MATHEMATICAL ANALYSIS OF DYNAMIC SPREAD OF PINE WILT DISEASE

DRAGOMIR D. DIMITRIJEVIC, JASMINA BACIC

Food and Agriculture Cloud Technology – FACT, Ltd.
Sajkaska 21, 11000 Belgrade, Serbia
Corresponding author E-mail: dragomir@dragomirdimitrijevic.rs

SUMMARY

Since its detection in Portugal in 1999, the pinewood nematode Bursaphelenchus xylophilus (Steiner and Buhrer), a causal agent of Pine Wilt Disease, represents a threat to European forestry. Significant amount of money has been spent on its monitoring and eradication. This paper presents mathematical analysis of spread of pine wilt disease using a set of partial differential equations with space (longitude and latitude) and time as parameters of estimated spread of disease. This methodology can be used to evaluate risk of various assumed entry points of disease and make defense plans in advance. In case of an already existing outbreak, it can be used to draw optimal line of defense and plan removal of trees. Optimization constraints are economic loss of removal of susceptible trees as well as budgetary constraints of workforce cost.

Key words: Pinewood nematode, differential equations, mathematical analysis

INTRODUCTION

Since its detection in Portugal in 1999, the pinewood nematode (PWN) Bursaphelenchus xylophilus (Steiner and Buhrer, 1934) Nickle, 1970, a causal agent of Pine Wilt Disease, represents a threat to European forestry. Significant amount of money has been spent on its monitoring and eradication.

In this paper we present a mathematical model of dynamic spread of pine wilt disease (PWD). Previous work in this area (Mao et al., 2012) used time only and studied the stability of system equilibrium under disease-free and disease-existing situations.

The life cycle of PWN and the vector beetle needed to model the process was described in details by various authors (Takasu, 2009; Togashi and Shigesada, 2006). We will concentrate on references that provide numerical parameters that will be used by our mathematical model.

In late June to early July, a large number of adult beetles emerge from pine trees that were infected and killed the previous year. These beetles carry PWN within their tracheal system and fly to healthy pine trees to feed on twig bark for maturation. During this feeding, PWN are transmitted to cortex and woody tissue through wounds on the twig made by beetles. Within 2-3 weeks infected trees lose the ability for oleoresin exudation. Soon afterwards, the trees emit ethanol and monoterpenes that attract mature beetles. Weakened trees eventually wilt and die and their foliage turns reddish brown, a typical symptom of pine wilt...
disease. A tree dies 30-40 days after infection, and may then contain millions of PWNs throughout the trunk, branches and roots.

Under ideal conditions with suitable temperature (20-25°C) and plentiful food, PWN can produce one generation every 4-5 days with each female laying up to 80 eggs (Mamiya, 1984). The life cycle has two different modes - propagative and dispersal (Wingfield, 1983). In both cases, PWNs are transmitted from one host to the next by Monochamus beetles. A different type of third-stage larva is produced - the "dispersal third-stage larva" which is effectively a survival stage as it can resist adverse conditions (Mamiya, 1983). The onset of dispersal mode is probably a response to reduced food availability once the fungus has fully exploited the wood resource. In the propagative mode, fourth-stage larvae of PWN are transmitted to recently dead or dying trees during oviposition by the female vector. The PWNs leave the beetle and enter the tree through the hole in the bark cut by the beetle to lay its eggs. Within the wood the PWNs feed on fungal hyphae (usually Ceratocystis spp.) which are also transmitted to the wood by ovipositing beetles. Immediately upon entering the wood, larval PWNs molt into adults and begin laying eggs. The population is composed of males, females and four larval stages in this propagative stage which shows rapid multiplication.

Beetle eggs laid on a weakened tree hatch after 1 week, and larvae feed on fresh inner bark of the tree to grow. By the end of autumn they construct pupal chambers in woody tissue, where they spend winter. The PWNs begin to gather around the pupal chambers during winter and enter the tracheal system of newly enclosed adult beetle present in pupal chamber next late spring and early summer. In June and July, adult beetles leave trees in search for new healthy trees where they will transmit PWNs loaded on them. These life cycles of the PWN and the beetle exhibit an obligatory mutualism in that the PWN supplies the beetle with newly weakened trees while the beetle transmits the PWN to a new host tree.

The reproductive cycle of female PWN starting from the moment she begins laying eggs until the moment her offsprings begin laying eggs includes the oviposition period of 28 days (Vicente et al., 2012). In the laboratory, PWN reproduces in 12 days at 15°C, 6 days at 20°C and 3 days at 30°C (Evans et al., 1996). Egg-laying starts on the 4th day after hatching and the eggs hatch in 26-32 hours at 25°C (Kobayashi et al., 1984). The temperature threshold for development is 9.5°C.

In the dispersal mode, third instar larvae present in the wood gather in insect pupal chambers, then molt in a special larval stage, “dau erlarvae”, which enter the callow adult insect through thoracic spiracles to settle, usually in the tracheae. As many as 100,000 dauerlarvae may enter an adult insect vector. Monochamus alternatus Hope is the primary vector of PWN in China and Japan and is known to be capable of carrying an average of 18,000 individual PWNs (USDA APHIS, 1999).

Species of Monochamus from conifers are its principal vectors (OEPP/EPPO, 1986), and of these M. alternatus is the major vector in Japan, whereas Monochamus carolinensis Olivier and Monochamus scutellatus Say are the major vectors in North America. Many of the Monochamus spp. from conifers have been recorded as having non-pathogenic Bursaphelenchus spp. as associates; it is supposed, therefore, that most, if not all, species
would also be capable of transmitting PWN to a greater or lesser extent. For example, the European Monochamus sutor L. and Monochamus galloprovincialis Olivier have been shown to transmit the related Bursaphelenchus mucronatus (Mamya and Enda, 1979) and could, therefore, transmit PWN if it were introduced into Europe, as happened with M. alternatus in Asia. In Portugal, the only known vector is M. galloprovincialis (Sousa et al., 2001).

The complete development of M. alternatus from oviposition to adult emergence takes 8-12 weeks. Females live for up to 83 days and continue egg laying until death, laying 40-215 eggs. Oviposition takes 4-12 days depending on temperature. Pupal stage lasts 19 days. Emergence of adult’s interval is 6-8 days. Initial feeding lasts about 10 days which is essential for sexual maturation. Female lays one egg per scar. Monochamus alternatus has one generation per year but may require 2 years for development especially in the cooler areas of Northern Japan. Adult emergence can begin in mid-April to late June, depending on weather conditions. Emergence lasts about 2 months (Kobayashi et al., 1984).

Adult Monochamus spp. tend to be strong fliers and capable of traveling several km in search of suitable host material. Studies conducted in Japan indicate that, although the adults are strong fliers and some individuals have been known to fly up to 3.3 km, most adults fly less than 200 meters (Kobayashi et al., 1984; USDA APHIS, 1999).

Monochamus alternatus adults can disperse over long distance 2-3 km by flight. A mathematical model indicated that long distance dispersal of M. alternatus contributes greatly to the spread of pine wilt disease (Takasu et al., 2000).

In Missouri, USA, M. carolinensis develops through two partially asynchronous generations per year. The average vector beetle carried 19386 PWN, 85% of which were in the thoracic tracheae (Kondo et al., 1982; Linit, 1987). The sexual maturation period ranged from 7 to 12 days (Walsh and Linit, 1985).

Monochamus galloprovincialis required ten to thirteen months to develop and had single generation per year. Emergence occurred from May to September with the peak in July. Emergences occurred slightly earlier for males than for females, with sex ratio of 0.48. Mortality was generally low for all developmental instars and the within log generation survivorship from egg to adult was 53% (Naves et al., 2008).

The maximum distance at which M. galloprovincialis could be recaptured was 7100 m (Hernandez et al., 2011).

Detailed studies (Evans et al., 2010) of the flight capabilities of Monochamus spp., especially M. alternatus in Japan and China, indicate that most of flights are very local (up to 100 m) but that longer distance flights (various estimates between 1.8 and 3.3 km) may also occur. The evidence of this comes from a number of studies on flight capabilities of Monochamus spp. that show the following distances:

- up to 2.4 km in experiment period (a release-recapture experiment in which one beetle from 756 released reached 2.4 km; 75.5% of the beetles recaptured within 100 meters (Ido and Kobayashi, 1977);
- 3.3 km/flight across open sea (Kawabata, 1979);
• 2 km/flight (Fujioka, 1993);
• 1.8 km/experiment period in average (Takasu et al., 2000);
• 2.3 km/flight (M. carolinensis) (Linit and Akbulut, 2003);
• 7-20 m/week (Togashi, 1990);
• 10-50 meters/flight (Shibata, 1986).

There is no reason for serious mortality of PWN and Monochamus vectors during transport/storage of all kinds of wood (round wood with or without bark as well as sawn wood). If the PWN and Monochamus are present in the wood, they are capable of surviving and reproducing for at least one year and can thus be expected to be present on arrival in the pest risk analysis (PRA) area (Kobayashi et al., 1984). Monochamus vectors present in wood could take up to 2 years to complete their life cycles (Linit, 1988).

**MATHEMATICAL MODEL**

Pine wilt disease is spread by random movement of vectors which carry PWN eggs. Random movement of particles and living organisms has been studied for almost two centuries. Scottish botanist Brown noticed irregular movement of particles of pollen in 1829 which is now known as Brownian motion (a.k.a. random walk). Research on this phenomenon under different names like diffusion or Wiener process led to applications in many areas like diffusion of particles (Einstein, 1905), movement of living organisms (Codling et al., 2008), transfer of heat (heat equation), etc. All results use in some form or shape Fick's laws of diffusion, partial differential equations (PDE) derived by Adolph Fick in the year 1855. They describe diffusion process and introduce the diffusion coefficient (diffusivity).

Usually, the Fick's law is applied to a single process like movement of certain type of particles. In this work we will describe three parallel processes. The first process is the life cycle of vectors which includes birth, transporting of PWNs, mating, and laying of eggs and later death. The second process is the life cycle of PWNs and the change in their number as a result of natural birth and death as well as a result of spread by vectors and removal of infected trees by humans. Birth of PWNs and vectors is dependent on available food provided by trees. The third process is the change (decrease) of the available food which is due use of food by PWNs and vectors and removal of healthy and infected trees by humans as a defense measure against further spread of disease. When an area is infected, the number of PWNs increases. As the number of PWNs increase, more and more of the available food is used until it is exhausted. Then PWNs and vectors gradually start dying out. At the end there is no more neither PWNs and vectors nor food.

In this work we shall assume that the area of land being considered is relatively small compared to the size of Earth so we can use Cartesian coordinate system and coordinates \((x, y)\) as an approximation to spherical coordinate system and longitude and latitude. First, we shall describe the tree processes as a set of PDEs using continuous space coordinates \((x, y)\) and time \(t\) as parameters.

In order to solve PDEs numerically, we shall divide land to \(N_x \times N_y\) cells with size \(\Delta y \times \Delta x\). Each cell at coordinates \((i\Delta x, j\Delta y)\) will be described with its own set of functions labeled with the subscript \(ij\). For each space dependent value, we shall implicitly assume a discrete
counterpart. In such a way, we shall approximate the system of partial differential equations with space and time as parameters with a system of ordinary differential equations with time as the only parameter. Such a system can be easily solved using numerically stable fourth order Runge-Kutta method (Kloeden et al. 1992). Note that in case of space-dependent parameters, they represent density of the corresponding value, i.e. the number of units per unit of land area. The discrete values represent the actual number of units at the corresponding cell of land. Let us introduce the following notation.

The $n(x,y,t)$ is the density of PWN at a geographical location $(x,y)$ at time $t$, i.e. the number of PWNs per unit of land area. The discrete counterpart of this value, $n_{i,j}(t)$, is the number of PWNs at land cell $(i,j)$.

Similarly, the $v(x,y,t)$ is the density of vectors at location $(x,y)$ at time $t$ and $v_{i,j}(t)$ is the number of vectors in the discrete land cell $(i,j)$ at time $t$.

The $p(x,y,t)$ is the density of pinewood trees at location $(x,y)$ and time $t$ and without further repetition the $p_{i,j}(t)$ is the discrete counterpart representing the number of trees in the cell of land $(i,j)$ at time $t$. Note that the land where this value is equal to 0 represents area without trees like urban area, lakes or fields where PWN cannot live.

Each tree has certain feeding capacity $N$, i.e., the number of nematodes it can feed and support. To be precise, in order to simplify the model, this model includes the feeding capacity of tree itself and the feeding capacity of fungi that develop later on a dead tree. A more precise model would model life cycle of fungi as the fourth process. The overall feeding capacity can be in the millions (Takasu, 2009; Togashi and Shigesada, 2006). Each PWN, during its life uses portion of food provided by the tree. As the number of PWNs that spend their life on an infected tree increase, its feeding capacity decreases. After all food available on the tree is used up, PWNs cannot survive on that tree and gradually start dying out. Vectors consume food provided by trees too. However, we will ignore this consumption due significantly higher number of PWNs.

The $f(x,y,t)$ is the feeding capacity of an area. For an area that is not infected, it holds

$$f(x,y,t) = N \cdot p(x,y,t)$$

The $r(x,y,t)$ is the rate of removal of trees at location $(x,y)$ at time $t$, i.e.

$$\frac{\partial p(x,y,t)}{\partial t} = -r(x,y,t)$$

This value is controlled by humans as a measure of blocking further spread of disease. Trees are removed from appropriate areas in order to cut pathways for further spread of disease.
If the stretch of land with no feeding capacity is sufficiently large, vectors cannot bridge the gap and disease cannot spread further beyond the gap. Note that when $\rho(x, y, t) = 0$ then it must be $r(x, y, t) = 0$, i.e. trees cannot be removed from areas where there are no trees.

The $F_x$ and $F_v$ are the ratio of the numbers of females to the overall populations of PWNs and vectors respectively (sex ratio). Obviously both parameters are between 0 and 1. In case of vectors, a value of 0.48 can be found in the literature and in absence of value for PWN, we will assume 0.5.

The $S_n$ and $S_v$ are the survivorship rates from egg to adult for PWN and vectors respectively. Both parameters are between 0 and 1. In case of vectors, a value of 0.53 can be found in the literature and in absence of value for PWN, we will assume 1.

The $\beta_n(t)$ is the number of PWN per time unit a single female PWN produces at time $t$ (time-dependent birth rate). During late spring and early summer its value is equal to $G_n/C_n$ while it is equal to zero during other time periods. The $G_n$ is the number of eggs laid by a female PWN which is between 80 and 150 (Vicente et al., 2012). The $C_n$ is the collective reproductive cycle of the $G_n$ siblings made by the same female PWN starting from the moment she begins laying eggs until the moment her off-springs begin laying eggs and, depending on temperature in laboratory conditions, it is between 3 and 12 days (Evans et al., 1996).

Similarly for vectors are defined $G_v$ (between 40 and 215 - Kobayashi et al., 1984), and $C_v$ (between 8 and 12 weeks).

The $V$ is the number of PWN juveniles picked up by vector and carried away and can range between 18,000 (USDA APHIS, 1999) and 100,000 (OEPP/EPPO, 1986).

The $L_v$ is life expectancy of PWN which is 2 years or 730 days (Takasu, 2009; Togashi and Shigesada, 2006). The $L_v$ is life expectancy of the vector. It is equal to $C_v$ because female dies after oviposition period (Takasu, 2009; Togashi and Shigesada, 2006).

The $H(a)$ is the Heaviside step function which is equal to 1 when $a > 0$ and 0 otherwise. We shall use it to include/exclude certain terms in our calculation in case $f(x, y, t)$ is greater/smaller or equal to 0.

The second Fick’s diffusion law defines incremental change of density of particles, or living organisms (vectors) due random motion (excluding other reasons for change such as birth or death) in time as

$$\alpha(x, y, t) = D \left( \frac{\partial^2 v(x, y, t)}{\partial x^2} + 1 \frac{\partial^2 v(x, y, t)}{\partial y^2} \right)$$

(3)
Per this equation, assuming that particles/organisms move randomly in all directions with equal probability, random movement statistically goes from more to less populated/infected areas and incremental change of density in time due to the random motion of vectors is proportional to the coefficient of diffusion (diffusivity), $D$ and the second order partial derivative of density over distance in both south-north and west-east directions. Data available from the literature do not indicate any preferential direction of movement of vectors and justifies assumption of equal probability of movement in all directions. In case a preferential direction of movement does exist, a biased variation of random walk may be applied (Codling et al., 2008).

The $D$ characterizes speed of diffusion (spread) of particles or living organisms. In a two-dimensional space it is equal to

$$D = \frac{E[s^2]E[\tau]}{4}$$  \hspace{1cm} (4)

The $E[s^2]$ is the mean square speed of vector and $E[\tau]$ is the mean time vector spends flying in one direction, i.e. time spent for one step in its random walk. This formula allows us to compare how efficiently different species of vectors spread disease. Faster vectors spread disease more efficiently. Furthermore, vectors that spend longer time flying in one direction before changing the direction are also more efficient in spreading disease. In other words, vectors that frequently change direction do not get far from its origin since they just hover around it.

The question is how to determine diffusivity experimentally. Several papers published how far were marked vectors found after their release. These values cannot be used in a straightforward manner since between release and capture, the vector flew a random walk changing directions in between. Therefore speed cannot be determined by simply dividing distance by time between release and capture. For that reason we propose two methods.

The first method is to somehow measure short distance flight of a vector. Measurement of short distance speed is straightforward. However it is more difficult to measure average duration of flight in one direction since it is more difficult to track vector over longer distance. A reasonable assumption is that vectors fly from a tree to tree, so duration of a flight may be calculated using average distance between trees, and determined speed of vectors.

$$D = \frac{E[s^2]d}{4E[s]} = \frac{E[s]d}{4}$$  \hspace{1cm} (5)

The second approximation holds in case the speed of vector is approximately constant, i.e. $E[s^2] \approx E[s]^2$.

The other method uses the fact that dispersal, distance between vector’s location and its origin, has a normal distribution with zero mean and variance $Dt$ where $t$ is time between
the vector is released at the origin and time it was captured at distance \( d \). In most cases, dispersal is only for a few hundred meters (Kobayashi et al., 1984). Let \( \pi \) be probability that dispersal will be larger than the observed value (tail of normal distribution). Then \( d \) can be obtained by solving the following non-linear equation

\[
\frac{1}{2} \text{erf}\left(\frac{d}{2\sqrt{2}\sigma}\right) = \pi
\]

where \( \text{erf} \) is the error function. A numerically easier way is to use approximation called Chernoff bound

\[
\frac{d}{\sigma} e^{-\frac{d^2}{8\sigma^2}} \geq \pi
\]

Note that variance of distance between place of release and capture of a vector increases as time between release and capture increase. For that reason, in order for two experiments to be comparable, time between capture and release must be same. Otherwise one can just assume value of \( \pi \) in (5) or (6).

The total incremental change of vectors in time can be described by the following PDE

\[
\frac{\partial v(x,y,t)}{\partial t} = \left( H(f(x,y,t)F_{x,0}^t, \beta(t) - \frac{1}{L} \frac{r(x,y,t)}{p(x,y,t)} \right) v(x,y,t) + \alpha(x,y,t)
\]

The left-hand side of (8) is the incremental number of vectors at the given time and location, i.e. the change in the number of vectors per unit of time. It is due factors in the right-hand side of (8).

The first term in the right-hand side of (8) is due birth of vectors. It is proportional to the number of female vectors in that area, survivorship rate, and time-dependent birth rate. The Heaviside function is to account that this factor is equal to zero when feeding capacity of the area is exhausted.

The second term in the right-hand side of (8) is the rate of natural dying of vectors which is also proportional to the number of vectors and inversely proportional to the average length of life.

The third term in the right-hand side of (8) is due removal of infected trees together with eggs of vectors. Depending on defense method, it can be replaced by a parameter with a value between 0 and 1 which would represent effectiveness of the eradication effort to reduce beetle density by spraying insecticide or fumigation of infected trees.

The fourth term is due Brownian motion of vectors as defined by the second Fick’s equation (3).
The incremental change of nematodes in time can be described by the following very similar PDE

\[
\frac{\partial n(x,y,t)}{\partial t} = \left( H(f(x,y,t)F_S, \beta_r)(t) - \frac{1}{L_n} \frac{r(x,y,t)}{p(x,y,t)} \right) n(x,y,t) + V_F \alpha(x,y,t) \tag{9}
\]

Except for the numerical values of parameters in the first three terms in the right-hand side of (9), the difference is that the fourth term in (9) includes parameters \( V \) and \( F \) to account that each female vector carries with it multiple juvenile PWNs. The first three terms model physical appearance/disappearance of PWN due various factors: birth, death, and physical removal. The fourth term models movement of PWNs loaded on vectors.

The rate of change of feeding capacity in time can be calculated as

\[
\frac{\partial f(x,y,t)}{\partial t} = -\frac{F_{in} n(x,y,t)}{C_n} - \frac{r(x,y,t)}{p(x,y,t)} f(x,y,t) - V_F \alpha(x,y,t) \tag{10}
\]

The first term in the right-hand side of (10) is due newly born nematodes which will in their life time use some feeding capacity. The second term is due removal of trees and the appropriate feeding capacity of the area. The third term is due nematodes brought by vectors. All three term have a minus in front of them since they reduce feeding capacity. Technically, it is possible to account for increase of feeding capacity due newly grown trees. However, this process is negligible due its length (years) compared to 30-40 days after which infected trees die (Takasu, 2009; Togashi and Shigesada, 2006). Once the feeding capacity is reduced to zero, it cannot be reduced any further and the remaining PWNs and vectors gradually die out.

The set of PDEs (8-10) has to be solved subject to three sets of initial conditions.

The first set of initial conditions is the initial distribution of pinewood trees, \( p(x,y,0) \), which describes areas under pinewood and areas that are not covered with pinewood (e.g., lakes, fields or urban areas). The most effective and accurate way is to use a digital geographic map. Consequently the initial feeding capacity can be calculated using (1).

The second and third set of initial conditions are the initial distribution of PWNs \( n(x,y,0) \) and vectors \( v(x,y,0) \). This can be defined in two ways. The first way is to assume initial distribution at a suspected risky entry point of disease (e.g., point of high trade) as a preparation for eventual future outbreak. The second way is to use actual observed distribution while drawing defense plan for the ongoing outbreak.

Since the set of PDEs (8-10) including initial boundary conditions cannot be solved as a closed form, it has to be solved numerically in discrete space and time domain. Given life cycle of PWN and speed of vectors, calculation in steps of one day is sufficiently precise.
Similarly, given usual density of pine trees (about 3,000 per hectare), square cells 5-10 meters wide containing 7-30 trees is sufficiently precise.

The transformation to discrete space domain is based on the following approximation:

\[
\frac{\partial^2 v(x,y,t)}{\partial x^2} \approx \frac{v_{i+1,j}(t) - 2v_{i,j}(t) + v_{i-1,j}(t)}{\Delta x^2}
\]  

The same approximation holds for \( y \).

The discrete set of PDEs becomes a set of ordinary differential equations with \( t \) as the only parameter. It can be solved as a set of consecutively calculated matrices using fourth order Runge-Kutta method. Each matrix represents one moment in discrete points of time spread one day apart while each matrix element represents one cell of land. Each cell is characterized by the estimated number of PWNs and vectors, the remaining cell feeding capacity and the time the cell is infected. As results are calculated as real (non-integer) numbers, the estimated infection time is time when the number of vectors in a cell becomes greater or equal to 1 or some other threshold. It is an important parameter in planning defense strategy against spread of disease. In order to optimally cut pathway for spread of disease, trees in a cell must be cut just in time before the cell is actually infected, i.e. before it becomes a springboard for further spread of disease. In other words, in order to minimize loss of healthy trees due cutting, trees must be cut as close as possible to the disease front line, i.e. as close as possible to the estimated infection time.

**NUMERICAL EXAMPLES**

In this section we demonstrate the methodology on a simple example as an illustration. The 50x50 meters area of land is divided to 5x5 square cells with size equals to 10 meters. Each cell contains 30 trees (3,000 trees per hectare). Initially only the cell in the upper-left corner is infected with 100,000 PWNs and 2,000 vectors. Calculation is performed in steps of 1 day until the cell in the lower-right corner (opposite of the initially infected cell) is infected. Other parameters are:

- \( L = 35 \), \( C = 5 \), \( C = 365 \), \( F = 0.5 \), \( F = 0.48 \), \( S = 0.53 \), \( G = 100 \), \( G = 150 \), \( V = 100,000 \), \( L = 365 \), and \( N = 20,000,000 \).

We varied parameters related to vector’s mobility, i.e. those that influence diffusivity and spread of disease and time a particular cell will be infected. Among data about vector mobility that is available in the literature, we have chosen the experiment in which a vector is recaptured one week after release 7 to 20 meters far from the origin (Togashi, 1990). We will use formula (6) to calculate variance and consequently diffusivity. In absence of probability (tail of normal distribution) in the literature that is required by formula (6) we calculated parameters for assumed values equal to 0.01 and 0.1. In other words, maximum distance from the origin was 20 meters for all of 100 (10) recaptured vectors. The corresponding diffusivity is 1.551 and 3.102 respectively. The lower-right cell is infected after 62 and 43 days respectively. The table below shows infection times for the two values of diffusivity and for each of the 25 cells.

| Table 1: Cell infection times in days |
Note that higher probability of normal distribution tail means higher diffusivity and shorter time of infection, i.e. faster spread of disease.

**CONCLUSIONS AND FUTURE WORK**

In this paper we presented a mathematical model of spreading pine wilt disease. Unlike in papers written by other authors, the model includes parameters of life cycles of PWNs and vectors as well limitation of food available to PWNs and PWNs eradication efforts by humans (cutting of trees and/or fumigation). Future work on this model should include verification and fine tuning using historical data on spread of earlier pine wilt disease outbreaks. The method can be used as a software tool in fighting against potential and ongoing diseases and drawing optimal defense plans. Such a software tool should include a database with geographic maps with disease susceptible areas with pine wood trees and areas that are not susceptible like lakes or urban areas. It can also include advices on eradication efforts like time and location of trees that should be cut or sprayed. Future enhancements can include PRA and automated creation of initial conditions of potential outbreaks using meteorological and other data that can be found in relevant databases.

**REFERENCES**


http://fabiserv.up.ac.za/webresources/pdf/05fd01bd7406bbf541f92c7e93875260.pdf