Contest and Scramble Competition and the Carry-Over Effect in *Globodera* spp. in Potato-Based Crop Rotations Using an Extended Ricker Model

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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 Bayesian 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 center of the infestation, optimal conditions existed for studying population response and damage in different cultivars. By using the empirical Bayesian 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 five 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: carry-over, contest competition, crop rotation, economic evaluation, gross margin, population dynamics, *Globodera* spp., Ricker model, scramble competition, sensitivity analysis, stability, steady state, yield loss assessment.

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. Presumably *Globodera pallida* was also introduced. In 1954, the first cultivars resistant to *G. rostochiensis* became available. Resistant cultivars cause potato cyst nematodes (PCN) 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 bases, 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 the 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 estimate nematode population densities from soil samples (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 the population dynamics of nematodes and their damage within a crop rotation scheme taking in account commonly measured quantities.

Nicholson (1954) recognized 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:

$$P_f = \frac{fHP_i}{1 + \frac{bHP_i}{h}}, \qquad (1)$$

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 et al. (1991) and assume the root density, h, to be an inverse linear function of P_i:

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

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:

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

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 and 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 nonhost crop. Because of the high estimates of C_p for resistant cultivars, Philips et al. (1991) propose C_p to be density-

dependent in future 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 that their algorithm did not converge. To overcome this problem they estimated the parameter c by 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):

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

where a equals the slope of the curve in the origin and M is the value of 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):

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

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

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

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

where T_e and T_h are threshold values above which density-dependent effects occur. Parameters m_e ($0 < m_e < 1$) and m_h ($0 < m_h < 1$) are asymptotes of y_e and y_h for P_i tending 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):

$$P_f = y_h(P_i)y_e(P_i)M\left(1 - e^{-\frac{a}{M}P_i}\right) + (1 - sy_h(P_i))bP_i, \qquad (6)$$

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

In this study, we will present an alternative model with fewer parameters that still describes dynamics of PCN in potato crop rotations over the whole range of prevailing densities. It will be shown that the density approaches a stable steady state that can be expressed in an analytical 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 in The Netherlands.

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 as 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 (Fig. 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 inflection equals $-\beta_1/e^2 + \beta_3$.

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

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

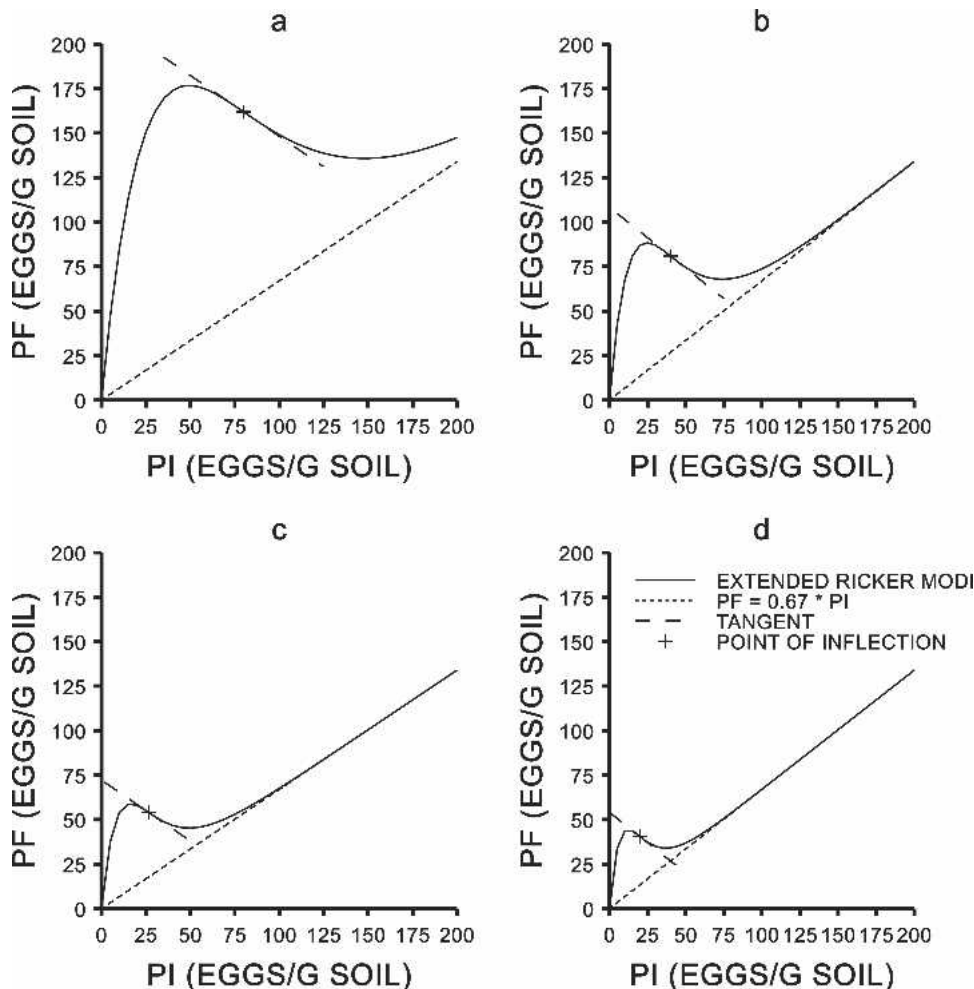meaning that the parameters β_1 and β_2 are 0. When resistant cultivars are grown on soils infested with *G.*

FIG. 1. The Ricker model according to Eq. (7) for $\beta_1 = 10$ and $\beta_2 = 0.025$(a), 0.05(b), 0.075(c) or 0.10(d) and $\beta_3 = 0.67$. Also shown is the tangent to the curve in the point of inflection. The slope of the line from the origin equals β_3.

rostochiensis, the nematode population will become extinct. So 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 the 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 function 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 the 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 declines due to nematodes. The price per unit product is kept constant; product quality considerations are ignored.

Dynamics of PCN 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 ($p = 0, \ldots, \infty$). 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 therefore be equal to:

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

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 $\overline{P}_n = g(\overline{P}_n)$ into Eq. (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 *G. rostochiensis* if 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 for $(\beta_1 + \beta_3) \rho^{n-1} > 1$. When this is not true, the population will become 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:

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

where GM_{Rn} is the mean gross margin of a rotation with n crops and $GM(r)$ is the gross margin of 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 inequality (18) holds.

The stability of the steady state in Eq. (15) is investigated as follows. The derivative of $g(P_n)$ at $\overline{P}_n$ is needed which equals:

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

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, β3, ρ, and λ are necessary. These derivatives are given in Appendix A.

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 × 1.5 m, 22 rows × 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 Bintje is susceptible for all pathotypes of *Globodera*, culivars Agria and Turbo, and Van Gogh are resistant to pathotype Ro1 of *Globodera*, cultivar Santé is resistant to

Ro1 and Pa2, and cultivar Darwina is resistant to Ro1, Pa2, and Pa3.

On each experimental unit, nematode density was measured before potatoes were planted (P_i) and also after they were harvested (P_f). Density, defined as the 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 plot. The experimental design allowed estimation of these parameters of the model describing the dynamics of the nematode. Equation (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 distributions of the parameters must be specified (Appendix B). The likelihood was calculated by assuming the data is 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 $N(\mu_{\beta1}, \sigma_{\beta1}^2)$, $N(\mu_{\beta2}, \sigma_{\beta2}^2)$, $N(\mu_{\beta3}, \sigma_{\beta3}^2)$, and $N(\mu_{\pi0}, \sigma_{\pi0}^2)$. 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 parameter sets for each iteration step were 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

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 × 4.5 m. Initial density is not mentioned when less 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	B
7	A	VG	B 1	A	S	B
8	A 1	VG	B 3	A 1	S	B
9	A 2	VG 2	B 4	A 1	S	B
10	A 3	VG 2	B 8	A 3	S 1	B 1
11	A 3	VG 3	B 6	A 4	S 2	B 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

wheat acted as a reference. The mean gross margin of this rotation when PCN is not present is equal to (3,490 + 2,867 + 1,330)/3 = 2,562 €/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 PCN, so for the 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. 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 inclusion in rotation *R*3, the necessary gross margin *GM*(4) was calculated with Eq. (18).

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 1989–90 increased from 5.9 to 8.7, due to removal of 32 experimental units with low population density from the experiment in spring 1990. The density of the remaining 106 experimental units was 7.2 eggs and larvae/g soil in autumn 1989. In winter 1990–91, 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 center of the

TABLE 2. Financial output (*FO*), specific costs (*SC*), and gross margin (*GM*) of crops in evaluated rotations (€ ha^{-1}) (based on Dekker (2001)).

Crops	FO	SC	GM
Ware Potato (average of all cultivars)	5,413	1,923	3,490
Sugar-beet			2,867
Winter-wheat			1,330
Onions			3,279
Chicory			1,611
Flax			983

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

Year Period	Spring	Autumn
1989	1.4	5.9 (7.2)
1990	8.7	23.3
1991	20.0	26.8

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 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 in 1990 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 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 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 $(\beta_1 + \beta_3)\rho^2$ or $(\beta_1 + \beta_3)\rho^3$ 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 three year 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 € for resistant cultivars Darwina and Santé (Table 5). However *GM*(4) was lower than 2,000 € for all four susceptible cultivars. According to 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

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
1991 Darwina	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

fourth crop because 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 €/ha/ yr is higher than *GM*(4) of some of the combinations of susceptible cultivar and year in Table 5.

In contrast to parameters β_1 and β_3, sensitivity of 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. 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.
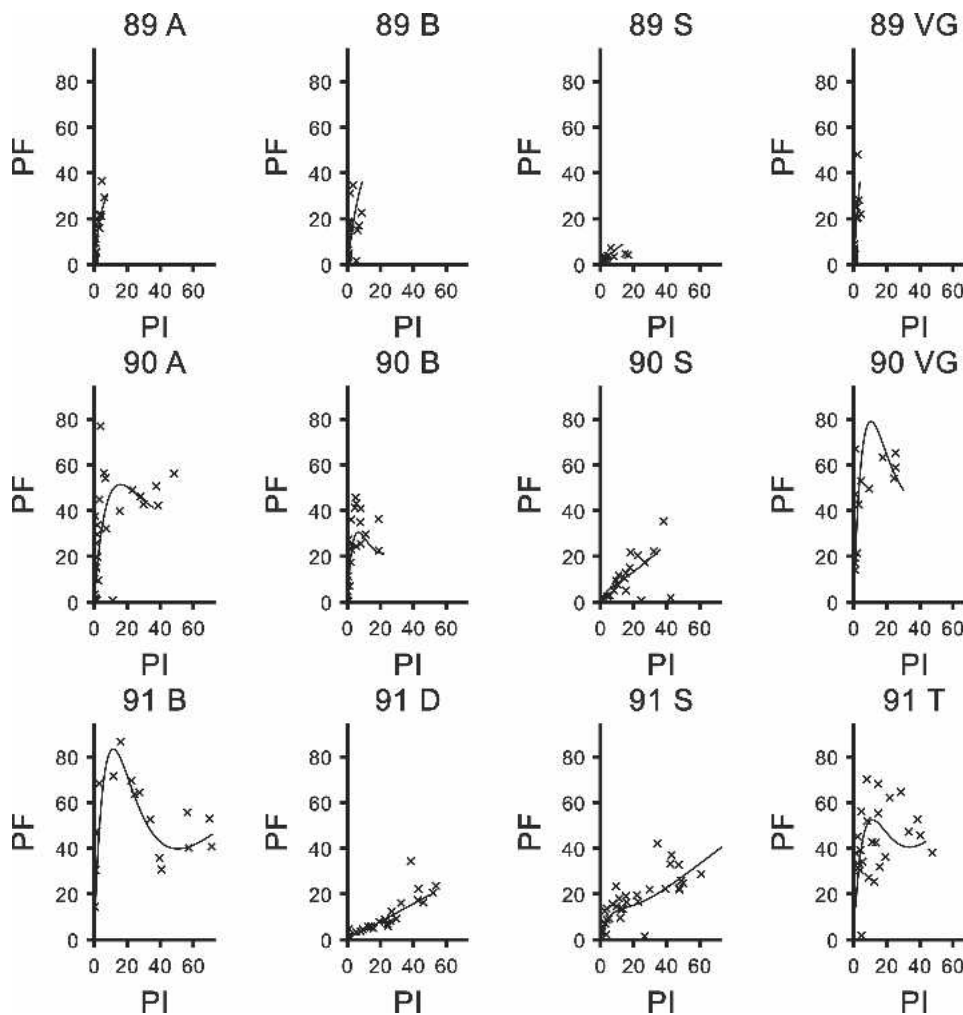

FIG. 2. Relation between final density (P_f) and initial density (P_i) (eggs per g soil) of *G. pallida* as observed (x) and estimated by regression (drawn line) for combinations of year and cultivar. Cultivar codes: A = Agria, B = Bintje, S = Santé, VG = van Gogh.

FIG. 3. Relation between tuber yield and initial density of *G. pallida* (P_i) (eggs per g soil) 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.
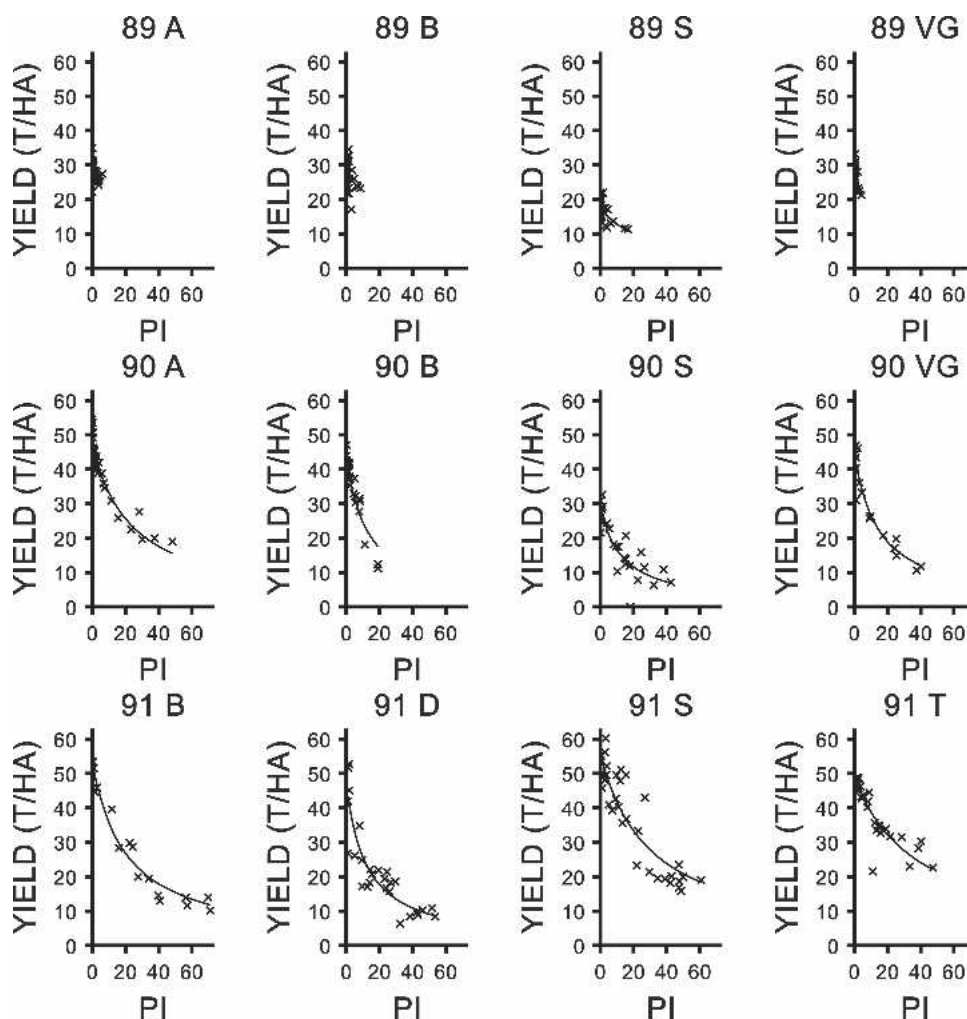
DISCUSSION

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 five

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	9.0 (1.0)cd	1,796	1,748
1989 Bintje	18.3 (2.5)ef	11.8 (1.5)de	2,128	1,914
1989 Santé	−2.1 (0.6)a	−3.6 (0.7)a	2,629	2,336
1989 van Gogh	41.1 (8.7)f	30.3 (6.4)g	1,344	1,331
1990 Agria	22.2 (0.6)f	15.8 (0.6)f	1,752	1,663
1990 Bintje	10.9 (0.6)d	8.3 (0.4)c	1,687	1,608
1990 Santé	−4.2 (0.9)a	−6.6 (1.3)a	2,540	2,264
1990 van Gogh	25.5 (1.0)f	19.6 (0.6)g	1,440	1,393
1991 Bintje	26.2 (0.7)f	21.0 (0.6)g	1,555	1,475
1991 Darwina	0.6 (0.3)b	−0.2 (0.4)b	2,380	2,093
1991 Santé	4.9 (0.7)c	1.4 (0.8)b	2,345	2,108
1991 Turbo	20.3 (0.6)f	15.1 (0.5)ef	1,922	1,761

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 a 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 of 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 of 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 state 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 behavior in our case study 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 from 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.

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 high for cultivar Darwina in 1991 (Table 4), whereas the high estimate of λ for Agria in 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 carryover 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 the 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 Monte Carlo Markov Chain using 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 the 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 Monte Carlo Markov Chain approach employed in this study. Biological prior knowledge about the parameters from the literature or former experiments may be included as prior distributions of the parameters. Calibration thus serves to assess to what 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 nonpotato 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 dy-

namics 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:

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

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

$$\frac{d\overline{P}_n}{d\beta_3} = \frac{\rho^{n-1}}{\beta_2(1-\beta_3\rho^{n-1})}. \tag{A3}$$

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

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

$$\frac{d\overline{Y}_n}{dp} = \frac{-\lambda\dfrac{d\overline{P}_n}{dp}}{(1+\lambda\overline{P}_n)^2}. \tag{A5}$$

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

$$\frac{d\overline{Y}_n}{d\lambda} = \frac{-\overline{P}_n}{(1+\lambda\overline{P}_n)^2}. \tag{A6}$$

The derivative of GMR to parameter p (p = β1, β2, β3, ρ) is equal to:

$$\frac{dGM_R}{dp} = \frac{d\overline{Y}_n}{dp} FO_{potato}.$$ (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, ß$_1$, ß$_2$ and ß$_3$:

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

$$\prod_{k=1}^{12} N(\beta_{2k}, \mu_{\beta_2}, \sigma_{\beta_k}^2) \prod_{m}^{12} N(\beta_{3m}, \mu_{\beta_3}, \sigma_{\beta_3}^2)$$

$$\sigma_{\pi_0}\sigma_{\beta_1}\sigma_{\beta_2}\sigma_{\beta_3},$$ (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}, $\sigma_{ß_1}$, $\sigma_{ß_2}$, and $\sigma_{ß_3}$ are the priors for $\sigma_{\pi_0}^2$, $\sigma_{ß_1}^2$, $\sigma_{ß_2}^2$, and $\sigma_{ß_3}^2$ (Gelman et al., 2004, paragraph 11.7).