沈聖娥 教授指導

碩士學位 請求論文

Mathematical Models of Animal Diffusion

동물확산의 수학적 모델

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誠信女子大學校 教育大學院

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金 涓 秀

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審査委員 ________________ 印

誠信女子大學校 敎育大學院

논 문 개 요

이 논문은 온도와 열 등의 물리적 확산에 대응되는 개념인 생물확산(bio-diffusion) 이라는 관점에서 서식지 내에서 동물 개체들의 분포의 변화를 설명하고자 한다.개체 밀도와 동물 확산의 관계에 대한 광범위한 연구들이 곤충을 이용하여 이루어졌다. 곤충류는 다른 동물들에 비해 개체 수가 풍부하고 또 운동성이 커서 확산에 관련된 연구에 적합하다. 곤충의 확산에 관한 연구는 새로 침투한 해충에 의한 지역적 피해를 추정하고, 또 동면 지점에서 깨어나 봄철 활동기 동안 곤충의 지역적 분포를 조사하는 데에 큰 역할을 하게 된다. 확산에 관련된 정량적인 정보들은 해충 조절 방법을 평가하는 데에도 핵심적인 역할을 한다.

이 논문에서는 곤충 확산을 기술하는 수학적 모델을 세우고, 이러한 모델들이 실제 현상들과 부합하는 정도를 측정할 것이다.

목 차

I Introduction

In his book Animal Ecology, Ito[1] classifies animal dispersal into random dispersal and density-dependent dispersal and emphasizes the importance of the latter from the standpoint of population dynamics.

The relationship between animal dispersal and population density has been studied extensively with insects. Because of their abundance and their high mobility as compared to animals of similar size, insects are suitable for the study of dispersal. Morisita[2] ascertained a relation between population density and dispersal in natural populations of water striders. Later,similar relations were recognized in experiments with aphids (Ito[3]) and with rice weevils (Kono[4]),from which it was concluded that for each species there exists an associated population pressure that enhances population dispersal.

Morisita[5] attempted to quantify this population pressure experimentally. He released ant lion larvae(Glenuroides japonicus)from a point and observed their dispersal. The movement pattern of individuals was classified as one of two types: one that dug holes in the vicinity of the release point("normal individual"), and the other that dug holes after having traveled large distances from the release point("abnormal individual").

The connection of population density with dispersal behavior has significance when viewed from the standpoint of social processes in communities (Ito[6]). Also, Andrewartha and Birch [7] attached great importance to dispersal as a reaction to crowding. Yet overpopulation does not necessarily lead to dispersal.

In lieu of fitting density-dependent models to insect dispersal, several experiments have directly manipulated the number of animals that were released, and then used the diffusion coefficient as a response variable to test whether diffusion coefficients varied with density (kareiva[8]). These experiments have typically found an increase in diffusion coefficients as density is increased. perhaps because the densities used as treatments are typically very high, and hence crowding effects might be expected. A dispersal experiment consists of releasing a great number of insects from a given source and of observing the spatial distribution at various subsequent times. Since three - dimensional dispersal is difficult to observe , we usually attempt to measure the two - dimensional distribution of dispersal by the use of traps placed near the ground. Sometimes the released insects are marked with radioactive tracers, etc., to distinguish them from others (Hawkers,[9]; Lamb et al. [10]).

The study of insect dispersal plays an essential role in estimating the areal spread of damage caused by a newly invaded pest or the spatial distribution of insects during the active period in spring subsequent to emergence from hibernation spots . Quantitative information concerning dispersal plays an essential role in the evaluation of pest control (Joyce,[11] ; Stephens and Aylor ,[12]). The work of Japanese entomologists on insect dispersal has enjoyed a good international reputation. Let's begin by first looking at a laboratory study by Watanabe et al. [13]. Under nearly constant temperature, humidity, and illumination,they investigated the pattern of dispersal of adzuki-bean weevils(Callosobruchus chinensis) on a piece of paper. They found the pattern of dispersal about the release point to be approximated by the two-dimensional normal distribution.

II Preliminaries

Considering only the dispersal of normal individuals, Morisita found that the number of individual, N, that settled inside a circle of area A centered at the release point could be expressed by

$$N = M\{1 - e^{-cA}\} \tag{1}$$

where M is the total number of normal individuals and c is a parameter associated with dispersal. Equation (1) agrees with the result obtained from a two-dimensional normal distribution, i.e., a two-dimensional simple random walk. Also, it is possible to express the horizontal variance σ_r^2 in terms of the parameter c in (1) by using the fact that number density S for the two-dimensional normal distribution is given by

$$S(x, y, t) = (\frac{M}{\pi\sigma_r^2}) \exp\frac{-(x^2 + y^2)}{\sigma_r^2} = (\frac{M}{\pi\sigma_r^2}) \exp(\frac{-r^2}{\sigma_r^2}).$$

Integrating the density function S over a circular area A around $r = 0$, we have that

$$
\begin{aligned}
N &= \int_A S\,dA \\
&= \int_0^{r_0} S\cdot 2\pi r\,dr \qquad (\pi {r_0}^2 = A, \quad r_0 = (\tfrac{A}{\pi})^{\frac{1}{2}}) \\
&= (\tfrac{M}{\pi\sigma_r^2}) \int_0^{(\frac{A}{\pi})^{\frac{1}{2}}} \exp(\tfrac{-r^2}{\sigma_r^2}) 2\pi r\,dr \qquad (r^2 = u, \quad 2r\,dr = du) \\
&= (\tfrac{M}{\pi\sigma_r^2}) \int_0^{\frac{A}{\pi}} \exp(-\tfrac{u}{\sigma_r^2})\,du \\
&= M\{1-\exp(-\tfrac{A}{\pi\sigma_r^2})\}.
\end{aligned}
$$

Comparing this with (1), we obtain that

$$\sigma_r^2 = (\pi c)^{-1}.$$

Analyzing data obtained with rice weevils Kono[4] and with adzuki-bean weevils(Watanabe[13])as well as those obtained with ant lions, Morisita[5] deduced the regression

$$\sigma_r^2(t) = \frac{\sigma_\infty^2 t}{(t+T)} \tag{2}$$

where t is time, and σ_∞^2 and T are parameters dependent on M. Morisita gave the following relationships:

$$\sigma_\infty^2 = \frac{M}{(\alpha+\beta M)}, \qquad T = \frac{\lambda}{(\alpha+\beta M)} \tag{3}$$

$$\sigma_r^2(t) = \frac{\sigma_\infty^2 t}{(t+T)} = \frac{Mt}{t(\alpha+\beta M)+\lambda}$$

where α, β , and λ are constants. From (2), for $t \ll$T , i.e., for initial dispersal,

$$\lim_{T\to\infty} \sigma_r^2(t) = \lim_{\alpha+\beta M\to 0} \sigma_r^2(t) = M\lambda^{-1}t. \tag{4}$$

The dispersal incresases proportionally with both population density and time. On the other hand, from (2) for $t \gg T$,i.e., for final dispersal,

$$\lim_{t\to\infty} \sigma_r^2(t) = \sigma_\infty^2 = \frac{M}{(\alpha+\beta M)}. \tag{5}$$

The dispersal becomes constant independent of time, and the dependence on M weakens as M increases. For high values of initial population density (M), the dispersion approaches the value $\frac{1}{\beta}$ independent of M. That is ,

$$\lim_{M\to\infty} \frac{M}{(\alpha+\beta M)} = \frac{1}{\beta}$$

The behavior of the initial variance is the same as that for Fickian diffusion so that the relation for diffusivity $D = \frac{M}{4\lambda}$ may be deduced ; note that D is thus proportional to the population density. Morista's empirical formulas (2) and (3) appear to be of general applicability in describing the time variation of the variance for insect dispersal from a point source. In other words, the dispersal pattern, assumed to be isotropic, is given by

$$S(r, \theta, t) = (\frac{M}{\pi\sigma_r^2}) \exp(-\frac{r^2}{\sigma_r^2}) \quad (6)$$

in polar coordinates(r,θ), where the origin is taken to be the release point, and where M is the total number of insects released and σ_r^2 is the horizontal variance.

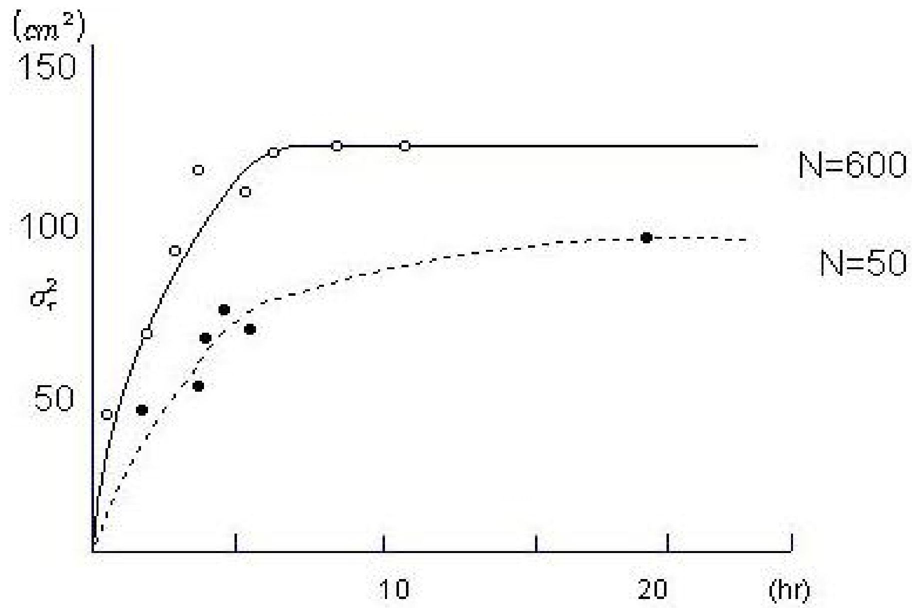

Figure 1: Time variations of the variance of the dispersal of adzuki-bean weevils: N denotes the number of individuals released (from Watanabe et al., 1952

Investigators often try to describe the vertical distribution of insects by empirical formulas such as that of (Wolfenbarger [14], [15]);

$$S = a + b\ logZ + \frac{c}{Z} \tag{7}$$

and of [16]:

$$S = c_1(Z + Z_e)^{-\lambda} \tag{8}$$

where S is the number density of insects, Z is the height from the ground, and a, b, c, c_1, Z_e and λ are constant parameters.

III Main Results

Dobzhansky and Wright [17] reason that *leptokurtic* distributions would result from heterogeneous population of insects, some dispersing rapidly and others dispersing slowly. The kurtosis of a spatial dispersal of individual insects is usually larger than 3.0 - the distribution is thus said to be l *leptokurtic*(Sokal and Rohlf, [18]). The kurtosis, β_2, is defined by $\beta_2 = \frac{\mu_4}{(\sigma^2)^2}$, where σ^2 is the variance and μ_4 is the 4th-order central moment.

If we express a density distribution function by $f = f_0 \exp(-cr^k)$, $\beta_2 = \Gamma(1/k)\Gamma(5/k)/\Gamma(3/k)^2$, where Γ is a gamma function. For a normal distribution, $k = 2$ and $\beta_2 = 3$. The distribution function for insects may be approximated by taking $k = 1 \sim 1/2$ .Thus, the spatial pattern of biodiffusion is generally leptokurtic. The superposition of two normal distributions with different values of variance produces a leptokurtic pattern. By the same token, a mixture of data from various experiments with widely different rates of dispersion gives a greater kurtosis than the separate components(Wright [19]). Also ,James([20]) has studied an inverse problem i.e., the estimation of the mixing proportion of two normal distributions by means of simple, rapid measurements.

Let us clarify the above matter in a more quantitative fashion. Take two populations that diffuse according to Fick's law with different diffusivities or variances. That is, the dispersal pattern of each population is Gaussian and given by

$$f_1 = \frac{n_0}{(2\pi)^{\frac{1}{2}}\sigma_1} \exp(-\frac{x^2}{2\sigma_1^2}) \tag{9}$$

$$f_2 = \frac{n_0}{(2\pi)^{\frac{1}{2}}\sigma_2} \exp(-\frac{x^2}{2\sigma_2^2}) \tag{10}$$

where the total number of individuals belonging to both population is assumed to be equal and is denoted by n_0, and σ_1^2 and σ_2^2 are the variances for both populations. Furthermore, suppose that $\sigma_1^2 \geq \sigma_2^2$.

When individuals from two such populations are pooled, the compound distribution is given by the mean of (9) and (10). That is ,

$$f = \frac{n_0}{2(2\pi)^{\frac{1}{2}}} \left\{ \frac{1}{\sigma_1} \exp(-\frac{x^2}{2\sigma_1^2}) + \frac{1}{\sigma_2} \exp(-\frac{x^2}{2\sigma_2^2}) \right\}. \tag{11}$$

The variance and the fourth - order central moments of (11) are given by

$$\sigma^2 = \frac{1}{2}(\sigma_1^2 + \sigma_2^2), \tag{12}$$

$$\mu_4 = \frac{3}{2}(\sigma_1^4 + \sigma_2^4), \tag{13}$$

respectively. Hence, we obtain the kurtosis

$$\beta_2 = \frac{\mu_4}{(\sigma^2)^2} = \frac{6(\sigma_1^4 + \sigma_2^4)}{(\sigma_1^2 + \sigma_2^2)^2} \tag{14}$$

As $\sigma_1^2 \geq \sigma_2^2$, we put $\sigma_1^2 = m\sigma_2^2$ $(m \geq 1)$ and substitute into (14). The result is

$$\beta_2 = \frac{6(1 + m^2)}{(1 + m)^2} \tag{15}$$

For $m = 1$, i.e., homogeneous populations, $\beta_2 = 3$ (normal distribution). For $m > 1$, $\beta_2 > 3$, and the value of β_2 increases with m. As $m \to \infty$, $\beta_2 \to 6$. Accordingly,

$$6 \geq \beta_2 \geq 3.$$

We are thus able to show that a compound distribution taken from heterogeneous populations, even though individual distributions are Gaussian with different variances, becomes leptokurtic. As long as the ratio m remains constant, the kurtosis will be invariant even if both and vary with time. on the other hand, the kurtosis decreases with time if m decreases with time; such a case will occur when the population having a larger variance, σ_1^2, thus dispersing faster, tends to settle sooner than the population having a smaller variance(Dobzhansky and Wright [17]).

Dispersal due to population pressure may be appropriately modeled by expressing the advection and diffusion terms as function of population density. Let us consider a one-dimensional case. The model equation can be written as

$$\frac{\partial S}{\partial t} = -\frac{\partial}{\partial x}(uS) + \frac{\partial}{\partial x}(D\frac{\partial S}{\partial x}) \tag{16}$$

where the advection and diffusivity generally depend on x, t, and S. The

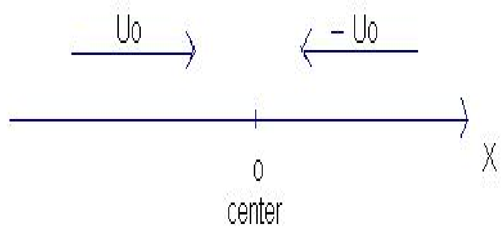

Figure 2: Diffusion model with the center of attraction The speed of attractive flow is U_0.

advection in (16) represents the effect of attraction of insects to a particular region. For instance, any tendency for concentration of insects around a point is interpreted to be the result of an attractive flow toward this point.

As a simple model, we take the center of attraction at the origin, $x = 0$, and assume that the speed of attractive flow is constant,

$$u = -u_0 \quad sgn(x) \tag{17}$$

where $sgn(x)$ is a function defined to be 1 if $x > 0$ and -1 if $x < 0$ (Figure 2). Assume the diffusivity to depend not on x and t, but on S alone. We thus take

$$D = D_0(\frac{S}{S_0})^m, m > 0 \tag{18}$$

where D_0 is the diffusivity for $S = S_0$(a reference concentration). As $m > 0$, the diffusivity increases with S. The effect of population pressure is thus incorporated into D. Substituting (17) and (18) into (16), we find

$$\frac{\partial S}{\partial t} = u_0 \frac{\partial}{\partial x}\{sgn(x)S\} + D_0 \frac{\partial}{\partial x}\{(\frac{S}{S_0})^m \frac{\partial S}{\partial x}\}. \tag{19}$$

The problem is to solve (19) under approprite intial conditional. However, the equation is nonlinear with respect to S, and in general an analytical solution is difficult to obtain. For such nonlinear problems, it may prove useful to pay attention to two limiting cases, i.e, small values of t (initial dispersal) and large values of t (final dispersal).

When the advection term is compared with the diffusion term , we realize that initially the concentration gradient, $\frac{\partial S}{\partial x}$, is very large near the origin from which individuals are released, and also diffusivity is high due to high density of individuals. Thus, we may ignore the advection term in the initial period of dispersal.

$$\frac{\partial S}{\partial t} = D_0 \frac{\partial}{\partial x}\{(\frac{S}{S_0})^m \frac{\partial S}{\partial x}\} \tag{20}$$

Pattle (1959) has given the solution to (20);

$$S = \begin{cases} S_0(\frac{t_0}{t})^{\frac{1}{m+2}}(1 - \frac{x_2}{x_1^2})^{\frac{1}{m}}, & \text{if } |x| \leq x_1, \\ 0, & \text{if } |x| > x_1, \end{cases} \tag{21}$$

with $x_1 \equiv r_0(t/t_0)^{\frac{1}{m+2}}$, $r_0 \equiv \varrho\Gamma(1/m + (3/2))/\pi^{\frac{1}{2}} S_0\Gamma(1/m + 1)$, and $t_0 \equiv r_0^2 m/2D_0(m + 2)$, ϱ being the initial flux of individuals from the origin and Γ being the gamma function. The population disperses only to a finite range $x = x_1(t)$, and the spatial pattern is consistent with the predictions of Aikman and Hewitt [21].

For the final period of dispersal, advection and diffusion play equally important roles. In fact, these two processes balance each other. Diffusion tends to spread the population from the center, while advection acts to attract it to the center. Eventually a steady state is established (Shigesada and Teramoto [22]), so that $\frac{\partial S}{\partial t} = 0$. Under this condition we integrate (19) once with respect to x:

$$u_0 \; sgn(x)S + D_0(\frac{S}{S_0})^m \frac{dS}{dx} = 0 \tag{22}$$

where the integration constant becomes zero insofar as $S = 0$ at $|x| = \infty$. Integrating (22) once more over x and seeking a symmetric solution around $x = 0$, we obtain

$$S = \begin{cases} S_0(1 - \frac{mu_0}{D_0}|x|)^{\frac{1}{m}}, & \text{if } |x| \leq x_b \equiv \frac{D_0}{mu_O}, \\ 0, & \text{if } |x| > x_b \equiv \frac{D_0}{mu_O} \end{cases} \tag{23}$$

where we take S_0 to be the population density at the center.

Another interesting problem is the spatial distribution of insects resulting from a combination of dispersal and intraspecific interaction. As a simple example, consider an insect population that is dispersing from a point according to Fick's law ,i.e , a random walk, and is reproducing at a constant rate. The mortality rate of parents is assumed to be constant. We may query as to what the distribution of eggs in space might be.

In one dimension the parent population obey the following diffusion equa-

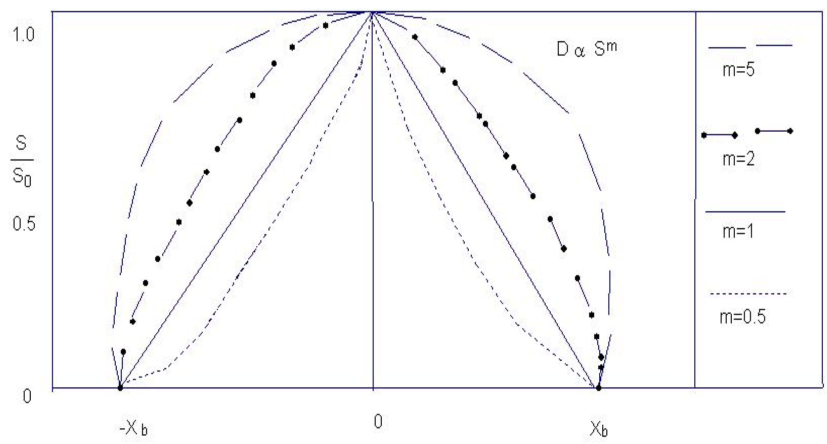

Figure 3: Spatial distribution of population under density-dependent diffusion and advection toward the center.

tion;

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} - \mu S \tag{24}$$

where S is the population density of parents, D is the diffusivity, and μ is the mortality rate. The equation for eggs is

$$\frac{\partial E}{\partial t} = \lambda S \tag{25}$$

where E is the population density of eggs and λ is the rate of egg deposition. The solution of (24) subject to the initial condition that,

$$\text{at } t = 0, \quad \int_{-\infty}^{\infty} S dx \;=\; \text{the initial total number of individuals} \;\equiv\; N_0$$

is given by

$$S(x,t) = \frac{N_0}{2(\pi Dt)^{\frac{1}{2}}} exp(\frac{-x^2}{4Dt} - \mu t) \tag{26}$$

Subsititution of (26) into (25) and integration over t yields

$$E(x,t) = \frac{\lambda N_0}{(\pi D)^{\frac{1}{2}}} \int_0^{t^{\frac{1}{2}}} exp(\frac{-x^2}{4D\eta^2} - \mu\eta^2) d\eta \tag{27}$$

which satisfies the initial condition that at $t = 0$, $E = 0$. Horenstein [23] provides a closed form of the integral of (27). The asymptotic form ($t \to \infty$) of (27) is given by

$$E(x,\infty) = \frac{\lambda N_0}{2(D\mu)^{\frac{1}{2}}} exp\{(\frac{-\mu}{D})^{\frac{1}{2}} |x|\}. \tag{28}$$

That is, the asymptotic distribution of eggs takes the form e^{-ax}, thus having a kurtosis of 6, characteristic of a leptokurtic distribution. This is one example which illustrates that in general a compound distribution differs from its parent distribution and often exhibits a leptokurtic pattern even if the parent distribution is Gaussian.

IV Further studies

The problem can easily be extended to two - or three- dimensional dispersal, where the asymptotic distribution is expressed in general by a modified Bessel function of the second kind,i.e, the so-called K-distribution. In this context, Yasuda [24] developed a mathematical model for a random walker who stop his movement at any time. The probability of stopping time of the walker is distributed according to a gamma law. The resultant distribution of dispersal distance is proven to be the K-distribution.

The present model, equations (24) and (25), is essentially the same as that of Broadbent and Kendall [25], who discussed the dispersal of larvae of the helminth $Trichostrongylus\ retortaeformis$.

The lavae are hatched from eggs in the excreta of sheep or rabbits and wander apparently at random until they climb and remain on blades of grass. There they may be eaten by another animal, in the intestines of which the cycle recommences.

The combination of (24) and (25) can be applied to the distribution of the larvae thus isolated on blades of grass. To this end, we regard S as the number density of lavae that are still free to perform a random walk,and E as the number density of the larvae that are settled upon blades of grass. Furthermore, we take $\mu = \lambda$. This means that the process of lavae climbing up and settling on blades of grass is considered as a loss of S with a constant rate μ, so that the population of free lavae lost becomes the population of lavae settled, E.

Williams [26] studied a similar problem, that of the distribution of larvae of randomly moving insects. Spatial distribution of eggs and larvae of insects constitute a subject of practical importance, and the study of mathematical modeling for them should be encouraged(e.g, a study due to Kuno [27]).

Other examples of dispersal problems are the propagation of plant or animal diseases carried by insects, and pollination by bees. Morris'[28] study of biased random movement in honeybees is noteworthy because it translated observations of individual bees into estimates of the advection velocity and diffusion coefficient in a standard advection diffusion model. By obtaining a numerical solution to this model, Morris [28] was able to predict the spread of pollen that had been marked with a dominant heavy anthocyanin gene and that hence showed up in progeny as "purplish" seedlings.

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ABSTRACT

Title of Paper

Kim,youn su

Major in Mathematics Education

Graduate School of Education

Sungshin Women's University

Supervised by Seong-A Shim, Ph. D.

The present thesis aim to explain the concept of "bio-diffusion" which is corresponding to the concept of physical diffusions like heat or temperature. Because of their abundance and their high mobility as compared to animals of similar size, insects are suitable for the study of dispersal. The study of insect dispersal plays an essential role in estimating the areal spread of damage caused by a newly invaded pest or the spatial distribution of insects. In this thesis we establish mathematical models that describes insect dispersal and estimate how accurate these models are compared to actual phenomena.