordt er in de Hoofdstukken 2 en 3 van uitgegaan dat een rotatie stationair is in de zin dat de cyclus oneindig vaak herhaald wordt. Dan kan een schatting van de totale gewasopbrengst over de cyclus gegeven worden. In Hoofdstuk 4 analyseren we een bestaand experiment en schatten de parameters in een model dat de gewasopbrengst en symptomen van ziekten voorspelt. Een veldproef gebaseerd op een optimaal ontwerp levert meer informatie gegeven een zeker financieel budget. In Hoofdstuk 5 wordt beschreven hoe zo’n opzet kan worden afgeleid door de instellingen van een behandeling zo te kiezen dat de proef als geheel kan worden uitgevoerd tegen de laagste kostprijs.

Curriculum vitae

Wim van den Berg werd geboren op 29 oktober 1957 te Pijnacker. In 1977 behaalde hij het diploma gymnasium-beta aan het Christelijk Lyceum voor Delft en Rijswijk. In 1987 werd de studie Landbouwplantenteelt & Graslandkunde afgerond met de afstudeervakken Landbouwplantenteelt (6 mnd), Agrarische bedrijfseconomie (3 mnd), Wiskundige statistiek (3 mnd) en Theoretische teeltkunde (3 mnd). In mei 1994 behaalde hij het diploma Statisticus bij de Vereniging voor Statistiek en Operationele Research. Sinds 13 februari 1989 is hij werkzaam als statisticus bij het Praktijkonderzoek Plant en Omgeving voor Akkerbouw, Groene ruimte en Vollegrondsgroenteteelt te Lelystad.

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Dankwoord

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Het samenvatten van de resultaten van de binnen het PPO-AGV uitgevoerde vruchtwisselingproeven was één van de fascinerende bezigheden gedurende mijn eerste jaren in Lelystad. Hoewel vruchtwisselingsproeven met een statistisch design, niet vaak meer worden aangelegd, blijft het onderwerp van belang. Immers de meerjarige effecten van behandelingen en gewasrotaties op de groei en gezondheid van de gewassen vormt een wezenlijk onderdeel van het landbouwkundig onderzoek, en maakt bij veel experimenten onderdeel uit van de vraagstelling. Daarom heb ik een aantal jaren geleden alweer, besloten om een proefschrift te wijden aan de dynamica van bodempathogenen in gewasrotaties en de daarmee gepaard gaande opbrengstderving.

Als promotor Johan heb je veel geduld gehad, maar steeds het einddoel voor ogen gehouden. Je toonde ook veel belangstelling bij onderdelen die buiten je eigen werkveld lagen. Je hebt niet alleen veel kennis van populatie dynamica maar bewaakte ook de dynamiek in mijn PhD proces.

Als co-promotor Walter zag je het belang van het onderwerp van begin af helder in. Je hebt er aan bijgedragen dat de statistische methodieken werden gerelateerd aan de reeds bestaande literatuur.

Dank Jan en Klaas, voor het beschikbaar stellen van de data van de vruchtwisselingsproef uit Achterberg, die is gebruikt voor de case study in hoofdstuk 4.

Bedankt Wampie, voor het verzorgen van de lay-out en de opmaak van dit boekje.

Vandaag is het hervormingsdag. Op 31 oktober 1517 spijkerde de monnik, Luther, 95 stellingen aan de deur van de slotkapel van Wittenberg, gericht tegen situaties in de Rooms-katholieke Kerk. Vandaag, 31 oktober 2011, aan de voet van de Wageningse Berg, volsta ik met 7 stellingen. Een 8^{e} stelling bleek niet te realiseren. Tijdens het afronden van het proefschrift las ik in de krant, dat in Nederland dit jaar, het besteedbare inkomen, gemiddeld daalt. Een Nederlandse uitdrukking voor gemiddeld is: ‘door de bank genomen’. Dit had als 8^{e} stelling kunnen opleveren: ‘Door de bank genomen, daalt het besteedbare inkomen.’ Het is beschrijvende statistiek, die de stochastische risico analyses van de financiële sector op de plek zet en een plaats geeft. Echter, hier stuitte de globalisering op haar grenzen: de stelling was niet goed in het Engels te vertalen en daardoor onbruikbaar. Zo bleef het aantal stellingen gelijk aan 7.

Op de 7^{e} dag rustte God, nadat hij in 6 dagen hemel en aarde geschapen had. Toevallig, gaat stelling 7 over de levensavond van de mens, waarin deze rusten wil zonder financiële zorgen. Op de 6^{e} dag had God de mens al aangesteld, om te heersen over de schepping. Zoals stelling 6 aan de orde stelt: met systeem theorie of door keuze van de rotatie? That is the question.

Lieve Marian, bedankt. Je bent geen vraag maar een antwoord.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)
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Writing of project proposal (4.5 ECTS)
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