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Managing the spread of alfalfa stem nematodes (*Ditylenchus dipsaci*): The relationship between crop rotation periods and pest re-emergence

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Abstract

Alfalfa is a critical cash/rotation crop in the western region of the United States, where it is common to find crops affected by the alfalfa stem nematode (*Ditylenchus dipsaci*). Understanding the spread dynamics associated with this pest would allow growers to design better management programs and farming practices. This understanding is of particular importance given that there are no nematicides available against alfalfa stem nematodes and control strategies largely rely on crop rotation to non-host crops or by planting resistant varieties of alfalfa. In this paper we present a basic host-parasite model that describes the spread of the alfalfa stem nematode on alfalfa crops. With this discrete time model we are able to portray a relationship between the length of crop rotation periods and the time at which the density of nematode-infested plants becomes larger than that of nematode-free ones in the post-rotation alfalfa. The numerical results obtained are consistent with farming practice observations, suggesting that the model could play a role in the evaluation of management strategies.

Keywords: alfalfa stem nematode management, alfalfa stem nematode model, crop rotation periods.

1 Introduction

The alfalfa stem nematode (ASN), *Ditylenchus dipsaci*, is a plant parasite that can dramatically reduce plant stand and forage yields, raising considerable concern in alfalfa producers. ASN attacks and reproduces only inside alfalfa (*Medicago sativa*) and sainfoin (*Onobrychis viciifolia*) plants [Evans et al. 2008]. ASNs are colorless non-segmented round worms that draw nutrients from the host cells. The nematodes feed in the parenchymatous tissues of stems, but they can also be found in foliage, inflorescences, buds, rhizomes, and stolons. Symptoms of stem nematode parasitism in alfalfa include stunted and swollen stems, stem necrosis, white flagging of leaves and stems, crown rot, and stand decline [Evans et al. 2008, Gray and Franc 1993], all of which are usually exacerbated by low temperatures [Williams-Woodward and Gray 1999]. Consequently, ASN-infestation in alfalfa crops results in a lower yield at harvest and induces economic losses [Koenning et al. 1994].

ASN has emerged as a major issue in the western United States during the last decade, with changes in insecticide usage and new ASN biotypes suggested as reasons for its renewed major pest status [Holin 2010]. There are no nematicides currently registered for use on alfalfa stem nematodes, making crop rotation and planting ASN resistant varieties the most practical ways to manage ASN invasions [Hafez 1998, Evans et al. 2008]. Briefly, crop rotation is used in pest management to disrupt the relationship between host plant and pest by planting a non-host crop. Crop rotation works well for ASN because the parasite is specific to its host. For other nematodes that have a broad host range, crop rotation is likely to be an ineffective pest control method [Duncan and Moens 2006]. In the absence of suitable hosts or during harsh environmental conditions, nematodes in the soil undergo a physical transformation that allows them to survive in a dormant state called *anhydrobiosis* [Evans et al. 2008]. An-

hydrobiosis is characterized by the almost complete desiccation of a nematode's body, which stabilizes its cellular structures and protects it from harsh environmental factors, such as extreme heat or cold. Because ASNs can stay dormant in the soil for long periods of time, waiting for the right host plant to appear, it may take several years of crop rotation to ensure that alfalfa can be planted again without the risk of a rapid nematode outbreak.

Therefore, knowing how long crop rotation should last to ensure that re-emergence of nematodes will not cause damage too soon becomes a significant issue. In other words, it would be beneficial to find a formal relationship between crop rotation duration and the time at which the density of nematode-infested plants becomes larger than nematode-free ones. In this paper we provide an approximate answer through the formulation of a discrete-time host-parasitoid model. As a consequence, the equations presented describe the time evolution of nematode-free and infested plant densities as well as nematode density in the rhizosphere of each alfalfa plant. We fit the model to published data in [Boelter et al. 1985] and observed that the outcomes from the resulting equations are comparable to what is actually seen in the field.

In relation with the conceptual framework proposed here, we remark that the invasion of stem nematodes in plants (onions) was first modeled in [Seinhorst 1965] by using similar ideas to those originally found in [Nicholson 1933] and has been studied extensively, see [Edelstein-Keshet 2005] for instance. Sienhorst's discrete time theoretical model has been used since then to relate crop yield losses with stem nematode population densities at the end of a harvest, [Schoemaker and Been 2006]. Our model is a variant of Sienhorst's, coupling the nematode infestation process with (i) the reproduction (and posterior spread) of nematodes from plants and (ii) the physiological changes that nematodes suffer in the absence of specific hosts, which alter their vital

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dynamics. The model proposed here incorporates more epidemiological realism than its predecessors so as to quantify the simultaneous impact of nematode population and host-nematode dynamics [Cunniffe 2015].

2 Biological background

ASNs are most active in the spring, with optimal temperatures around 5°C-18°C [Norton 1978]. They usually begin to leave infested alfalfa plants when conditions in the plant tissue become unfavorable [Hafez 1998], moving towards the soil in search of roots of nematode-free hosts. Nematode movement between plant hosts generally occurs through irrigation water. Once a new plant host is found and invaded, females lay eggs that hatch inside the stems. The offspring quickly develop through a number of juvenile stages until they reach adulthood in about 19-23 days [Evans et al. 2008]. Eventually, the last juvenile stage leaves the stem and returns to the soil to repeat the cycle [Evans et al. 2008, Norton 1978]. As the season progresses, however, reproduction slows down as a result of the rising temperatures and lower soil moisture [Williams-Woodward and Gray 1999]. Increased levels of nematode infestation results in a decreased yield during harvest season (summer). Also, if plants are damaged to a certain point before winter, most likely there will be a decreased yield the following year.

Under reasonable biological assumptions, our theoretical structure attempts to provide a closer dynamical description corresponding to the process detailed above by establishing quantitative relationships between (a) the mechanism of nematode invasion of new hosts, (b) the release of nematodes from infested plants and (c) survival of nematodes during crop rotation periods.

3 Model formulation

Let S_t and I_t be the density of nematode-free and infested alfalfa plants, respectively, at times $t = 0, 1, 2, ...$, where the sampling time unit is equal to two months and corresponds to the interval between harvests during the summer. We emphasize that the unit of time does not represent generations as is usual in host-parasitoid models. The nematodes that are potentially harmful to the plants are those located in the soil volume immediately surrounding the root known as the *rhizosphere* [Williams-Woodward and Gray 1999], usually within 2 cm of the alfalfa stem node and about 15 cm deep. Let W_t be the average density of nematodes in the rhizosphere surrounding one plant's roots at time t. As a first approximation, we make the following reasonable assumptions: (i) the probability that a host is attacked by nematodes located in its rhizosphere is Poisson distributed, (ii) only contaminated hosts die and there is no winterkill of hosts, (iii) plants are homogeneously distributed in space, (iv) the density of nematodes is independent of the soil temperature and moisture, (v) nematodes that leave an infested host are relocated to the rhizosphere of any other plant with the same probability, (vi) there is no immigration of nematodes from other sources, (vii) a fraction of the nematode population can survive the harsh winter conditions.

In our model, the density of nematodes in the rhizosphere of one plant changes due to nematodes either immigrating from other hosts or dying with average rate μ_W. Considering the total area A of the field to be relatively small, we can also assume that the average nematode contribution from each infested plant to the rhizosphere of any other one (nematode-free or infested), C, is proportional to the number of surviving nematodes coming out of the infested plant, c. Therefore we can approximate $C = c/(\text{total number of plants in the area } A)$, which is justified in part from the observation that, in addition to nematode dispersal through flood irrigation, the tools employed

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in harvesting for cutting the plants are also responsible for nematode transport over relatively large distances [Evans et al. 2008]. Thus, the total number of new nematodes surrounding a host's root becomes $C \times$ (number of infested hosts), with the number of infested hosts given by $I_{t-1} \times A$. Finally, we assume that the small fraction of surviving nematodes already surrounding the new host's root have gone underground and will only perform chemotactic movement searching for the roots. For our model we will use a relative value of $A = 1$, which corresponds to 0.065 hectare used in the experiments of ASN spread reported in [Boelter et al. 1985]. Therefore, the density of nematodes in *one* host's rhizosphere can then be described by

$$W_t = (1 - \mu_W)W_{t-1} + CI_{t-1}. \tag{1}$$

When there are no infested plants to contribute new nematode offspring, i.e. during crop rotation, we instead use

$$W_t = (1 - \mu_{W_2})W_{t-1} \tag{2}$$

for the nematode population, where μ_{W_2} is the ASN death rate during anhydrobiosis.

Next, we approximate the density of nematode-free and infested plants with the equations

$$S_t = S_{t-1}e^{-aW_{t-1}}, \tag{3}$$

$$I_t = (1 - \mu_I)I_{t-1} + \left(1 - e^{-aW_{t-1}}\right)S_{t-1}, \tag{4}$$

where $e^{-aW_{t-1}}$ represents the probability that a nematode-free host is not reached by any nematode in its rhizosphere in a single timestep, a is a parameter measuring the nematode efficiency in finding hosts and μ_I is the death rate of infested plants. Notice that the number of total number of host plants does not change over time so a growth rate term is absent. We also emphasize that the model assumes no new nematodes

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introduced into the field by means of runoff irrigation from other infested fields or from human activity, and that the initial nematode population comes from the use of infested seeds. Thus, the system's dynamics are described by equations (1), (3) and (4) when nematodes are active and by (2) together with $S_t = I_t = 0$ during crop rotation periods. Although nematode infestation will stop when all nematode-free hosts are infested in the absence of crop rotation, an analytical description of the steady states in its presence becomes convoluted, thus suggesting a numerical approach.

4   Parameter estimation

To estimate the unknown parameters in the model we used experimental data from [Boelter et al. 1985], where an experimental field with nematode-free and nematode-infested plants was harvested twice a year, in July and September, for two years. The disease progression was recorded by counting the number of new plants that presented symptoms. Unfortunately, the information was restricted to only two harvests per year for two years. Low temperatures dramatically decrease ASN activity so we assumed that no new infections occurred during fall/winter.

The average lifespan of ASN is between 45-75 days in adequate temperature and moisture conditions [Hafez 1998]. However, they can survive the winter in parasitized alfalfa tissues, as well as in the rhizosphere of parasitized plants [Gray and Franc 1993]. Therefore, we neglect nematode winterkill for the calibration of our model. Taking the worst case scenario of an averaged lifespan equal to 75 days in normal conditions, the corresponding average death rate is $\mu_W = 0.8219$ (time units)$^{-1}$ (≈ 0.0137 (days)$^{-1}$). The average death rate for infested hosts was approximated using data from [Boelter et al. 1985], and is equal to $\mu_I = 0.0994$ (time units)$^{-1}$ (≈ 0.0017 (days)$^{-1}$).

Table 1: Parameters for the model and their estimated values. The time unit used for the approximate rates shown is sixty days.

Parameter	Description	Approximate Value	Source
a	nematode efficiency in finding host's root	0.001	Estimated in this paper
C	incoming new nematodes into a plant rhizosphere	1.202	Estimated in this paper
μ_W	death of nematodes per unit of time	0.822	[Boelter et al. 1985]
μ_I	death of contaminated plants per unit of time	0.099	[Boelter et al. 1985]
μ_{W_2}	death of nematodes during anhydrobiosis per unit of time	0.056	[Gray and Franc 1993]

Unconstrained nonlinear optimization was used to find values for a and C that minimize the error between the values computed with the model and those from the literature. Parameter values are shown in Table 1.

Figure 1 (A) shows the model fitting to the data from [Boelter et al. 1985]. The lower panel (B) shows the ASN density in the rhizosphere, which reaches values consistent with those observed in experimental fields [Williams-Woodward and Gray 1999]. We computed nematode incidence progression using the adjusted parameters with initial plant densities $S_0 = 300$, $I_0 = 0$ and initial nematode density $W_0 = 100$ (Figure 2).

5 Turning times for crop rotation periods

Since there are currently no nematicides on file approved by the Environmental Protection Agency for outdoor use, crop rotation is one of the main methods for managing an ASN invasion. Crop rotation is successful due to the nematode's inability to re-
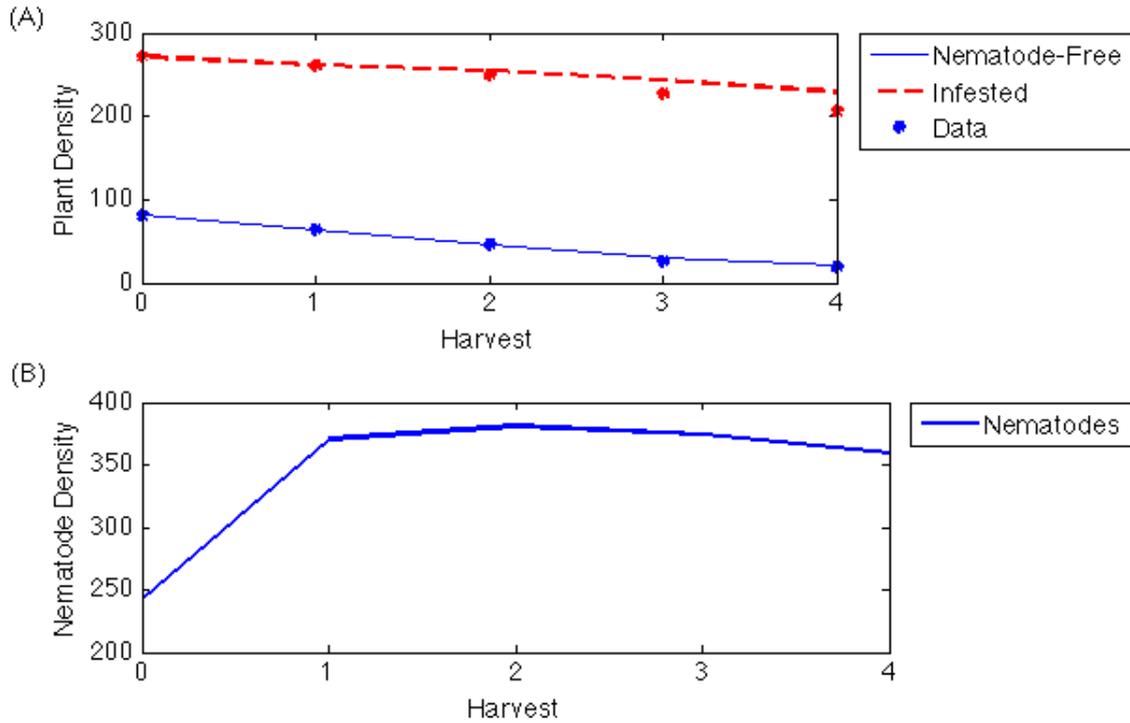
Figure 1: **(A)** Data from [Boelter et al. 1985] is presented in asterisks (*), model computations appear as a continuous line for nematode-free hosts and a dashed line for infested hosts. In the numerical solution winter is excluded and time steps are taken equal to two months, as this interval is approximately the time between harvesting in the experiments [Boelter et al. 1985]. In the Figure,the horizontal axis represents time (two years) but appears with superposed marks for the harvesting events. Marks 1 and 2 are the first and second harvests in the first year which occur around July and September. Marks 3 and 4 are the first and second harvests of the second year. Notice that the interval from mark 2 to mark 3 includes winter and spring of the second year. We assume that there is no winterkill of infested plants and that nematode spread ceases during this time. **(B)** Average density of nematodes in the rhizosphere of an alfalfa plant.
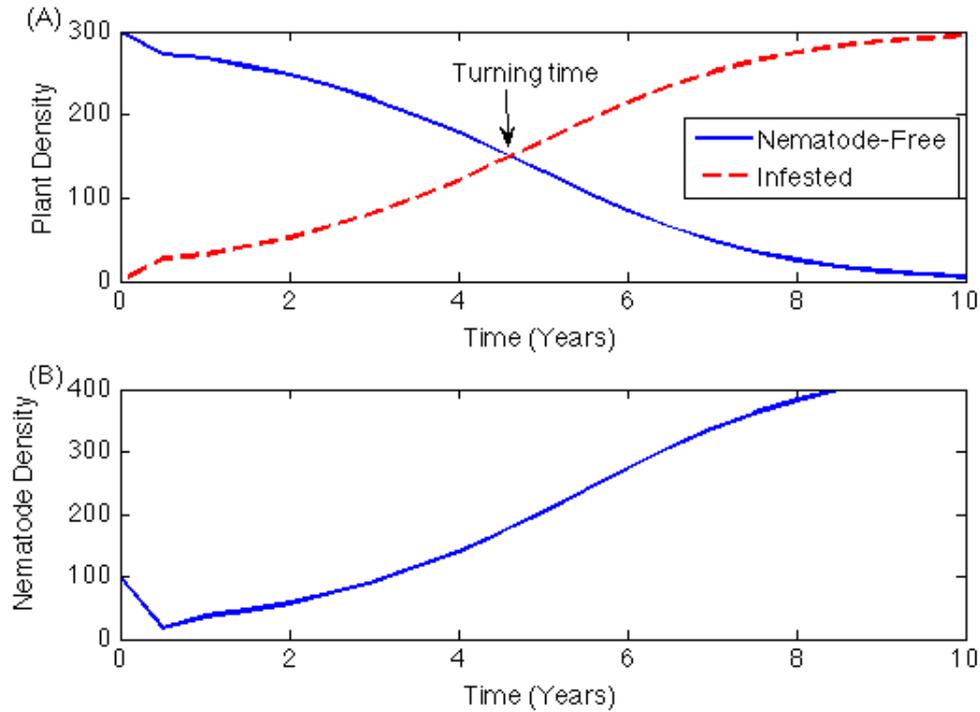
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Figure 2: **(A)** Progression of nematode infestation (without crop rotation) in an alfalfa field using the estimated parameters a and C, see Table 1. The computations are made using initial plant densities $S_0 = 300$ and $I_0 = 0$. The turning time happens during the fifth year, in agreement with common farming practice observations. **(B)** Nematode density trend in the rhizosphere, with initial condition $W_0 = 100$. The drop in nematode density at the start is explained by the initial absence of infested hosts.

produce within other cultivars. When non-host crops are grown in an infested field, the nematodes enter a state of anhydrobiosis, which is characterized by the removal of all body water together with a dramatic change which causes the metabolism to come reversibly to a standstill, [Wharton 1996]. In this state nematodes can stay alive in the soil for longer periods of time with a decreased natural averaged death rate, μ_{W_2}. It has been suggested [Gray and Franc 1993] that it takes around three years for the density of nematodes to decrease sufficiently so that new alfalfa crops can be planted. The death rate for nematodes in the anhydrobiosis state is $\mu_{W_2} \approx 1/3$ (year)$^{-1}$.

Although there is no formal procedure that farmers follow to decide when to introduce crop rotation, long-established growing practices suggest that having more than fifty percent of plants infested is likely to reduce the yield to less than seventy percent of normal. Thus, for many growers, four tons per acre per year is the cut off used to decide crop rotation time in fields that initially have yields up to seven tons per acre per year. Once production drops below four tons, farmers figure they are experiencing economic losses that justify starting crop rotation. This suggests we choose initially a 1:1 ratio of infested to nematode-free plants as a rough approximation to a threshold for rotation that is close to experienced farmers practices. We thus define the *turning time* to be the length of time it takes for an initial healthy alfalfa field to reach a 1:1 proportion between infested and nematode-free plants. The turning time obtained from the simulations using the model (1)-(4) is on the order of four to five years, see Figure 2. Experienced growers usually grow alfalfa continuously for five or six years before introducing crop rotation. Figure 3 shows the differences between turning times after the implementation of crop rotation periods with variable time lengths.

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(a) One year rotation.

(b) Two year rotation.

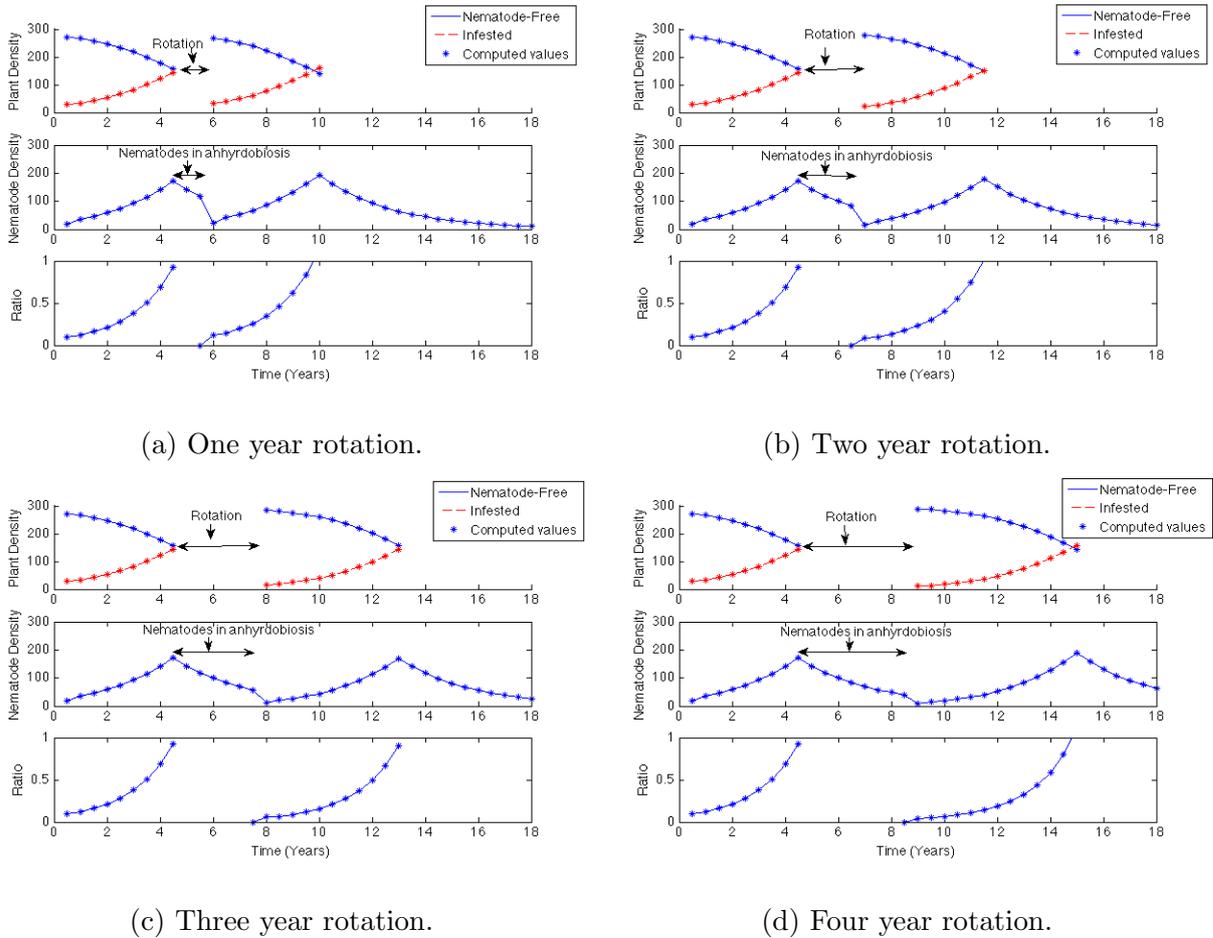(c) Three year rotation.

(d) Four year rotation.

Figure 3: Effects of crop rotation on progression of ASN. The curves interpolate the densities at harvest events, which are marked with asterisks. In the model there are two harvests per year. Crop rotation occurs once the alfalfa field has at least 50% infested plants. This happens when the corresponding nematode-free and infested curves intersect. The program will wait until the end of a growing year to make a rotation. Computations made for different rotation period lengths illustrate the effects of the rotation on turning time: (a) one year of rotation produces a turning time for the new, replacing field of approximately four years. (b), (c) and (d) show results for two, three and four years respectively. The bottom graph in each panel shows the progresion of the ratio infested:nematode-free. We assumed new and re-planted fields free of infested host and used $S_0 = 300$ as initial plant densities. The initial nematode density for the first planted field was $W_0 = 100$. For subsequent plantings the initial nematode density was based on how many nematodes were left in the soil after the previous rotation period ended.
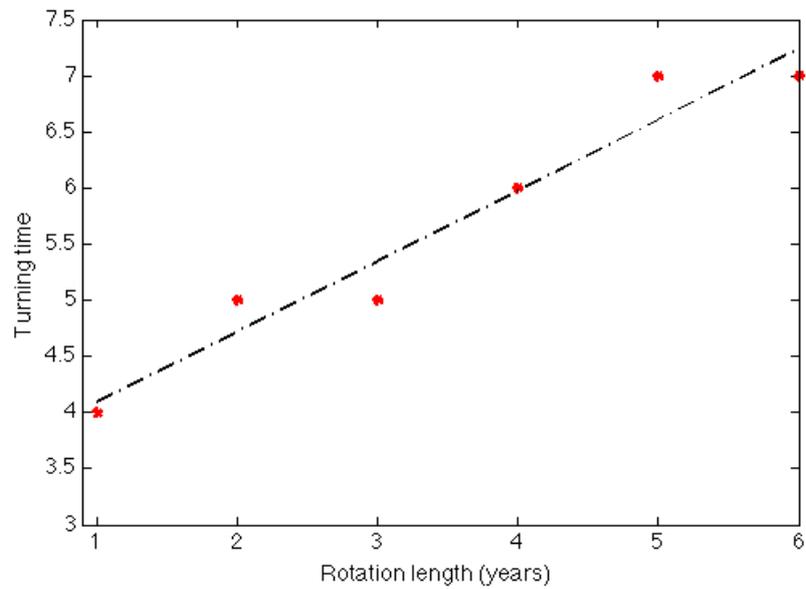
Figure 4: Turning time (in years) for new alfalfa fields as a function of previous crop rotation period length. The model suggests that 3–4 years of crop rotation will provide an alfalfa field that will last 5–6 years before it becomes half infested. This criterion coincides with common practices used by farmers.

6 Conclusions

We presented a theoretical model that characterizes the spread of alfalfa stem ne-
matodes in alfalfa crops, adapted from the more general Nicholson–Bailey model
[Edelstein-Keshet 2005]. The model consists of difference equations describing the
progression in time of affected plants and free nematodes on hosts' rhizospheres. The
parameter values for the equations were obtained by fitting the model to published data
of nematode incidence on alfalfa in experimental trials [Boelter et al. 1985]. With the
calibrated model we were able to compute the progression of nematode infestation and
determine the times at which the ratio of infested to nematode-free hosts is larger
than one (the "turning time"). The computations are made for crop rotation periods
of different duration. We established an approximate relationship between the crop
rotation period and the projected turning time for the new alfalfa field that follows
crop rotation, Figure 4. Common field practices suggest rotation with non-host crops
for a period 2 to 4 years [Hafez 1998] before planting fresh alfalfa and a waiting time of
5 to 6 years to re-initiate crop rotation. Our model approximates these field practices
very well, despite the restrictive assumptions.

Further refinements could be incorporated into the conceptual framework presented
to address important issues related to the management of ASN infestations. For in-
stance, it would be of interest to include the possible influx of new nematodes carried
by irrigation water runoff from neighboring infested fields (an important cause for re-
infestation in several parts of the country [Evans et al. 2008, Gray and Franc 1993]),
and contamination due to inappropriate cleaning of farm equipment or the use of
cheaper non-certified seeds [Hafez 1998]. In addition, it would be of interest to address
the impact of ANS-resistant varieties of alfalfa, which are known to provide longer
turning times, by appropriate modifications to the model.

The costs of crop rotation to control ASN spread must be continuously adjusted with the costs of yield reduction in comparison with the scenario where no rotation is needed. Our model could potentially be combined with known techniques of optimization for crop rotation scheduling [Dos Santos et al 2012] for achieving an economically optimal rotation schedule for protection of alfalfa crops against ASN invasions.

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