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The Development of a Spatially Explicit Landscape-Scale Model of Migration and its Application to Investigate the Response of Trees to Climate Change

by

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Declaration

The material contained within this thesis has not previously been submitted for a degree at the University of Durham or any other University. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Abstract

A spatially explicit model (MIGRATE) was developed to simulate the spread of a single species at the landscape scale. Current models such as forest stand models operate at a very small scale (typically less than one hectare) or at a very large scale as in the case of biome models. The biome models predict the final outcome to environmental change but give no indication as to how this state may be reached or how long it will take. The forest stand models show how successional changes may occur at a small scale but can not be used to predict changes involving species migrations that occur over tens of kilometres or more. MIGRATE is an attempt at bridging the gap between these two scales of modelling. It incorporates biologically meaningful parameters that have been identified as being the most important factors in determining migration rates and patterns.

The two-dimensional version of MIGRATE was applied to the particular problem of the response of trees to changes in both climate and land use. Data from the Institute of Terrestrial Ecology were used in order to create a model landscape that could be considered to represent a real landscape. The use of these data enabled both the effects of habitat loss and fragmentation and the effects of climate change to be explored. The simulation modelling work concentrated on the migration of *Tilia cordata* since its ecology is particularly well documented and its response to climate well understood. Results from these simulations showed that habitat loss and fragmentation could have a significant effect on the ability of trees to respond to future climatic change.

A one-dimensional version of MIGRATE was also developed as a tool for investigating the sensitivity of the model to the values given to its parameters. The palaeoecological record of the response of trees to past climatic change has indicated that they migrated at the remarkably rapid rates of 100 - 2000 m yr^{-1} (Huntley and Birks, 1983). However, due to difficulties in interpreting the fossil record there are areas of uncertainty regarding the exact nature of their migration. MIGRATE was used to attempt to address the particular question of whether migration occurred as a continuous front or by the establishment of small isolated populations with gradual infilling.

Attention is given both in the literature review discussed in Chapter 1 and in the field work described in Chapter 3 to the measurement of propagule dispersal distances since dispersal is believed to have played an important role in facilitating the rapid migration of trees in response to past climatic change.

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Table of Contents

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 1

INTRODUCTION

This chapter starts with a brief introduction to the subject area focussed on by the research presented in this thesis. The remainder of the chapter then provides reviews of the various topics relevant to the research.

1.1. General Introduction to the Area of Research

It is known from palaeoecological evidence that species responded to post-glacial climatic change through shifts in their distribution which enabled them to track the climate to which they are adapted. This change in distribution has been referred to as migration (Huntley and Webb, 1989). The research presented in this thesis has focussed on the development of MIGRATE, a simulation model which produces graphical output of the rates and patterns of the migration of a single species based on its reproductive and dispersal ecology and its interaction with the environment. It was intended that MIGRATE should be a spatially explicit model, operating at the landscape-scale. Current models operate at a scale which is either very small (for example, forest stand models) or very broad (for example, biome models). MIGRATE therefore represents an intermediate between these two extremes. Existing models will be discussed in order to put the MIGRATE model into context. It was the hoped to use MIGRATE to try to provide answers to some of the questions that the palaeoecological record can not satisfactorily answer alone, for example, did post-glacial migration occur by the progression of a steep continuous population front or by the establishment of small isolated populations with gradual infilling. In addition to using MIGRATE as a tool for investigating the processes involved in migration it was hoped to carry out some simulations which would enable investigation of the response of trees to both the effects of habitat loss and fragmentation as seen in the modern day landscape and the effects of anthropogenically induced global climatic change predicted for the next century. In conjunction with the modelling work, it was hoped to obtain values for the dispersal parameters required by MIGRATE through field studies. This area of research was given particular attention since early work by Skellam (1951) showed the importance of dispersal in facilitating the rapid rate of post-glacial migration of oaks.

1.2. Introduction to Ecological Modelling

The application of models to scientific problems is an area which has grown rapidly during the last forty years. Its development has been enhanced by advancements both in mathematical techniques and computer technology. A model may be defined as any abstraction or simplification of a real system (Hall and Day, 1977). A mathematical model is one in which the relationship between defined entities is described by a mathematical expression. One of the earliest and best known biological models is the Lotka-Volterra model which uses a pair of simultaneous differential equations to describe the relationship between predator and prey. Since this early model, ecological models have been developed to simulate a wide variety of ecological processes. The journal "Ecological Modelling" is dedicated to the subject.

Models provide scientists with a means of conceptualising, organising and communicating complex phenomena. This is particularly relevant to ecologists since ecological processes are often very complex and involve the interactions between a wide variety of organisms and their abiotic environment. Such interactions may be dynamic (i.e. vary with time) and may exhibit feedback mechanisms. In developing and experimenting with ecological models, ecologists may also increase their understanding of ecological systems. Many ecological problems are too complex to be solved by commonsense rules of thumb or by intuition. Models therefore provide a tool for predicting the consequences of an action that would be expensive, difficult or destructive to perform upon the real system. Ecological models have been used to predict the environmental impact of proposed actions by man, for example, in assessing the effect of electric power plants on aquatic environments. Hall and Day (1977) give case histories of the development and use of various ecosystem models.

More recently, spatially explicit models have been used as a tool for studying population dynamics in a heterogeneous landscape (Dunning *et al.*, 1995). These models incorporate the reproductive and dispersal characteristics of the species being modelled. The real environment is represented as a grid-based map which is created using a geographic information system. Such models have been used for making qualitative predictions regarding the response of one or more species to environmental change. In order to obtain quantitative predictions more accurate estimates of the parameter values are needed together with testing and further refinement of the models themselves. Some spatially explicit models are currently being applied to species conservation problems, for example, the effect of land management plans on the distribution of the northern spotted owl (*Strix occidentalis*) in Oregon and the control of the exotic bush lupin (*Lupinus* *arborea*) in California with the view to conserving the native dune plant, Menzies' wallflower (*Erysimus menziesii*) with which it competes (Turner *et al.*, 1995).

The use of sensitivity analysis in which parameter values are varied in isolation and combination enables identification of those parameters where accurate values are most important (Conroy *et al.*, 1995). Most ecological data, especially those on dispersal distances, are of poor accuracy (Mollison, 1991) so sensitivity analysis is a useful tool for determining where efforts in improving parameter estimates are best targeted. Model validation involves comparing the output of the model with independent observations. However, a good agreement does not necessarily imply that the model is correct, it could be coincidental. It is also possible for more than one model to give the same outcome (Conroy *et al.*, 1995).

Theoretical modelling and experimental research should be considered to share many similarities (Caswell, 1988). Models are constructed to improve our understanding of theoretical problems in the same way that experiments are used to increase our understanding of empirical problems. The same general principles which are used in experimental research can be applied to modelling.

1.2.1. Modelling Terminology

Stochastic versus Deterministic Models

There are two main types of model, deterministic and stochastic. Deterministic models always produce the same output for any given input. They do not therefore take into account the inherent variability of natural systems. Stochastic models, however, incorporate probabilities and random numbers with a statistical distribution. They are usually executed several times in order to obtain an average or 'most likely outcome'. The main advantage of stochastic models is that they can give an indication of the range and frequency of possible outcomes. It may be very important to know what the rare extremes might be. Stochastic models should only be used when chance plays an important role in the problem being modelled (Starfield *et al.*, 1990). Mollison (1986) stresses the importance of incorporating the effects of chance, especially when populations are small. The case for using a stochastic model needs to be carefully considered. In some cases deterministic models can be regarded as approximating a more detailed stochastic model. For example, if a population never becomes too small, then a deterministic model may closely resemble its stochastic equivalent (Renshaw, 1991). In order to test whether or not a deterministic model is an accurate predictor of what may happen in reality it is necessary to check that a series of results from a stochastic version of the model lie close to that predicted by the deterministic model (Renshaw, 1991).

Simulation versus Analytical Models

Models may also be classified as analytical or simulation models. Analytical models attempt to describe the whole problem using a single mathematical equation. Simulation models, however, break the problem down into smaller components, each of which is then represented mathematically. Models may be subdivided further according to the branch of mathematics they employ (Jeffers, 1982).

Variable Types

Models are composed of state variables, driving variables and output variables. The measurable properties (for example, biomass, age, number of individuals etc.) are the state variables. Their value varies with time in accordance with changes in other variables which constitute the system. The complexity of a real-world system may be simplified by aggregating processes and components that are similar into single state variables. Some aggregation may be necessary as data may not be available to provide estimates for all the required parameters. The degree of aggregation possible also depends on the output required. Driving variables are those which act upon the system from outside, for example, climatic factors. They may also be referred to as forcing functions or exogenous variables. The output variables are the quantities that the model is required to predict.

1.2.2. Outline of the Tasks Involved in Modelling

The process of developing a mathematical model may be broken down into a series of logical steps (Jeffers, 1982).

1. The setting of goals and objectives and definition of boundaries.

2. The production of a written description ("word" model) which describes what is known about the system to be modelled. This should include the components, interactions and mechanisms that operate and may state any assumptions that are to be made. It may be based on pure logic or experience/data already collected.

3. The production of a diagrammatic model which takes the form of a flow chart and may use special symbols to indicate the relationship between variables.

4. The construction of mathematical formulae which describes the relationships between the variables.

5. The implementation of a computer program which incorporates the mathematical relationships.

6. The validation of the model. This may involve checking the results of the model against existing data which have not been used in the determination of any of the model's parameters or using the model to make predictions which may be compared with the real system when such conditions occur or are made to occur in the future.

The Institute of Terrestrial Ecology has produced a checklist of points to consider when modelling (Jeffers, 1982).

1.2.3. Simple versus Complex Models

Ecological models have been the subject of much criticism, often on the grounds that they are not sufficiently realistic to be applied to real situations. Even some of the most widely accepted models such as the Lotka-Volterra predator-prey model and the density dependent stock recruitment model used in fisheries are only superficially supported by data from the literature (Hall, 1988). The data used to support some of the historically most influential models used in ecology are reviewed by Hall (1988). Abstract models such as these are often so general that they omit the key factors of specific situations. In order to make abstract models more realistic they need to explicitly consider the individual processes which make up the system. A realistic model is one that accounts for as much of the knowledge of a population or community structure and function as possible. Therefore in order to be realistic, models are often complex (Onstad, 1988). DeAngelis (1988) discusses an approach based on envirograms for breaking up the problem to be modelled into its mechanistic components. An envirogram has been described as "a dendrogram whose branches trace the pathways from distal causes in the web to proximate causes..." (Andrewartha and Birch, 1984). Only when a model includes all of the process known to be involved in the system being modelled can the model be used as a tool for making predictions. However, before this is done, the model should be tested as far as possible using data from the field in order to verify that all the important processes are being correctly modelled. In the absence of sufficient data and/or tested ecological theories, it may be necessary to develop simple models and then let empirical testing indicate the limits of applicability (Onstad, 1988).

Mollison (1986) emphasises the importance of keeping the structure of models as clear and simple as possible. For example, the components of a model of population spread should have straightforward ecological interpretations such as, net population growth rate, dispersal distribution etc. It may be found that the results of a model with a large number of parameters actually depends on a subset of parameters which dictate the model's behaviour. It may also be more difficult to analyse the behaviour of a model with a large number of parameters. In modelling the spread of rabies, Murray (1987) warns that:

"a model which incorporated all the possible aspects of the epidemic would be impossible to use, since nothing would be known about many of the parameters, nor would there be much hope of estimating them with the data available."

Rastetter *et al.* (1992) discuss ways in which fine scale ecological knowledge can be aggregated and used in coarser scale ecosystem models. They suggest that aggregation is likely to result in some loss in model accuracy, however, this may be balanced by the loss in precision which would have arisen through the accumulation of errors associated with the estimation of the larger number of parameters in the more complex model.

More complex models are usually easier to relate to realistic situations and have parameters which are easier to measure (Onstad, 1988). However, if the required parameters are difficult to measure or have a high degree of variability then the predictive value of the model will be reduced. Simple models are highly aggregated and can therefore only be applied to the specific situations for which their parameters were determined. They can, however, be useful in enabling one to understand the relative importance of the components making up the system being modelled.

In conclusion, it seems that a sensible compromise needs to be made in deciding how complex a model should be. This decision should be based upon the depth of understanding of the system being modelled and the accuracy with which the required parameter values can be determined.

1.3. Historical Record of Tree Response to Climatic change

There is a large amount of fossil evidence mostly in the form of pollen which can be used to gain an insight into the post-glacial response of plants to climatic change. In particular the pollen record provides data on the rates of geographic spread, population growth and the competitive interactions of migrating plants (MacDonald, 1993). It has been suggested that palaeoecological studies of the response of plants to post-glacial climatic change may provide an understanding as to how plants may respond to future climatic change. However, the interpretation of the pollen record is not easy as there are many potential sources of uncertainties. The application of palaeoecology to the study of plant invasions and the problems involved in interpreting the pollen record have been reviewed recently by MacDonald (1993).

1.3.1. Past and Predicted Future Climatic change

According to the Milankovitch Theory, historical climatic changes have been induced by changes in the orbital geometry of the Earth. These cycles produce glacial periods lasting approximately 100,000 years and interglacial periods lasting approximately 15,000 years (Gribbin, 1988). It is now generally believed that the anthropogenic increase in the concentrations of greenhouse gases will cause a warming of the Earth in the next century (Ratcliffe, 1995). The Intergovernmental Panel on Climate Change (IPCC) predict that an effective doubling of carbon dioxide concentration will occur by between 2030 and 2050 if present trends continue. Predictions made using General Circulation Models suggest that a doubling in the concentration of carbon dioxide will cause global mean temperatures to rise by around 1.5-4.5°C. The IPCC best guess is a 2.5°C increase in global mean temperature (Houghton *et al.* 1990, 1992). The variations in the GCM predictions are largely a consequence of the uncertainties associated with the modelling of moisture, clouds and changes in albedo (Ratcliffe, 1995). The GCMs also predict that the warming will be greatest near the poles and that there will be changes in precipitation and prevailing winds. There may also be an increase in the number of storms. The rate of predicted climatic change due to an increase in greenhouse gases is likely to be 10-100 times faster than the rate of post-glacial warming (Schneider, 1989).

1.3.2. Palaeoecological Evidence of Past Response to Climatic change

The palaeoecological record provides a valuable resource for studying the response of plants to the climatic changes of the past. Much of the evidence comes from the palynological record as pollen grains have been well preserved in the fossil record. Various workers (for example, Huntley and Birks, 1983; Birks, 1989; Davis *et al.*, 1991) have used pollen data to map the range extension of trees since the last glacial maximum (18,000 yr. BP). The remains of fossil tree stumps have also been studied (Gear and Huntley, 1991). The results of such studies have enabled ecologists to understand how trees have responded to climatic change in the past and therefore predict how they may respond in the future.

The palynological record has been used extensively to show the response of different taxa to climatic change. Huntley and Birks (1983) have produced isopoll maps for European taxa. These show the spatial distribution of a pollen taxon and its relative abundance pattern. A similar technique adopted by Davis for North America uses isochrone maps in which isolines are drawn to connect localities showing a first consistent sharp ten fold increase in pollen values at the same time (for example, Davis 1981, 1983a). Birks (1989) has also used isochrone maps to show the migration of trees in the British Isles.

1.3.3. Difficulties in Interpreting the Pollen Record

Very low pollen counts may be due to either the presence of small local source populations or long-distance dispersal from a large population. It is often not possible to decide which case applies. The use of different criteria for determining the presence of a plant species near a fossil pollen site may result in markedly different reconstructions of plant migration. For example, Davis (1983b) mapped the spread of *Fagus grandifolia* in North America as occurring as a gradual northward migration, however, Bennett (1985) produced a map for the same region and concluded that there had been an early rapid spread of *Fagus grandifolia* through the establishment of small isolated populations. These two different reconstructions are a result of the fact that Davis (1983b) used the time at which there was a sharp increase in *Fagus* pollen whereas Bennett (1985) used the first continuous deposition of pollen (MacDonald, 1993). Davis considers the early deposition of small quantities of pollen to have been a consequence of dispersal from large distant populations, whereas Bennett believes it to have been due to the local presence of trees.

Davis *et al.* (1991) have investigated the problem of determining range boundaries from the fossil record. They compared U.S. Public Land Survey maps of tree distribution prior to clearance by man with pollen data from the same period. This enabled them to identify an area 20 km wide which enclosed the range limit of *Fagus* and *Tsuga.* Pollen counts were expressed as percentages of the total arboreal pollen grains present in the sample. At least 300 arboreal pollen grains were counted. Intermediate pollen of 1-4% lying within 20 km of the limit were bounded by high pollen counts of greater than 4% within the species range and very low pollen counts of 0-1% 20 km beyond the range limit. It was not possible to identify small outlying populations within 20 km of the main population limit due to the blurring effects of pollen from the main population. Very low pollen counts (0-1%) outside the main population limit may provide evidence for small outlying populations or a very sparse distribution of the taxa. However, in order to support the hypothesis of the existence of small outlying populations it is necessary to use a dense sampling grid in order to show that the proposed outlying population is surrounded by an area of consistently lower pollen count. This is not often possible due to a lack of suitable sites (MacDonald, 1993).

Taxa also vary in the relative amounts of pollen they produce, how far their pollen may be dispersed and how well it is preserved in the fossil record. All these factors need to be taken into account when interpreting the fossil record (Sauer, 1988 pages 145-146). For example, the pollen deposited in lakes comes from plants growing within a few metres to tens of kilometres from the shore. It has been shown that the size of the pollen source area for a lake is dependent on the settling velocity of the pollen taxon and the diameter of the lake (for example, Prentice, 1988).

Plant population densities of less than 1 ha^{-1} can not be reliably detected in the pollen record. This means that a species could exist undetected outside the range boundary determined from the pollen record (Bennett, 1986). Differences in population growth rates might affect the time between when a species first invades and when it is detected in the pollen record. This time lag is of the form:

$$t_{lag} = a\alpha^{-1} \tag{1.1}$$

where t_{lag} is the lag between the establishment of the species and the time when the population density reaches the required size for registration in the pollen record, a is a constant related to the population density required for the detection of the species in the pollen record and α is the intrinsic rate of population increase (MacDonald, 1993). Regional differences in population growth rates may therefore produce spurious estimates of migration rates.

Another area of uncertainty lies in the form of the relationship between pollen abundance and plant population size (Huntley, 1992). Bennett (1983, 1986, 1988a), suggests that the sigmoid curve of pollen accumulation rates is a result of local population growth whereas Davis and Sugita (submitted) suggest that it is a consequence of the linear increase in the area occupied and that the actual shape of the sigmoid curve is determined by the migration rate, the dispersability of the pollen and the size of the lake from where the pollen sample was taken. However, in contrast to Bennett (1983, 1986, 1988a), Davis and Sugita (submitted) consider migration to occur by the progression of a well-defined steep population front. MacDonald (1993) suggests that the form of the relationship between pollen abundance and population size could be highly dependent on the spatial configuration of invading plants relative to the sampling site. If population growth occurs by the establishment of many small populations then the pollen record may provide a reasonable estimate of plant population growth rates. Under these circumstances the potential bias introduced by the leptokurtic pollen depositional gradients will be mitigated by the contemporaneous establishment of both nearby and distant individuals (MacDonald, 1993).

Other areas of uncertainty include the reliability of the radiocarbon dates from lake sediments and the effect of sediment mixing. Finally, some pollen grains can only be identified down to the level of genera (for example, *Pinus* and *Quercus*) so any reconstructions based on the pollen record may reflect the response of more than one species and must therefore be interpreted with caution (MacDonald, 1993).

1.3.4. The Response of Trees to Climatic Change (Migration versus Evolution)

The palaeoecological record indicates that species respond to climatic change by "migrating". Palaeoecologists have used migration in this context to describe the movements of populations of forest trees in response to long-term environmental change (Huntley and Webb, 1989). Migration enables species to track environmental change and thus continue to occupy the environmental space to which they are adapted (Huntley, 1989). Some workers prefer to refer to "spread" or "range extension" to describe the establishment and directional movement of a taxon into a new geographical area (for example, Bennett, 1985; Birks, 1989). Diffusion has also been used to describe species spread by Pielou (1977).

Huntley *et al.* (1989) have used pollen response surfaces for *Fagus* to show that climate is the major determinant of its distribution and that it responded to past climatic change by migration rather than evolution. Pollen abundance was plotted onto a graph with mean July temperature and mean January temperature forming the axes. Response surfaces produced for *Fagus* spp. using contemporary data have been used to successfully predict the present pollen abundance pattern using current climatic data. This implies that climate plays an important role in determining the present patterns of distribution and abundance. In addition, response surfaces for *Fagus* in North America correctly predict the distribution of *Fagus* in Europe and vice versa, despite the two species having been separated between 25 and 10 My ago. This therefore supports the theory that trees respond to climatic change by migration and not evolution.

Present knowledge of dispersal, vegetation dynamics and population growth also supports the hypothesis that trees respond to climatic change by migration and not evolution. The long life span of trees probably acts as a major limitation on their ability to evolve. The rates of evolutionary change are too slow to enable species to respond to climatic change (even though the cycles of climatic change are in the order of 100,000 years). However, species have evolved over time to deal with climatic change by developing mechanisms which facilitate migration (Huntley and Webb, 1989).

A comprehensive account of plant migration is given by Sauer (1988). The descriptions of migration illustrate the importance of long-distance dispersal agents. Birds and humans are thought to have often played a significant role. In the northern hemisphere, north flowing rivers were also believed to have been important.

1.3.5. Rates and Patterns of Migration

From isopoll and isochrone maps it is possible to calculate the migration rates of trees as being in the order of 100-2000 m yr^{-1} (Huntley and Birks, 1983). The consistency of these realised rates between different geographical areas implies that these rates may be the maximum achievable. Bennett (1986, 1988a) suggests that these rates may not be equal to the rate of migration at the range margin because pollen levels there are too low to be recorded in the fossil record. He therefore suggests that rates of spread determined from the pollen record should be referred to as rates of spread of the taxon at a given threshold density above which the taxon can be detected. It is quite possible that the spread of a species may have taken place at population densities too low to be visible in the pollen record (Bennett, 1986, 1988a, b).

The maximum migration rates simulated by a model of tree migration in response to climatic change should be comparable with those estimated for post-glacial migration since these are thought to represent the maximum rates achievable. However, it is unlikely that trees will be able to migrate as fast as they did during post-glacial warming due to a reduction in natural dispersal agents and a decline in the availability of suitable sites (Davis, 1989). Man-made features of the modern environment, such as areas of intensive agriculture and urbanisation may pose significant barriers to species trying to migrate between fragmented habitats. Future changes in land use could be important in governing the rates of migration, for example the creation of wildlife corridors and tree planting schemes such as the creation of community forests.

Two models have been suggested for the pattern of tree migration. The outlier model suggests that populations spread by the formation of small outlying populations with gradual infilling. Supporters of this model (for example, Godwin, 1975; Watts, 1973; Tsukada, 1982a, b; Bennett, 1983, 1986, 1988a, b) believe that the initial low pollen abundance values are due to the presence of a small number of local trees and that the subsequent sigmoid pollen abundance curve is a direct result of local population increase. The continuous front model supported mainly by Davis (for example, Davis, 1976, 1981, 1983a, b; Davis and Sugita, submitted), predicts that migration occurs as a more or less continuous front and that the initial low pollen abundance values are due to the long distance dispersal of pollen. It is important to consider the pattern of migration in the context of scale, since the discontinuous expansion of a range limit may appear to be continuous at a broader scale.

Isopoll and isochrone maps imply that populations migrate as a continuous front, however, if as Bennett (1983, 1986, 1988a, b) suggests, there is a sparse distribution of trees beyond the range limit deduced from the pollen record, then migration may have occurred by the expansion of small populations of trees beyond the range boundary of the main population. If Bennett is correct then the rate of migration as detected by the pollen record will be limited by the rate of population increase and not by dispersal. The realised rate of spread may also be greater than the rate determined by the pollen record if spread occurs by the establishment of small outlying populations with gradual infilling.

Mack (1985) has shown that many small isolated populations spread faster than a large single population. This is because many small populations have a greater total circumference than a single large population occupying the same total area, therefore a greater proportion of their propagules fall into the adjacent unoccupied areas. Therefore relatively rare long-distance dispersal events coupled with local population increase and spread may help to explain how the fast post-glacial migration rates were achieved

1.3.6. Individualism

Isopoll and isochrone maps also show that species exhibit very individualistic responses to climatic change (Davis, 1976; Huntley and Birks, 1983; Birks, 1989). The individualistic nature of the response means that species have different time constants of response resulting in lags in range expansion in the order of years to decades (Davis, 1976). This results in communities being temporary assemblages of taxa (Huntley, 1989, 1991).

1.3.8. Lags in Migration

Migration rates may have lagged the rates of climatic change resulting in a disequilibrium between the migrating species and climate. The extent and cause of such lags is still under debate. One school of thought believes that lags may not have represented disequilibrium but may have been due to the different regional patterns of temperature and precipitation change i.e. climatic restrictions prevented migration into areas which may superficially have seemed suitable. Another group believes that the lags were real and caused by factors such as limitations in dispersal, rate of population increase, soil development, disturbance and problems in establishing and competing with the present occupier of space. Prentice *et al.* (1991) have used response surfaces which describe the relationship between surface pollen percentages and climate to infer past climates from palynological data. Their results lead them to conclude that at the continental-scale with a time resolution of 3000 years, vegetation patterns responded to continuous changes in the climate from the last glacial maximum to the present, with lags no greater than about 1500 years.

The role of dispersal and climate in the range expansion of *Fagus* has been investigated in North America (Davis *et al.*, 1986). Johnson and Webb (1989) have reviewed the role of blue jays (*Cyanocitta cristata* L.) in the post-glacial dispersal of fagaceous trees. They conclude that dispersal by blue jays should have allowed *Castenea, Fagus* and *Quercus* to migrate in equilibrium with climate.

1.3.9. Comparison with Succession

Much of the subject matter on recent plant migrations is shared with ecological studies of succession. However, succession is usually regarded as a change in a community as a whole within fixed spatial borders (Sauer, 1988).

1.4. Factors Controlling Rates and Patterns of Spread

Both biotic (for example, dispersal and competition) and abiotic (for example, climate and soil) constraints may have played important roles in influencing the patterns of spread at different spatial and temporal scales (Birks, 1989).

Work by Brubaker (1986) indicates that the following factors were probably important in controlling the response of trees to climatic change:

- life spans and length of juvenile period;
- seed productivity;
- seed dispersability;
- phenotypic plasticity;
- genetic variability;
- competition;
- disturbance.

The ecological literature holds a wealth of data on the life history characteristics of many tree species. There is also a great deal of data to be found in the silviculture literature, for example, Savill (1991). Researchers at the University of Sheffield have constructed a database on the field behaviour of most native plants which include some tree species (Grime *et al.*, 1988; Grime, 1992).

1.4.1. Role of Climate in Controlling Species Distribution

The distribution of species is primarily governed by climate. Minimum winter temperature, growing degree days and water balance have been shown to be the most important factors in determining broad-scale vegetation patterns. Evidence supporting this comes from the results of global vegetation prediction models based on the response of major vegetation types to climatic variables (for example, Woodward and Williams, 1987; Woodward and Mckee, 1991; Prentice *et al.*, 1992) and from work on climate response surfaces (for example, Huntley *et al.*, 1989; Beerling *et al.*, 1995).

Studies of physiology and growth response of species have shown the importance of:

- freezing tolerance;
- growing season length;

- drought intolerance;
- critical conditions for the completion of particular stages in the life cycle.

1.4.2. Rate of Population Increase

If trees did exist as small isolated populations then the rate of population increase could have been a major factor limiting spread. The major factors limiting the rate of population increase are the time taken to reach reproductive maturity, reproductive output and probability of survival to maturity (Brubaker, 1986).

Bennett (1988a, b) suggests that some species may have existed for some time at population densities too low to be recorded in the pollen record. As the climate improved, these populations would have increased in size. Their rate of migration as determined from the pollen record would therefore have been limited by the intrinsic rate of population increase.

Bennett believes that the early low levels of pollen recorded in the fossil record represent the expansion of local tree populations and not long-distance dispersal from a large distant population as is thought by other workers (for example, Woods and Davis, 1989). He has plotted graphs of pollen accumulation rate against time and fitted exponential or logarithmic curves to the data as appropriate. He has then used the data to determine population doubling rates in the order of 20-500 years.

$$\text{doubling time} = \frac{\ln 2}{\alpha} \qquad (1.2)$$

where α = intrinsic rate of population increase.

These results agree with those from modern day observations (Bennett, 1986, 1988). This approach has also been used by Tsukada (1982a, b), who obtained similar results.

1.4.3. Competition

Competition from existing vegetation may have been an important factor where trees were migrating into forested areas. In particular, light limits the establishment of new trees (Brubaker, 1986). Therefore the migration rate of late successional trees may have been slowed down by competitive interactions with existing species. For example, Kullman (1981) noted that the rate of expansion of *Pinus sylvestris* was faster in sparse stands of *Betula pubescens* than in dense stands. In general, however, competition is not thought to have played an important role in controlling the response to climatic change during the Holocene. For example, Davis (1976) suggests that the rapid rates of migration and the apparent ease with which established communities were invaded are indications that competition was not a major barrier to most invaders. Huntley *et al.* (1989) have used climate response surfaces to show that the distribution of *Fagus* is primarily determined by climate in both North America and Europe. The distribution is insensitive to the presence or absence of *Tsuga* which has a close association with *Fagus* in eastern North America.

Evidence of the occurrence of interspecific competition may also be obtained from the pollen record. If the arrival of a new taxon corresponds with decreases in pollen concentrations or accumulation rates of taxa already present then there is evidence that competitive displacement has occurred. For example, Bennett and Lamb (1988) analysed pollen sampled from sites in Fennoscandia and observed a decrease in the pollen accumulation rate for *Betula* which was accompanied by an increase in the pollen accumulation rate for *Pinus*. They suggested that this could be explained as the competitive displacement of *Betula* by *Pinus*. Delcourt and Delcourt (1987) used a population model to test for a competitive interaction between *Fraxinus nigra* and the taxa *Ostrya* and *Carpinus*. Using values of the intrinsic rates of population increase and equilibrium densities obtained from the pollen record they fitted values for the interspecific competition coefficient by *Ostrya/Carpinus* on *Fraxinus nigra* and found that it was nearly twice as high as the coefficient of intraspecific competition for *Fraxinus nigra*. MacDonald (1993) warns that care should be taken in attributing such observations to competition as other factors such as climate could be involved in the apparent concurrent rise in one taxon and fall in another.

Prentice (1989) suggests that the broad-scale distribution of taxa is controlled by climate and not by competition because within large areas of vegetation there are a range of microhabitats which are suitable for the establishment and growth of different taxa. However, at the smaller scale of the stand or vegetation patch the species composition will be determined by several non-climatic factors such as interspecific competition, succession and time since disturbance. Malanson (1993) suggests that competition will probably play an important role in the future, since the predicted climatic changes are likely to occur over a much shorter time scale than those of the Holocene. Competition is thought to be more important than climate in determining the southern range limit of species (in the northern hemisphere).

1.4.4. Disturbance

Those trees which invaded later were forced to migrate across forested terrain. Huntley (1989) refers to them as secondary migrants and proposes that their rates of migration may have been limited by the rate of gap formation in the existing forest canopy.

Experiments with forest simulation models have shown that disturbance plays an important role in facilitating the change in community composition in response to climatic change (Overpeck *et al.*, 1990). Disturbance probably increases the response time of ecosystems to climatic change by eliminating resident long-lived individuals and allowing organisms which may be better adapted to the changed climate to invade (Davis, 1989). It is probable that the future climate will show an increase in disturbance events. In addition to an increase in the number of gales which create gaps caused by windthrow, there may be an increase in fire due to a combination of summer drought and thunderstorms.

1.4.5. Dispersal

The first species of trees to migrate had to become established in unforested terrain. Huntley (1989) refers to these as primary migrants and suggests that their rate of migration was limited by their dispersal capacity.

The definition of dispersal as given in the Oxford dictionary implies that something which was concentrated is spread about more evenly. However, dispersal usually achieves a strikingly uneven distribution (Harper, 1977). Seed dispersal may be classified into local dispersal within the present habitat and long-distance dispersal outside the present habitat. Local dispersal enables propagules to escape competition with parent plants and reduces density dependent mortality. In contrast, long-distance dispersal may bring about the colonisation of new habitats. The distinction between local and long-distance dispersal may be quite arbitrary (Sauer, 1988). Some examples of observations of long-distance dispersal are given in Table 1.1.

The modern existence of outlying populations of beech and the establishment in the past of outliers beyond water barriers, implies that long-distance dispersal occurs at a non-trivial frequency (Woods and Davis, 1989). Palaeoecological research by Davis *et al.* (1986) suggested that *Fagus* (animal dispersed) and *Tsuga* (wind dispersed) were dispersed distances of over 100 km. They argue that such long dispersal distances were not unreasonable as colonies of *Tsuga*, apparently established within the last several thousand years, exist today in Minnesota, 50-150 km west of the main range limit in Wisconsin. Kinloch *et al.* (1986) have also suggested that the establishment of a disjunct population of *Pinus sylvestris* in Scotland 300 km from the main population in England was most likely to have been due to rare long-distance dispersal. The alternative hypothesis that the Scottish population expanded from a small indigenous source which survived the last glacial period is considered to be very unlikely. Webb (1986) suggests that tornadoes at the right time could transport seeds of all sizes 50 km or more.

In Europe, the rapid migration rates of *Alnus* (500-2000 m yr^{-1}) and *Corylus* (1500 m yr^{-1}) may be explained by transport along rivers. Even a relatively slow flowing river (1 m s^{-1}) would carry fruit 3.6 km in 1 hour and over 80 km in a single day (Huntley and Birks, 1983). This mechanism may also explain why such rapid rates of spread are not observed in eastern North America since many of the major rivers flow eastwards or southwards (Davis, 1976).

The recolonisation of the volcanic island of Krakatau also illustrates how effective long-distance dispersal can be (Ernst, 1908). All the vegetation on Krakatau was destroyed by the volcanic eruption which took place in 1883. Krakatau is separated by 19-25 km from the neighbouring islands of Sebesi and Seboekoe (half-destroyed by the 1883 volcanic eruption) and 35-45 km from the nearest points of the Java and Sumatra coasts. However, despite this an expedition three years after the 1883 eruption found algae, ferns, mosses and eight species of flowering plants, six of these (two grasses and four compositae) were obviously transported by air currents since their seeds are light and show special adaptations to wind dispersal.

Several classic studies on dispersal have been carried out. For example, Ridley (1930) gives values for the furthest distance covered by a seed from its source for various species. He notes that the height of a tree is important in determining its maximum dispersal distance and that the size of a tree (not its age) will determine when it will first fruit. Another classic account of dispersal is given by Van der Pijl (1972) who describes in detail the various modes of dispersal. Mechanisms for dispersal include sea and rivers (hydrochory), animals (zoochory), wind (anemochory) and humans.

Table 1.1. Some observations of long-distance dispersal events for various wind and animal dispersed trees.

Species	Observed long-distance dispersal event
Acer pseudoplatanus	Seeds carried 85 m in a 'tolerably' strong breeze (Ridley, 1930).
Acer spp.	Maple samaras found in the Alps which were 4 km from their nearest source (Vogler, 1901).
Betula pendula and *Betula pubescens*	Establishment at low densities at 500+ m from parent trees (Miles, 1988).
Fagus grandifolia	Jays observed to carry nuts up to 4 km from source (Johnson and Webb, 1989).
Pinus edulis	Clark's nutcracker observed caching seeds 22 km from source area (Vander Wall and Balda, 1977).
Pinus sylvestris	Saplings found over 3 km from the nearest seed source (Welch et al, 1990).
	Young trees found up to 810 m from the forest edge in Tentsmuir in Fife (Smith,1900).
	Establishment at low densities at 500+ m from parent trees (Miles, 1988).
Pinus spp.	Individuals frequently recorded at distances of up to 8 km from nearest source (Ledgard, 1988).
	Individuals observed up to 25 km from source (W.G. Lee pers. comm. in Richardson *et al.*, 1994).
Quercus palustris	Jays observed to carry nuts up to 1.9 km from source (Johnson and Webb, 1989).
Quercus spp.	An isolated tree on the island of Hoy in Scotland must have dispersed at least 16 km (Jones, 1959).

1.5. Field Studies of Seed Dispersal

Most dispersal studies on trees have involved either single isolated trees (for example, Cremer, 1965; Augspurger, 1984) or dispersal from the edge of a forest clearing. Isolated trees may be difficult to locate, especially in regions of low tree diversity and they may not exhibit recruitment processes which are representative of the species being investigated. The pattern of seed dispersal from forest margins may be different to that of isolated trees (Harper, 1977). It is difficult to study a tree in a more or less continuous stand because of the problem in distinguishing its seed from that of others of the same species which are dispersing into the same area. This problem could be overcome by using paints, dyes or isotopes to mark seeds before dispersal (Harper, 1977). Another approach to this problem has been the application of maximum likelihood analysis to match values in dispersal functions to observed field observations (Ribbens, 1994). Most field studies have looked only at primary dispersal i.e. the movement of seeds from the parent plant to their first site of repose (Chambers and MacMahon, 1994). The subject of secondary dispersal is reviewed by Chambers and MacMahon (1994) who conclude that this is an area where much more research is needed if the ultimate fate of seeds is to be understood.

Various workers (for example, Roe, 1967; Boyer, 1958; Hughes and Fahey, 1988) have carried out seed trapping experiments which have shown that seeds are dispersed according to a negative exponential distribution (i.e. seed density decreases at a constant percentage over equal units of distance) with half distances occurring in the range 8-68 m. Results from these studies have lead to the conclusion that most seeds fall within a few hundred metres of the canopy (for example, Boyer,1958; Brown and Neustein, 1972; Mair, 1973; Miles, 1988; Pigott, 1991). Most of the studies on seed dispersal by trees have been done on commercial forest species since foresters need information on seed dispersal in order to be able to effectively use natural regeneration as a means for restocking areas cleared of trees. Isaac (1930) claims to have done the first field study on seed dispersal. He carefully details the procedures he used, including how to construct the seed traps, so that they may be followed by subsequent workers. A large number of studies have since been carried out in the United States, mainly by their Forestry Service. Very few British studies have been done and most of these have focussed on sitka spruce (Mair, 1973).

Isaac (1930) carried out experiments in which seeds were artificially released under known conditions. He showed that a doubling of the height of release more than doubles the distance of seed dissemination. This is largely due to the higher wind velocities at greater elevations. He also collected data which showed that an increase in wind speed had it greatest effect on the maximum dispersal distance. These results are given in Table 1.2.

Table 1.2 Relationship between wind speed and dispersal distance for Douglas fir.

wind speed (miles per hour)	mode (m)	maximum distance (m)
6.5	300	540
8.0	390	780
23.0	480	960

Mair (1973) used seed traps to investigate the dispersal of sitka spruce (*Picea sitchensis*) seeds from the forest edge. A small artificial trial was carried out in which seeds were released from a height of 15 m under three different, but known wind speeds. The results from the artificial trial were similar to those obtained from the seed trapping studies of the natural seed fall. Both studies showed that most of the seed is deposited within 20 m of the source. During his field studies, Mair (1973) observed the effects of turbulence which caused seeds to be lifted higher into the air thus increasing their dispersal potential. Siggins (1933) observed the same phenomenon when carrying out experiments on the dispersal of conifer seeds.

The dispersal distances measured by Isaac (1930) and Mair (1973) are considerably shorter than those noted as examples of long-distance dispersal. This may be because the occasional high winds that result in long dispersal distances occur too infrequently to be observed during field studies. Turbulence is also thought to be responsible for the occasional long-distance transport of seeds.

Johnson (1988) has studied the dispersal of *Acer saccharum, Fraxinus pennsylvanica* and *Tilia americana* in abandoned agricultural fields in Wisconsin. The seed source was either an isolated individual or a row of trees in a hedge row (linear source). Instead of carrying out seed trap studies, Johnson counted the number of seedlings occurring in quadrats along transects from the seed source into the abandoned fields. It was found that the seedling density curves for one-year old and all aged seedlings approximated to the negative exponential. However, if the survival of the seedlings was followed over a longer time period then the shape of the recruitment curve could alter significantly due to density and distant dependent mortality. Johnson (1988) also suggests that the slope of the seed and seedling density curves should be similar if the micro-environmental conditions for germination and survival and the spatial distribution of seed predators are both reasonably uniform along the distance axis. A similar study has been carried out by Welch *et al.* (1990) on the invasion of Scots pine (*Pinus sylvestris*) into moorland in the Cairngorms National Nature Reserve in Scotland. They found saplings at distances greater than 3 km from the source. The major problem with this method of investigating dispersal is therefore the selection of a suitable study site where these conditions apply. This type of study could be used to give estimates for the dispersal parameters of trees. However, the values estimated would depend on the environmental conditions affecting germination and recruitment as well as the initial seed distribution. It would be better to separate seed distribution from seedling recruitment since they are affected differently by environmental conditions. If, however, the initial seed distribution were known then the probabilities of seedling survival with respect to dispersal distance from the parent plant could be quantified.

Some work has also been done on the dispersal of seeds by animals. This has either involved direct observations of animals dispersing propagules or the use of radioactive isotopes to label propagules. The former technique has been successful in recording long-distance dispersal events (for example, Vander Wall and Balda, 1977) whereas the latter has been used to look at more local dispersal distances (for example, Vander Wall, 1992). Johnson and Webb (1989) suggest that for bird dispersed species such as the Fagaceae the observed dispersal distances will depend on the habitat structure of the landscape. For example, maximum dispersal distances would be expected in a landscape where large isolated nut sources are intervened with habitat suitable for nesting. Propagules dispersed by animals are also often cached in places favourable for regeneration.

1.6. Models of Seed Dispersal

It is generally accepted that the deposition of seeds dispersed by wind decreases exponentially from the source. However, the pattern of seed dispersal by animals may be different since seeds are more likely to be dispersed at centres of animal activity (Stiles, 1989). Despite this, dispersal models based on stochastic diffusion processes which may seem more appropriate for wind-dispersed propagules may be a good approximation for animal-dispersed propagules since, for sufficiently large distances enough "random" effects would occur to make such models a good enough representation of reality (Portnoy and Willson, 1993).

Most anemochorous seeds and fruits are adapted for wind dispersal by having features which reduce their rate of descent. This makes them sensitive to variations in wind velocities which are of the same order of magnitude as their terminal velocities (Burrows, 1975). The pattern of propagule dispersal is therefore dependent on air flow and can be expected to vary between sites depending on meteorological conditions, local topography and the aerodynamic characteristics of the surface over which dispersal is occurring.

1.6.1. Empirical Models

Empirical models attempt to fit mathematical formulae to experimentally measured dispersal gradients. The main disadvantage of this type of model is that they provide no way of extrapolating from one situation to another based on independently measured parameters. Empirical models include the inverse power law ($y = ax^{-b}$) and the negative exponential ($y = ae^{-bx}$) both of which have been widely used in dispersal modelling. These describe the asymptotic distribution of seeds, spores or pollen from a point source (McCartney and Fitt, 1985, 1986; Okubo and Levin, 1989). Both these models predict that seed density decreases by a constant percentage over equal units of distance. They are also examples of the general exponential model:

$$y = ae^{-bx^{n}} \tag{1.3}$$

where y = density associated with dispersal, x = distance from source, n = power function which determines the shape of the curve and a and b are constants (McCartney and Fitt, 1985).

In the case where $n = 2$, the corresponding model is a bivariate normal distribution:

$$y = \frac{a}{2\pi s^2}\exp\left(\frac{-x^2}{2s^2}\right) \tag{1.4}$$

This assumes that there is a normal distribution around a point source with variance s^2.

Although the inverse power law and the negative exponential have been more widely used, the general exponential model may give a better fit to a given set of data since the curve can take variable shapes. The inverse power law tends to over estimate deposition near the source since as $x \rightarrow 0$, $y \rightarrow \infty$. It may therefore be unsuitable for spread with steep density gradients. In contrast, the exponential model tends to under estimate deposition near the source, but does predict finite values for y at all distances (McCartney and Fitt, 1985).

McClanahan (1986) has developed a simple model of seed dispersal based on the negative exponential model. This model simulates the dispersal of seeds to the surrounding environment based on the size of the seed source(s) and their proximity to the area under investigation. The density of seeds arriving at a location is given by:

$$Q_d = \sum_{i=1}^{n} Ce^{-kd_i} \tag{1.5}$$

where Q_d = density of seeds at distance d_i from the seed source; k is a measure of the species dispersal capacity and C = density of seeds at distance zero from the source.

k is equal to the gradient of the logarithmically transformed dispersal curve. It may also be calculated from:

$$k = \frac{\ln 2}{d_h} \tag{1.6}$$

where d_h is the half distance of dispersal or the distance where the seed fall is half that of the source.

This model assumes k to be constant although in reality it varies not only between species but also as a function of location and time. Therefore if the model is to be used under different environmental conditions a new value for k must be determined.

McClanahan (1986) used data from the literature on the longleaf pine (*Pinus palustris*, Mill.) to assign values to the model's parameters. The results from the model compared well with the field data although the model had a slower decay rate than is found for field data. It was suggested that this may be due to the fact that k was estimated from seed trap studies using a forest edge as the seed source and that the value used for k should be that determined from a single source as this is likely to differ from that of a linear source. McClanahan (1986) recommends the use of a curve-fitting procedure which varies the individual values of k until there is a good agreement between the predicted dispersal curve and the field observations.

Another technique which has more recently been used for looking at seed dispersal and seedling recruitment patterns is that of maximum likelihood analysis (Ribbens *et al.*, 1994). This involves identifying values for the parameters in a function describing seedling distribution so that the model output most closely matches the observed distribution This technique does not require the identification of the parent of each recruit. Field data were collected by counting the number of seedlings in successive 1m^2 quadrats along a transect running through mixed stands of adult trees. The location and size of every reproductively active tree within 20 m of the quadrat was mapped. The basic equation for the distribution of seedlings used by Ribbens *et al.* is:

$$P = STR\left(\frac{dbh}{30}\right)^{\beta}\frac{1}{n}e^{\left(-DM^{\theta}\right)} \tag{1.7}$$

where P = number of recruits; STR = number of recruits produced by a tree of standardised dbh, in this case 30 cm; dbh = diameter at breast height; β = a number which modifies the STR according to a power function of the actual dbh observed; n = normaliser (ensures area under curve = 1); D = rate of decline in recruitment number with increasing distance from parent; M = distance from parent; θ = determinant of the shape of the distribution.

The approach used by Ribbens *et al.* does not deal well with long-distance dispersal events. They also stress that their results only apply to dispersal and recruitment within forest stands since more open areas are subject to different weather and wind dynamics. They found that values of $\beta = 2$ and $\theta = 3$ tended to produce models with the highest likelihood. By simulating dispersal patterns around single trees, they were able to use the model to estimate values for the mean dispersal distances of various trees in North America.

Portnoy and Wilson (1993) have looked at the tail of the distribution curve for various plant species. The tail was defined as the part of the dispersal curve beyond the modal distance value. They developed a four parameter model which may have an algebraic or exponential tail:

$$f_{R_T}(r) = Br^{-a}e^{-br^{c}} \tag{1.8}$$

where R_T = horizontal distance; B, a, b and c are constants and r is at least 2 or 3 standard deviations bigger than the mean of R_T. Algebraic tails tend to be longer than exponential tails and have greater reach. They suggest that since the ratio of algebraic to exponential tail probability tends to infinity, the nature of the tail behaviour can have important implications. They carried out statistical tests to see whether dispersal was exponential, algebraic or both. For example, if the tail is algebraic then a is not equal to 0. Their results indicated that algebraic tails tend to be more common than exponential tails, but more data were needed in order to confirm this.

Peart (1985) examines five hypothetical dispersal density functions and their associated probability functions. The graphical illustrations of the dispersal curves show that the use of seed density rather than seed number can change the overall shape of the curve, including the proximity of the peak to the source.

1.6.2. Mechanistic Models

Mechanistic models attempt to describe dispersal mathematically using theories based on the laws of physics. They therefore must incorporate the effects of wind, turbulence and gravity. The physical models include those based on ballistics and atmospheric diffusion.

The distances seeds are dispersed by wind depends on (Cremer, 1977):

- how fast seed falls through air (terminal velocity) - this depends on the morphology and weight of the seed (V_f);
- height of release (H);
- speed and turbulence of wind between ground and point of release (μ).

These variables are related by the simple ballistic equation:

$$x \approx \frac{\mu H}{V_f} \tag{1.9}$$

where x is the predicted horizontal distance from the seed source to the deposition site (Pasquill and Smith, 1983). This model has been extended by Greene and Johnson (1989) to give:

$$\frac{dQ}{dx} = \frac{Q}{x\sigma_u\sqrt{2\pi}}\exp\left\{-\left[\frac{\ln\left(x\overline{V_f}/H\overline{u}_g\right)}{\sqrt{2}\sigma_u}\right]^2\right\} \tag{1.10}$$

where Q = total number of propagules to be dispersed; x = predicted horizontal distance from point source; H = release height; V_f = constant descent velocity (terminal velocity); $\overline{u}_g$ = geometric mean horizontal wind speed assuming the distribution of wind speeds to be lognormal; σ_u = standard deviation of ln(u).

Variation in the terminal velocity between seeds from the same source results in a distribution of dispersal distances even under steady winds (Isaac, 1930). From equation 1.9, it would be expected that seeds with a low terminal velocity (V_f) would be dispersed further than those with a higher terminal velocity. However, field studies by Johnson (1988) found that *Fraxinus* disperses further than *Acer* despite *Fraxinus* having a higher terminal velocity. Johnson suggests that this is due to the samaras of *Fraxinus* having a greater stability in gusty high speed winds. In addition to this, *Fraxinus* disperses its seeds later in the season after leaf abscission and when the average wind velocities are higher.

Sharpe and Fields (1982) have used the simple ballistic model in SEDFAL to simulate the dispersal pattern for a single isolated tree. They reasoned that not enough is known about wind in forests to enable dispersal to be modelled in a forested environment. A comparison between simulated results and published data for Douglas fir (*Pseudotsuga menziesii*) revealed some disparities. It was suggested that these could have been due to atmospheric turbulence affecting the length of time in the air, errors in measuring wind speed during seed flight or not assigning the correct variability to the terminal velocity. They suggest that a seed dispersal model should account for:

- variable terminal velocity;
- phenology of seed release;
- effect of humidity, temperature and wind speed on seed release;
- coincidence of events leading to seed release with wind speeds and direction leading to dispersal;
- average wind speeds between the height of release and the ground.

Atmospheric diffusion models have been used to describe the dispersal of light particles such as fungal spores (McCartney and Fitt, 1986; McCartney, 1991a), pollen (McCartney, 1991b) and air pollutants (for example, the UK-ADMS model developed by Meteorological Office). They assume that the particles being dispersed are light enough to follow air currents exactly and include gradient transfer theory models, Gaussian plume models and random walk models.

Gradient transfer theory (K Theory) models are based on an analogy with molecular diffusion as described by the classical diffusion-advection equation. In three dimensions this equation is very complex, however, it can be simplified to consider particle movement in the direction of the mean wind speed only. It has been applied to the dispersal of plant pathogens. Gaussian plume models have been widely used for predicting the concentrations of atmospheric pollutants, but can also be applied to the dispersal of other light particles. They assume that the average distribution of particles across the height and width of a plume downwind from a continuous point source can be described by Gaussian curves. Both these models assume that the particle release rate is independent of wind speed which may often be an invalid assumption. They are both mechanistic models which consider the horizontal and vertical distribution of particles under the influence of advection and diffusion. The horizontal advective force is mean wind speed and the vertical advective force is gravity.

The Gaussian plume model has been modified to derive the tilted-plume model which takes into account the gravitational settling of heavier particles such as seeds (Pasquill and Smith, 1983):

$$Q(x) = \frac{n\bar{V}_f}{\sqrt{2\pi}\sigma_z}\exp\left\{-\frac{(H-\bar{V}_f x/\bar{u})^2}{2\sigma_z^2}\right\} \tag{1.11}$$

where $Q(x)$ = concentration of seeds at distance x downwind from point source; H = source height above ground; $\bar{V}_f$ = settling velocity of seeds; $\bar{u}$ = mean wind speed in the direction x; n = effective source strength at distance x; $\sigma_z^2 = 2Ax/\bar{u}$ where A is the coefficient of diffusion in the vertical direction. A further refinement of this model which incorporates vertical variation in wind velocities is given by Godson (1957).

Gaussian plume models have been used to predict the mode of the dispersal distances (Okubo and Levin, 1989; Andersen, 1991). Unlike empirical models they relate dispersal distance to measurable parameters such as wind speed and settling velocity. They are both more appropriate to the dispersal of light particles since due to the effects of inertia, large or heavy particles do not follow air currents exactly. They have been mainly used for predicting dispersal over flat, uniform terrain.

Andersen (1991) has compared seed dispersal data with the predictions of the Gaussian tilted-plume, Godson, Weibull and stochastic differential equation (SDE) models. Seed shadows were generated analytically for the first three models and by the simulation of a large number of trajectories for the SDE model. The Weibull model assumes that wind speeds are Weibull-distributed and that seeds are too heavy to be buffeted about significantly by wind turbulence. The SDE model incorporates the effects of turbulence by using Brownian motion as a model for the vertical positions of seeds. Andersen (1991) found that although none of the four models satisfactorily fitted the distribution of artificially released seeds the SDE model performed the best. The discrepancies were attributed to inaccuracies in the modelling of turbulence, variations in wind speed during seed flights and imperfect transfer of momentum from moving air to suspended seeds. Andersen (1991) considers that the SDE model could be refined to take into account these factors as well as variations in settling velocities and release heights. A threshold wind velocity for seed release could also be incorporated in the SDE model. Despite the promising results obtained from the SDE model, Andersen (1991) concludes that secondary dispersal may be responsible for the final distribution of many seeds.

A mathematical model has also been developed for the dispersal of seeds by animals from a single source of a given size (DeAngelis *et al.,* 1977; Johnson *et al.,* 1981). The model traces the movement of an animal assumed to be dispersing seeds through a grid of cells. The movement of an animal to an adjacent cell is determined by a combination of its preference for certain habitat types, its tendency to continue forward in the same direction and the presence of 'attractors' and 'repellers'. At each cell there is a certain probability that a seed will be deposited. In order to develop a realistic model, quantitative information is needed on the behavioural interactions of the dispersing animals with the environment. In the absence of such data, the values of various probabilities which determine animal movement were estimated using what information there was in the literature. Further field studies need to be done in order to test the model and improve its paramaterisation.

Both the animal dispersal model developed by DeAngelis *et al.* (1977) and the wind dispersal model developed by Sharpe and Fields (1982) have been considered to be too unwieldy for use in simulating the dispersal of seeds from more than one tree.

As has already been noted by Andersen (1991), secondary dispersal may determine the final resting place of seeds. Following initial settlement, seed may blown along the ground by wind etc. Dispersal along the ground depends on the morphology of the seed and the nature of the ground's surface. Animals may also play an important role in the secondary dispersal of seeds, for example, Vander Wall (1992) found that between 95% and 99% of artificially distributed Jeffrey pine *(Pinus jeffreyi)* seeds were removed within two days by rodents. The dispersal models described in this section may predict the general dispersal pattern, however, in reality this will vary between sites depending on the speed and direction of local winds and the topography of the area.

1.7. Relationship Between Dispersal and Recruitment

The pattern of regeneration is likely to be highly variable depending on both the shape of the dispersal curve and the availability of sites suitable for establishment. Bunce *et al.* (1990) suggest that the distribution pattern of established plants is unlikely to reflect that of the seed rain since many factors such as density dependent seed predation, caching by seed-feeding animals and subsequent density dependent mortality of seedlings and growing plants are involved in determining the final pattern. The number of trees regenerating depends also on the number of seeds dispersed, the quality of the seed bed and the proportion of the seeds that will grow into trees (Cremer, 1977).

Stiles (1989) has suggested that the probability of recruitment should reach a peak at some distance from the parent. This peak is a consequence of the interaction between the decreasing dispersal curve and the increase in the probability of escaping predation due to density dependent mortality.

Howe and Smallwood (1982) discuss three hypotheses for the advantages of dispersal. The escape hypothesis implies that there is a greater probability of survival for those propagules that escape the vicinity of the parent. The colonisation hypothesis supposes that dispersed propagules may arrive in habitats that have recently become suitable and the directed dispersal hypothesis assumes that propagules possess special adaptations which ensure they reach sites suitable for establishment. These three hypotheses are not mutually exclusive. However, they suggest that as forest trees tend to recruit best in disturbed areas the colonisation hypothesis offers the strongest explanation for dispersal.

Augspurger (1984) has looked at the relationship between initial seedling density and seedling survival after two months and one year in nine species of wind dispersed tropical trees. All but one species supported the escape hypothesis i.e. dispersal increases the probability that offspring escape density dependent and/or distance dependent mortality that may be higher near the parent.

The final recruitment pattern is therefore determined by the distribution of dispersed and germinated seeds and the relative survival probabilities of seeds and seedlings at various distances from the parent. In addition, recruitment may be enhanced for seedlings which germinate in favourable conditions (colonisation hypothesis), for example, for a shade intolerant species light gaps would be particularly favourable. In this case, the recruitment pattern would be dependent upon the location of light gaps.

Ribbens *et al.* (1994) list the following sources of spatial variation in recruitment:

- abundance and fecundity of parents;
- primary dispersal patterns;
- secondary dispersal agents;
- seed predation;
- distribution and frequency of microsites favourable to establishment.

Harper (1977) suggests that it is quite possible that seed predators fail to affect plant distributions because they rarely push the density below that at which competition ultimately limits occupation of space. A recent review of seed dispersal and regeneration by Willson (1992) concludes that there is still much remaining to be discovered in the field of dispersal ecology. In particular, very little is known about how the probability of survivorship changes with increasing dispersal distance (Willson, 1993).

1.8. Models of Range Expansion/Invasion

Much work has been done on the spread of invading organisms (for example, the SCOPE programme on ecology of biological invasions). Such studies could be applied to tree migration in response to climatic change and are reviewed in this section. Hengeveld (1989) provides a comprehensive review on the subject of biological invasions.

Mollison (1986, 1995) breaks down invasion into four phases:

- arrival;
- competitive ability to succeed initially;
- rate and manner of spread;
- competitiveness to persist.

The first three of these show similarities with the spread of disease. Studies in epidemiology have helped improve the understanding of invasion and some of the most sophisticated models have arisen in the context of epidemics (Mollison, 1986). The application of contact models and diffusion models are reviewed by Mollison (1977). Diffusion models have been extensively applied to population spread. They may be considered to be an approximation of the contact models which have been used in epidemiology studies (Mollison, 1977). Some examples of the application of diffusion models to biological invasions will be given in the following section.

1.8.1. Application of Knowledge from Diffusion Studies

The simplest model of spread relates to the spreading out of a homogeneous population into a homogeneous environment. If the size of the population is assumed to remain constant and to be spreading in a homogenous environment then the following equations can be applied (Levin, 1986 and Pielou, 1977 p 170). In one dimension:

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} \qquad (1.12)$$

This equation is often referred to as Fick's equation of diffusion. It can be extended to a two dimensional system as follows:

$$\frac{\partial S}{\partial t} = D\left(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2}\right) \tag{1.13}$$

where S = population density; t = time; x and y are the spatial coordinates; D = dispersion rate which is analogous to diffusivity or coefficient of diffusion and is sometimes also referred to as the mean square dispersion per unit time.

When the spreading population is moving randomly (i.e. behaving in a Brownian fashion) then a solution for equation 1.13 is a normal probability function with mean zero (Okubo, 1980):

$$S(x,t) = \frac{M}{\sqrt{4\pi Dt}}\exp\left\{\frac{-x^2}{4Dt}\right\} \tag{1.14}$$

where M = total number of individuals at time $t = 0$ and variance = $\sigma_x^2 = 2Dt$

In two dimensions, the corresponding solution is:

$$S(r,t) = \frac{M}{4\pi Dt}\exp\left\{\frac{-r^2}{4Dt}\right\} \tag{1.15}$$

where horizontal variance = $\sigma_r^2 = 4Dt$

These basic equations can be easily modified to take into account variations in the coefficient of diffusion (for example, due to variation in habitat) and also population growth, for example, see Levin (1986) and Okubo (1980). The latter gives a comprehensive account of the application of mathematical models of diffusion to ecology. Hengeveld (1989) also discusses the application of diffusion models to the topic of biological invasions.

Two density distributions may be pooled together to form a compound distribution. This may be particularly useful if a population has two or more diffusion coefficients. This approach has been adopted by Allen (1991) in the modelling of active and passive diffusion of *Opuntia imbricata*. The shape of the compound distribution has been shown to be leptokurtic (Okubo, 1980). A compound distribution could be used to model local dispersal events coupled with rare long-distance dispersal events.

These diffusion equations predict that the population (at a given threshold density for detection) will spread forwards as a continuous front with a velocity of:

$$C = 2\sqrt{\alpha D} \qquad (1.16)$$

where C = rate of spread; α = intrinsic rate of population increase and D = coefficient of diffusion. This simple equation illustrates the importance of both population growth and dispersal in range expansion.

The diffusion equation was first studied by Kendall (1948) and then independently by Skellam (1951) and is a simplification of the earlier genetic equations used by Fisher (1937) and Kolmogoroff *et al.* (1937). Skellam was able to use the diffusion model to show that animals must have played an important role in the dispersal of oak during its post-glacial migration.

A graph of the square root of the area occupied against time is linear, the gradient being equal to:

$$\frac{d\sqrt{Area}}{dt} = 2\sqrt{\pi\alpha D} \qquad (1.17)$$

(Okubo, 1980 p108). This equation assumes that the population is increasing as a series of continually expanding circles. An incorrect formula for the gradient ($\sqrt{\alpha D}$) has been used by several workers including Williamson and Brown (1986) and Birks (1989). Equation 1.17 can be confirmed as correct as follows:

$$\sqrt{Area} = r\sqrt{\pi}$$

Putting r/t = C into equation 1.17 then:

$$r = 2t\sqrt{\alpha D}$$

$$\therefore \sqrt{Area} = 2t\sqrt{\pi\alpha D}$$

$$\therefore \frac{d\sqrt{Area}}{dt} = 2\sqrt{\pi\alpha D}$$

The assumption of random movement may be a valid simplification when looking at population spread. Although the individual patterns of movement may not be random (for example, an animal may use information from its surroundings when moving around the environment), the overall pattern produced by the population may approximate to randomness. This simplification offered by the diffusion model does seem to offer a good approximation to population spread (for example, Lubina and Levin, 1988; Andow *et al.*, 1990)

The range expansion of the sea otter has been investigated by Lubina and Levin (1988). One of the reasons for choosing this species was that its spread can be considered to be one-dimensional (i.e. along the coast). This therefore avoids the complications that occur with two-dimensional spread such as physical barriers obstructing the diffusion process and causing a distortion in the spread of the population. They predicted rates of spread by substituting estimates for α (rate of population increase) and D (movement in north and south of range) in equation 1.16. The predicted rates compared well with those observed. The model correctly predicted the faster rate of expansion in the south. The faster expansion rate in the south can probably be accounted for by the difference in the diffusion constants which arise because the otters move around more in the less suitable habitat in the south of their range. Other explanations could include habitat differences in mortality and ocean currents (advective force) tending to promote southward movement. More studies need to be carried out to provide the independent parameters necessary to resolve this issue.

Diffusion models have also been successfully applied to the spread of invading organisms in two-dimensions. For example, Andow *et al.* (1990) have examined the match between the observed rate of spread of the muskrat, the cereal leaf beetle and the cabbage white butterfly and that estimated using equation 1.16. They used microscale observations to estimate α and D. For the muskrat and the cabbage white butterfly the predicted rates compared well with the observed rates. However, for the cereal leaf beetle the theory was wrong by two orders of magnitude, this was thought to be due to processes not observable at the microscale level (for example, long range movements on air currents and hitch hiking on human transport).

Reeves and Usher (1989) have used a diffusion model for the spatial spread of an invasive species through the cells of a grid. They parameterised the model for coypu using data from the literature to estimate values for α, D and K_{max} (maximum carrying capacity per 10 km square). The environment of East Anglia was represented by assigning values for diffusivity and carrying capacity to each cell according to the extent of the distribution of suitable coypu habitat. Values for these parameters were estimated from 1:50,000 O.S. maps. They considered their model to be successful since it was able to predict the coypus' range reasonably well. Their model predicted a distribution with a continuous front, whereas the actual distribution of coypu shows the presence of some outlying populations. They suggest that a stochastic element should be added in order to more realistically model the process of dispersal. In addition to carrying out simulation runs, sensitivity tests were made in which the values of parameters were varied in relation to each other (other parameters were held at their default values). The resulting expansion rates were then analysed by analysis of variance. Significant results were obtained for the principle dispersal and reproductive parameters, α, D, and K.

The models discussed so far have all been single species models. However, Okubo *et al.* (1989) have used a competition-diffusion model to examine the spread of the grey squirrel (*Sciurus carolinensis*) in Britain through habitat already occupied by the red squirrel (*Sciurus vulgaris*). In addition to the usual parameters of the diffusion model, their model included competition coefficients. They were able to show that the spread of the grey squirrel was slowed down by the presence of the red squirrel. From this they concluded that simple diffusion, logistic population growth and some form of competition were sufficient to account for the progressive replacement of the red squirrel by the grey in England and Wales.

Van den Bosch *et al.* (1990,1992) have developed models for range expansion based on the population growth/diffusion model. They reformulated equation 1.16 to give:

$$C = \frac{\sigma}{\mu}\sqrt{2\ln R_0} \tag{1.18}$$

where R_0 = net reproductive rate; $\overline{\mu}$ = mean age at child bearing; σ^2 = variance of marginal dispersal density.

They claim that this equation gives a good approximation for C when $R_0 \leq 1.5$. For populations with larger net reproductive rates the following formula was developed:

$$C = \frac{\sigma}{\mu}\sqrt{2\ln R_0}\left\{1+\left[\left(\tfrac{\nu}{\mu}\right)^2-\beta+\tfrac{1}{12}\gamma\right]\ln R_0\right\} \tag{1.19}$$

where ν^2 = variance of age at child bearing; γ = kurtosis of marginal dispersal density; ß = measure of the interaction between dispersal and reproduction.

These models can be applied to any organism which disperses once only during its life history. They both use reproductive parameters which can be estimated from data in life tables and allow for variations in fecundity and survival throughout the species' life history. Values for the dispersal parameters can be derived from observations on dispersal distances. The model given by equation 1.19 no longer assumes that dispersal distances are normally distributed so strictly speaking this model should not be referred to as a diffusion model, but rather a spatial spread model (Hengeveld, 1989). The predicted value of C from these equations showed a good approximation to the observed values for the five animal species Van den Bosch *et al.* (1992) investigated. Both equations tended to predict lower rates than those observed. This was believed to be due to an underestimate of the dispersal distances. In most cases equation (1.19) gave a better prediction than equation (1.18). This was thought to be due to the incorporation of the kurtosis of dispersal density. This supports the earlier work of Van den Bosch *et al.* (1990) which concluded that the parameters of dispersal density are more critical than the demographic parameters in determining the rate of spread. With a slight modification, equation 1.19 can be adapted for use with species which disperse throughout their life (Marinissen and Van den Bosch, 1992).

Diffusion and spatial spread models that incorporate population growth can therefore provide a useful first approximation to rates of spread. In some instances it may be relevant to construct models that incorporate variations in α and D. Where movement occurs on two different scales it may be appropriate to use two-phase models which couple models for long-distance jumps forward with diffusion models representing the short range spread from a point of introduction (Andow *et al.*, 1990). Most of the work done with diffusion models and similar mathematical models of spread has assumed the environment to be homogeneous. However, some recent work has used these models to look at spread in a heterogeneous environment (for example, Reeves and Usher, 1989; Holmes *et al.*, 1994; Van den Bosch and Hengeveld, submitted). Most of these models (with the exception of that by Reeves and Usher, 1989) are not spatially explicit, i.e. they allow predictions to be made about the rate of spread but do not incorporate any graphical display showing the actual pattern of spread.

Auld and Coote (1980) have produced computer generated simulations for population spread in a homogeneous environment. They looked at the effects of varying the population growth rate, the fraction of population dispersing (s) and the distance over which the dispersing fraction is distributed (d). Results from their simulations showed that the rate of spread and total population growth depended on both mobility (determined by values of s and d) and population growth rate. The distribution patterns were also more complex when growth rates and mobility were high. Comparisons of spread in central and scattered initial populations showed that the scattered populations had a greater rate of spread. The inverse cube law for seed dispersal predicts that spread occurs as an advancing front (Harper, 1977). However, the curve describing the distribution of daughter plants could be less steep and therefore imply that spread may occur as a ragged edge. Empirical data on the distribution of daughter plants would enable the model to be refined. This model could also be developed to simulate spread in a heterogeneous environment.

The rates of spread of trees in the British Isles during the Holocene are high compared with theoretical predictions based on diffusion models (Skellam, 1951; Birks, 1989). This implies that chance, long-distance dispersal events by birds, small mammals, rivers, ocean currents and possibly man were important. By plotting the square root of the area occupied against time, Birks (1989) has estimated the velocity of expansion of various forest trees in the British Isles during the Holocene. Using estimates of α derived by Bennett (1983), Birks also derived estimates for the diffusion constants of the different taxa (using equation 1.17). The results obtained assume that the population was expanding into an area unpopulated by that taxon. However, if trees were distributed sparsely beyond the range determined using the pollen record than the model would be inappropriate and the estimates derived too large. Unfortunately Birks used the formula gradient = $\sqrt{(\alpha D)}$ in his calculations rather than the correct formula as given by equation (1.17). However, his approach is still valid and the same conclusions would have been reached with the correct formula.

The diffusion model has also been used in conjunction with other models to investigate the relative importance of adaptation and dispersal as mechanisms for responding to environmental change (Pease and Lande, 1989).

1.8.2. Possible Alternatives to Diffusion Models

Particle Dispersion Models

Woodward and McKee (1991) have adapted the particle dispersion model used by Solomon (1975) to produce a simple dispersal model which predicts the rate of spread of trees:

$$C = -\frac{\bar{u}H}{TV_f}\ln F \tag{1.20}$$

where C = migration rate; $\bar{u}$ = mean wind velocity; T = source longevity; H = release height; V_f = terminal velocity; F = proportion of deposited seeds necessary to cause an individual tree to regenerate. They used parameter values for spruce to obtain a migration rate of 115 m yr^{-1} which is at the low end of the range estimated by Huntley and Birks (1983). It was suggested that this was because the model ignores the effects of turbulence which is believed to be important in rare long-distance dispersal events.

Gap Dynamics Models in Conjunction with Dispersal Models

Dispersal models have been used in conjunction with gap models (see section 1.9) which simulate the dynamics of small plot (typically 1/12th of a hectare) in order to look at vegetation change at a large spatial scale. The gap models are arranged in a grid with dispersal occurring between them (for example, Coffin and Lauenroth, 1989). By modelling dispersal between a large number of gap models it would be possible to investigate tree migration. However, due to the fine resolution of the forest gap models it would be virtually impossible to simulate landscape dynamics at the broad-scale due to both computational and data limitations (Smith *et al.*, 1992).

More Explicit Mathematical Models

Smith (1975) has developed a model which explicitly models the process of invasion. He gives the following mathematical models for the input (I), germination and first year survival (G) and survival to maturity for a plant species (M):

Input to each site:

$$I_x^j = \sum_{\substack{i=1 \\ j=1}}^{n} (S_x^i P_{dx}^{ij}) \tag{1.21}$$

where I_x^j = input of viable seeds per site j of species x; S_x^i = number of viable seeds of species x per source i; P_{dx}^{ij} = probability of dispersal of species x from source i to site j.

Germination per site:

$$G_x^j = I_x^j \prod_{\substack{k=1 \\ j=1}}^{n} P_x^k \tag{1.22}$$

where G_x^j = number of seedlings produced per site; I_x^j = seed input per site; P_x^k = probabilities per seed of each factor determining G, includes ability to germinate (P_g), ability to escape predation (P_e) and location of safe sites (P_s).

Adults per site:

$$M_x^j = G_x^j \prod_{\substack{l=1 \\ j=1}}^{n} P_x^l \tag{1.23}$$

where M_x^j = number of plants maturing per site per cohort; G_x^j = number of seedlings produced per site; P_x^l = probabilities for yearly survival including first year of reproduction.

These models are intuitive and simplistic, however, the major problem with them will be that of estimating the values for the various probabilities. Smith has made an attempt at doing this for a selection of bird dispersed woody plants by carrying out a series of field observations and experiments. Although he was able to estimate I, G, P_g and P_e it was not possible to estimate probabilities for yearly survival beyond the first year since this requires studies of a longer duration (Smith, 1975). Another limitation of this model is that the values for the probabilities are site specific and therefore the model can not be used in other situations since the environmental variables which determine the probabilities will be operating at different intensities.

More recently, Schwartz (1992) has used a similar but less detailed spatially explicit model in which dispersal occurs by either a negative exponential function or an inverse power function. Population growth occurs by assuming that newly colonised sites have an initial density of 6% of the maximum. The density is then doubled in each of the four following generations to reach the maximum value. Schwartz was able to use this model to show that tree migration rates fall well below historically observed migration rates at low levels of habitat availability, regardless of the dispersal function that was used.

1.9. Models used to Predict the Effect of Climatic Change on Plant Distribution

These have recently been reviewed by Malanson (1993) who recognises three general types of model:

- transfer functions;
- gap dynamics models;
- physiological models.

None of these models project spatially, temporally and biologically detailed responses to climatic change at the continental-scale. One of the main reasons for this is the need for more computational resources. The direct effects of an increase in carbon dioxide concentration is incorporated into very few models. These effects are reviewed by Eamus and Jarvis (1989) who conclude that the effects of the rise in carbon dioxide concentration may be relatively small in relation to impending changes in land use and management practices.

Transfer Functions

These predict the future distribution of vegetation based on the present day relationship between vegetation and climate. These models are known as static or equilibrium models since they predict the final vegetation pattern produced as a result of climatic change. They give no indication as to how this change may occur or how long it may take. They are, however, useful in predicting the magnitude of potential changes. Examples of these models include climate response surfaces which predict the future distribution of a species or taxon based on its current distribution with respect to selected climatic variables known to be important in determining its present day range (for example, Beerling *et al.*, 1995; Huntley *et al.*, 1995; Carey *et al.*, 1995).

Physiological Models

Models based on plant physiology and dominance, soil properties and climate have been developed to predict global vegetation patterns (Prentice *et al.*, 1992; Woodward and Williams, 1987; Woodward and Rochefort, 1991; Woodward and McKee, 1991). Such models are often mechanistic using rules which are derived from experimental information and not from correlations. They include parameters such as cold tolerance, chilling requirement, heat requirement, moisture requirement and dominance hierarchy. They may be considered to be a more complex and sophisticated form of transfer function model. As for transfer functions, physiological models at the global-scale are static models. Some physiological models have also been developed at smaller scales.

Gap Dynamics Models

Another approach has been to use gap dynamics models to predict the effect of climatic change on the forest ecosystem. Most of the research in this area has focussed on forest ecosystems and in this context gap dynamics models are often referred to as forest stand models. Models such as JABOWA and FORSKA have been used to simulate the forest dynamics in a gap (usually less than 1 hectare) by considering the birth, growth and death of individual trees. A major limitation of most of these models is that they assume that the seed bank consists of all species of trees that could grow in the changed climate (Pacala *et al.*, 1993). This assumption is clearly not valid as some species would have to migrate great distances before they could start establishing themselves in the simulated forest.

A few stand models do however, consider limitations in the seed supply. For example, FORET (Shugart and West, 1977) allows seed source limitations to be specified for 6 old-field successional species. The FOREST stand development model (Ek and Monserud, 1974; Monserud, 1975) explicitly models local seed production and dispersal. Seed production can either be held constant or allowed to vary stochastically based on the frequency of good and bad seed years. Johnson *et al.* (1981) have further developed FOREST to enable it to handle exogenous seed dispersal into the sample plot. They simulated the invasion of *Acer saccharum* into a pure stand of *Prunus serotina* under three levels of exogenous *A. saccharum* seed supply. The results supported the hypothesis that seed source proximity can significantly affect the vegetation dynamics of forest islands. Johnson *et al.* (1981) suggest that the use of seed dispersal models in conjunction with forest gap models may provide a basis for simulating forest dynamics in patchy landscapes.

A more recent forest stand model (SORTIE) developed by Pacala *et al.* (1993) includes the spatial position of all trees and explicitly models recruitment by simulating the seedling recruitment pattern for each individual tree. They are trying to use field data to estimate values for parameters used in forest dynamic models which can not be determined from the published literature and which have been insufficiently dealt with in earlier stand models. By doing this they are hoping to develop a more realistic model of forest stand dynamics.

Hanson *et al.* (1990) have used FORFLO, a forest gap model derived from FORET in conjunction with a dispersal model to look at the effects of habitat fragmentation on forest composition. They used a 3 x 40 array of 30 m x 30 m simulation plots to model an area of 90 m x 1200 m. In the modern landscape where forests often occur as fragmented islands separated by large areas of unsuitable habitat, the dynamics of the individual islands may be significantly affected by the degree of isolation from neighbouring islands. They chose not to use the models of wind dispersal and animal dispersal developed by DeAngelis *et al.* (1981) since these were considered too complex to be applied to the situation they wished to investigate. They also rejected the negative exponential model used by McClanahan (1986) on the basis that the values for the dispersal capacity and seed production were too variable under the conditions of their model. Instead they used a simple model based on a set of rules for different modes of dispersal. Their results supported the theory that an increase in fragmentation will result in a decrease in species diversity due to a reduction in the immigration rate of species into patches.

Some forest stand models have also attempted to include the direct effect of carbon dioxide on vegetation by modifying the growth equation (for example, Kienast, 1991). Another effect which is associated with an increase in greenhouse gases is the depletion of the ozone layer, this may have an effect on plant productivity.

Stand models predict forest dynamics on a very small scale and would become computationally complex if applied directly to larger scales such as the landscape. For example, a personal computer operating at 0.2 Mflops takes 1 hour for SORTIE to simulate one year's forest dynamics in a 1 km square.

Markov Models

Another type of model which is frequently applied to succession are Markov models. In these models each tree is given a probability of being replaced by another tree of a different species. Most of these models assume that the replacement probabilities do not change over time (Horn,1975, 1981). The replacement probabilities for each species of canopy tree is determined from the percentage of saplings of each species found growing beneath it. It is assumed that every sapling has an equal chance of replacing the canopy tree.

1.10. Outline of the Structure of this Thesis

Chapter 1 reviews the literature relevant to the research presented in this thesis. Topics covered include the palaeoecological record of post-glacial tree migration, existing models of species' spread and the dispersal of propagules.

Chapter 2 describes the implementation of the model of species migration developed as part of this research project. The model (MIGRATE) exists in the form of a one-dimensional and a two-dimensional model. The two-dimensional version is a spatially explicit model designed to simulate the spread of a species across a heterogeneous landscape. The use of environmental data such as land cover, climate and probability of occurrence values for simulating migration across a realistic landscape is described.

Chapter 3 describes the field work which was carried out in order to obtain seed dispersal curves for sycamore (*Acer pseudoplatanus*), Scots pine (*Pinus sylvestris*) and larch (*Larix decidua* Mill.). Computer simulations are described in which an attempt is made at investigating the relationship between the seed dispersal curve produced by a forest edge and the seed dispersal curve produced by an individual tree. Most field studies, including those carried out for this research, have looked at dispersal from a forest edge. However, the dispersal function required by MIGRATE is that for an individual tree.

In Chapter 4 the results from MIGRATE are examined. The initial simulations were carried out with a single cohort, single dispersal function system, as this represents the most simplistic case. Further simulations were then carried out using multiple cohorts and two dispersal functions as this is more representative of reality. An attempt was made at investigating some of the issues raised in Chapter 1 regarding the post-glacial migration of trees. Finally, two-dimensional simulations were carried out in which the spread of the small-leaved lime (*Tilia cordata*) was investigated under various environmental conditions.

Chapter 5 draws together the major conclusions that have arisen from this research and suggests areas where further work is needed.

CHAPTER 2

Model Development and Parameter Estimation

This chapter describes the design and implementation of the MIGRATE model and the assumptions which are made. The one-dimensional and two-dimensional versions of the model are compared and the estimation of the reproduction and dispersal parameters discussed with particular reference to trees. The problem of scaling with respect to dealing with local and long-distance dispersal is addressed. For the two-dimensional model details regarding the creation of habitat suitability maps are given. Two approaches for the investigation of the response to climate are discussed. These include the use of climate response surfaces to modify the relative carrying capacity values and the creation of climate suitability maps to determine whether or not reproduction can occur.

2.1. The MIGRATE Model

MIGRATE is a simple deterministic model which can be used to simulate the migration of any sessile organism. For the purposes of the MIGRATE model, a sessile organism is defined as one which disperses once during its life history and then settles down. Therefore MIGRATE may be applied to many animal species as well as all plant species. For example, many bird species disperse once during their life cycle and then settle down in a relatively confined area to breed. In section 4.3 the migration rates predicted by the one-dimensional version of MIGRATE for the collared dove, house sparrow and muskrat are compared with the rates predicted by the analytical models of migration developed by Van den Bosch *et al.* (1992). MIGRATE currently allows the investigation of the migration of a single species across either a homogeneous or a heterogeneous environment. It does not take into account interspecific competition, this is assumed to be incorporated into the relative carrying capacity values. Intraspecific competition does, however, occur in the form of competition for available space. MIGRATE has been implemented in the C programming language. Routines from the Uniras subroutine library are called from within the program to produce a graphical display of the simulation results.

Two forms of MIGRATE have been implemented, one for simulating migration in one-dimension and the other for simulating migration in two-dimensions. If the environment is assumed to be homogeneous then the one-dimensional version of MIGRATE is the most appropriate model to use since this is less computationally demanding. In this case the environment is represented by a single row of cells which are labelled cell_i (where $i = 1, ..., m$). However, for a heterogeneous environment it is necessary to use the two-dimensional version, in which the environment is represented by a grid of cells made up of m rows and n columns. These are labelled cell_{ij} (where $i = 1, ..., m$; $j = 1, ..., n$). Although the formulation of both models is the same, it should be noted that one-dimensional dispersal functions do not always give rise to the same migration rate in two-dimensions. This phenomenon will be explained in section 2.1.4.

The two-dimensional version of MIGRATE also has the facility to explore the effects of climate on migration. This may be done either by the use of a climate map which assigns cells as either suitable or unsuitable for reproduction or by the use of a probability of occurrence map whose values act directly on the relative carrying capacity values of the cells.

The output from the one-dimensional version of MIGRATE takes the form of two graphs. The upper graph shows the wave-like progression of the population front over successive generations. The lower graph shows the change in population density with time at various distances from the origin. Unless otherwise stated the lines represent the population increase at distances of 100 km, 110 km, 120 km 130 km and 140 km from the origin. The population densities are plotted as natural logarithms so that the gradient of the line is an estimate of the intrinsic rate of population increase. A threshold value of -5 was set so as to avoid the plotting of large negative values. In most cases the lines will appear as five evenly spaced parallel lines. However, in cases where the chance long-distance dispersal events play an important role the spacing between the lines becomes erratic. Various analytical models have been developed which use mathematical equations to calculate migration rates. The main advantage that the one-dimensional version of MIGRATE has over these analytical models is that the graphical output it produces enables the shape of the wave front to be readily visualised. In particular, the extent of the wave front can easily be measured. It is possible to derive so called "travelling plane wave solutions" which describe the shape of the migration front in mathematical terms (for example, Van den Bosch *et al.* 1990, 1992 and references therein). However, the mathematics involved are quite complex and probably only accessible to those in the field of mathematical biology.

The parameter values used in the simulation are printed above the upper graph. The notation is as follows:

Line 1: L = cell length; a = area occupied by an individual; T = generation length.

Line 2: An ordered list of the survival probabilities for each cohort class starting with the probability of a propagule recruiting to the first cohort class.

Line 3: A list of the number of propagules (S) produced by an individual in each cohort class during a generation length starting with the first cohort class.

Line 4: A dispersal parameter (for example, RMSD if a normal distribution is being used) followed by the probability of dispersal by that dispersal function. Parameter values are given for each dispersal function. Any number used as a suffix to the parameter name refers to the dispersal function number. In most cases it is necessary to use only one or two dispersal functions.

Line 5: A list of the dispersal sums for each dispersal function. These should be the same as their corresponding dispersal probabilities. The sum of all the dispersal probabilities (this should add up to 1.0). The furthest cell from the parent cell for which a dispersal probability is calculated. Cells beyond this value do not receive any propagule input.

Line 6: K = relative carrying capacity (i.e. the fraction of each cell which is available for colonisation). If the number of individuals was rounded to a whole number then the random number used in this process is given. Details of any climatic restraints which were operating during the simulation are given.

Line 7: The interval in generations between each successive migration front. The number of generations over which the simulation occurred.

A typical output of the upper graph from the one-dimensional version MIGRATE is shown in Fig. 2.1. Each line represents the population density at the end of a generation. The number of generations which are output and the time interval (in terms of generations) separating them are specified by the user at the start of the simulation. The extent of the population front is the distance between the leading edge of the front and the point where the population stabilises at its maximum value. The migration rate is determined by dividing the distance between migration fronts (d) by the time interval which separates them. Fig. 2.2 was taken from Van den Bosch *et al.* (1992) and shows how an observer at position x will observe local exponential population growth. In the lower graph of the one-dimensional version of MIGRATE, the population density is expressed as a natural logarithm so that the gradient can be used as an estimate of the intrinsic rate of population increase.

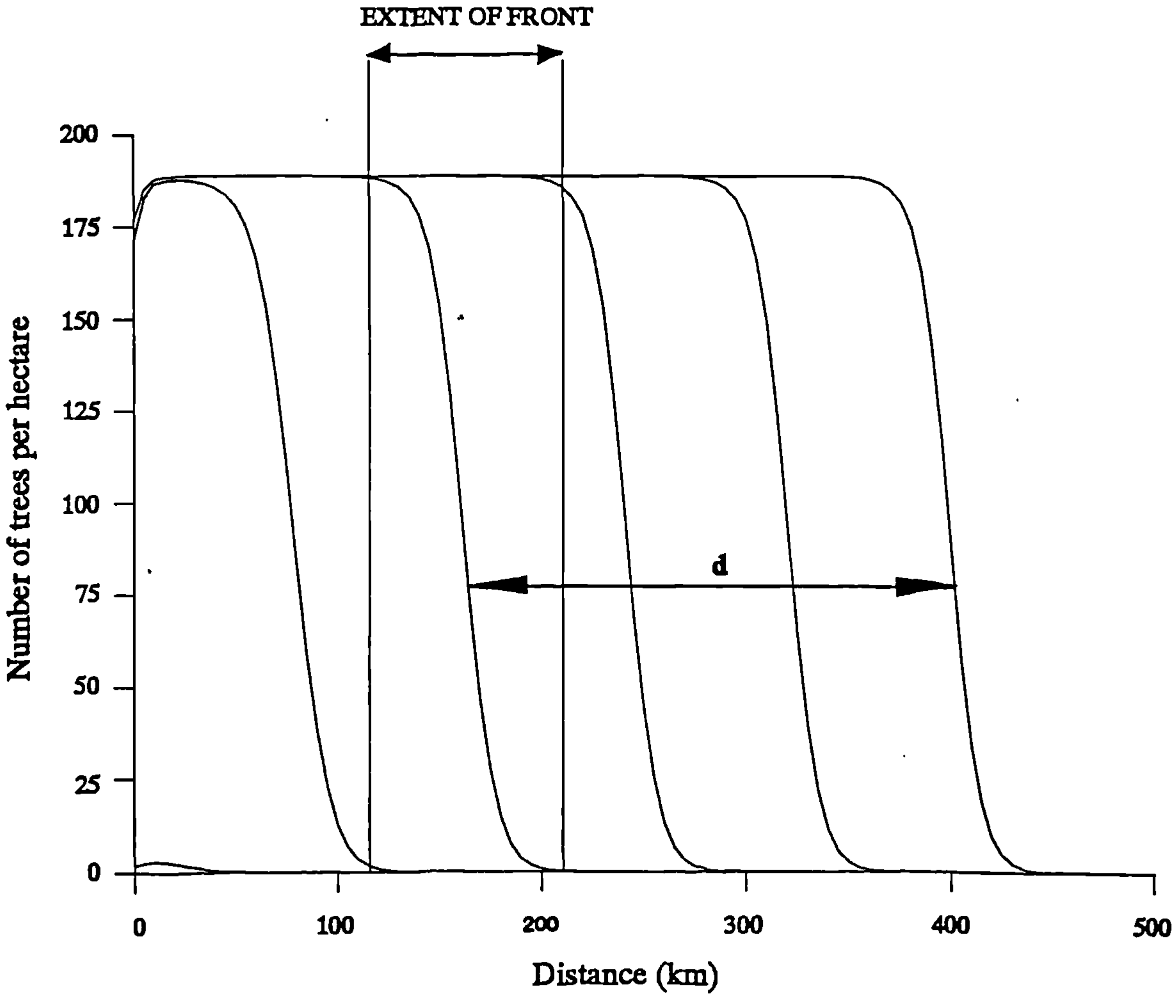

Fig. 2.1 A typical output of the upper graph of the one-dimensional version of MIGRATE. Each successive migration wave shows the density of individuals at increasing times from the start of the simulation.

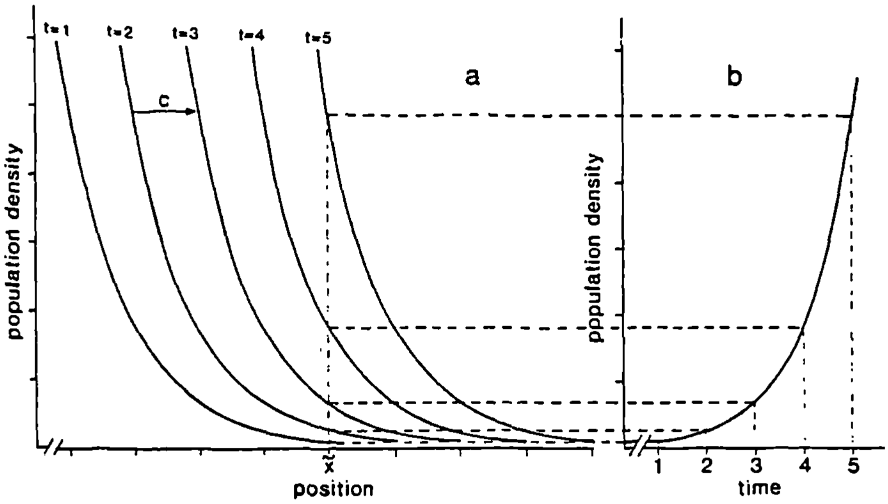

Fig. 2.2 The mechanism by which a population front having an exponential shape in space and travelling at a constant velocity induces apparent local exponential population growth (from Van den Bosch *et al.* 1992).

a: population density as a function of position in space at different times.

b: Population density as a function of time at position x.

2.1.1. Parameters used in MIGRATE

One of the first tasks in developing the MIGRATE model was to identify the biological and environmental components which have been shown to be important in species migration. Once these elements and their interactions were identified then it became possible to begin to formulate the model. There is an extensive amount of literature on biological invasions and species migration some of which was reviewed in Chapter 1. Hengeveld (1994) suggests that invasions can be conceived to consist of two processes, that of spatial spread followed by local population increase. The earliest models of spread were the reaction-diffusion models such as the classic model of Skellam (1951) and Fisher (1937). These combined local population growth with Brownian random dispersal. Since then, models of spread have become more advanced in that they allow for more complicated life histories and dispersal functions. The analytical models developed by Van den Bosch *et al.* (1990, 1992) and Mollison (1990) consist of a reproduction kernel and a dispersal distribution. The reproduction kernel describes the production of offspring throughout a species' life time. This incorporates parameters which can be obtained from life table data i.e. the number of offspring produced by each age class and the probabilities of survival between successive age classes. These parameters are the average values for the species and are assumed to be constant, therefore density dependent factors which may affect survival are not taken into account.

The dispersal function describes the distribution of propagules about their parent and incorporates the variance and kurtosis of dispersal. In some models, a carrying capacity has been included so as to set an upper limit on the population density. For models which predict migration rates only, this parameter is not essential as by the time the population has increased above what may be considered to be a realistic density it is so far away from the migration front as to have no effect on the migration rate. Most models have concentrated on the migration of a single species, however, some models have been developed which use competition coefficients to model the interaction between two species, for example Okubo *et al.* (1989). Despite the poor accuracy of most ecological data (Mollison, 1991) the models of spread using the parameters described so far have been used successfully to predict the spread of a wide variety of species. (for examples see Van den Bosch *et al.*, 1992; Okubo *et al.*, 1989; Andow *et al.* 1990; Reeves and Usher, 1989; Marinissen and Van den Bosch, 1992).

In view of the recent success in the modelling of biological invasions and the desire to keep the model as simple as possible, it was decided to restrict the model to the parameters listed in Table 2.1. They have been categorised into reproductive, dispersal and landscape parameters. From these parameters, the following secondary values are derived:

A	Cell area i.e. L^2;
F	Potential number of offspring produced by an individual during one generation i.e. $S.P_1$;
α	Intrinsic rate of population increase i.e. approximately $\ln(F)/T$.

MIGRATE calculates the number of propagules $M_{ij}(t)$ arriving in each cell$_{ij}$ at time t (i = 1, ..., m; j = 1, ..., n) and from this updates the number of individuals $N_{ij}(t)$ in each cell$_{ij}$

In order to take into account variations in fecundity and survival throughout a species' life history the facility to use more than one age class has been implemented. Each age class is given its own value for survival ($P_{\text{cohort no.}}$) and propagule output ($S_{\text{cohort no.}}$).

Table 2.1 The parameters required by the MIGRATE model.

Parameter Type	Parameter Description	Parameter Name
Reproductive Characteristics	Time in years to reach the age of first reproduction i.e. generation length.	T
	Number of propagules produced per individual during one generation length.	S
	Probability of propagules establishing and surviving to the age of first reproduction in the absence of self thinning.	P_1
	Probability of mature individuals surviving a further interval of one generation length.	P_2
Dispersal Characteristics	Number of dispersal functions.	N_DISP
	Dispersal parameters which define the distribution of propagules from their parent (e.g. root mean square displacement for a normal distribution, half distance for a negative exponential distribution or shape and scale parameters for a Weibull distribution).	RMSD (for normal distribution) or D_H (for negative exponential distribution)
	Probability of dispersal for each dispersal function (must sum to 1.0).	P(RMSD), P(D_H)
	Maximum distance (in terms of number of cells) over which dispersal is calculated.	FURTHEST_CELL
Landscape Characteristics	Area occupied by a mature individual.	a
	Cell length.	L
	Number of cells in the north-south direction.	j_max
	Number of cells in the east-west direction.	i_max
	Relative carrying capacity for each cell (i.e. the area available for occupation by the species or taxon being simulated expressed as a proportion of the total cell area).	K_{ij}

2.1.2. Word Description of MIGRATE

MIGRATE is a cell-based model with the real environment being represented by a grid of square cells. Each cell has a relative carrying capacity associated with it which determines the fraction of that cell which is available for occupancy. The number of individuals in each age class and the number of propagules arriving are MIGRATE's state variables. The values of these variables for each cell are calculated at intervals of one generation length.

MIGRATE takes each cell in turn and calculates the total number of offspring which will reach the age of first reproduction produced by that cell i.e. the number of potential new recruits. If the number of potential recruits is greater than zero then the recruits are dispersed into the neighbouring cells according to the dispersal distribution specified by the user. The area over which dispersal can occur is controlled by the value given to 'furthest_cell'. Some of the individuals in each age class are then removed according to the probability of survival value assigned to that age class. As there is a difference in the recruitment process of the model when only a single age class is used compared with multiple age classes the two cases will be described separately.

In single cohort simulations, MIGRATE keeps a tally of the number of individuals who are older than the age of first reproduction. Following removal of some individuals due to death, the arriving offspring are recruited according to the amount of space available. This means that the offspring are able to reproduce themselves in the next cycle of the model i.e. it has been implicitly assumed that all the offspring were produced at the beginning of the time step.

In multiple cohort simulations, MIGRATE starts with the oldest age class and works through to the second age class and recruits all the surviving individuals from the immediately younger age class i.e. the third age class receives all the surviving individuals from the second age class and the second age class receives all surviving individuals from the first age class. During this stage there is no competition for space since it is assumed that all individuals occupy the area of an adult. Therefore competition needs to occur only during recruitment into the first age class. The number of individuals recruiting to the first age class depends on the amount of space available in the same way as it does for single cohort simulations. The advantage of using multiple cohorts compared with just a single cohort is that the assumption that all the offspring were produced at the beginning of a time step and can therefore reproduce in the next cycle of the simulation can be relaxed. By assigning a non-zero fecundity value to the first age class the fact that individuals were born continuously throughout the previous time step can be taken into account i.e. the propagule output of the first cohort class can be estimated as:

$$S_{(\mathrm{cohort}\ 1)} = \frac{1+2+3+\dots\dots\dots+T}{T} . \frac{S_{(\mathrm{cohort}\ 2)}}{T} \qquad (2.1)$$

The value of $S_{(cohort\ 1)}$ is approximately half of the value of $S_{(cohort\ 2)}$.

If at the end of the time step that particular generation is to be output then the density values expressed as the total number of individuals per hectare in all age classes is plotted.

A flow chart illustrating the processes which occur during a simulation is given in Fig. 2.3. The incorporation of changes in the relative carrying capacity and climate will be discussed in sections 2.3.2 and 2.3.3.

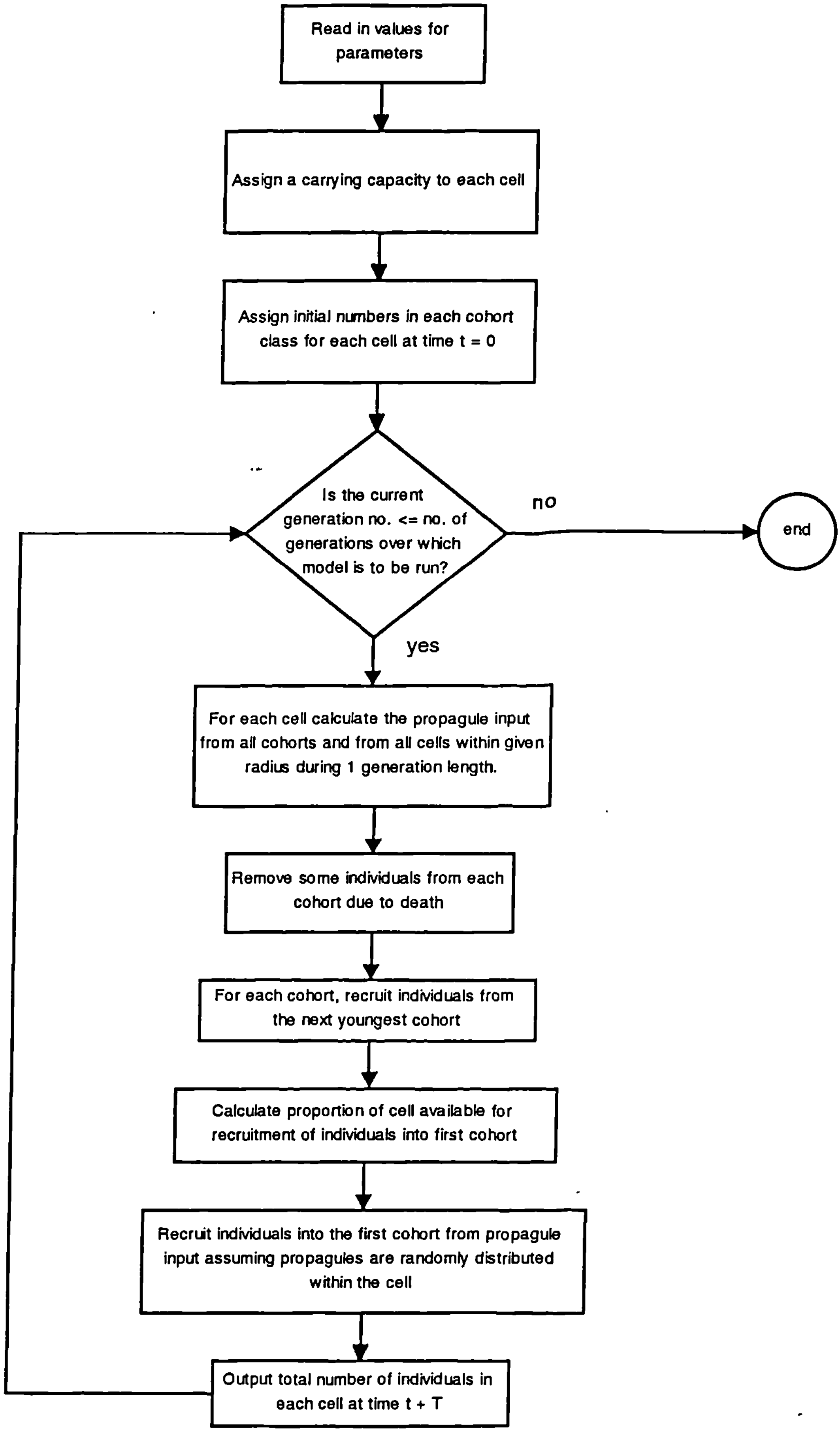

Fig. 2.3 Flow chart showing the sequence of events occurring in the MIGRATE model.

2.1.3. Mathematical Description of MIGRATE

In this description, in order to keep the equations as easy to understand as possible, it is assumed that there is only one cohort consisting of the number of reproductively mature individuals. The dispersal function f(*r*) can be any function which gives the probability of arrival with respect to distance (*r*) from the parent. The sum of the dispersal probabilities should be 1.0. The notation below refers to the two-dimensional version of MIGRATE. The one-dimension version of MIGRATE functions in the same way as the two-dimensional version, but summation occurs over cell_i only.

The number of propagules arriving in each cell is calculated from the following summation over all cells:

$$M_{ij}(t) = \sum_{i'} \sum_{j'} f(r).A.N_{i'j'}(t).S \tag{2.2}$$

where r is the distance between propagule source and cell receiving dispersed propagules, calculated by Pythagoras's formula ($r^2 = L^2((i-i')^2+(j-j')^2)$). For a bivariate normal distribution it can be shown that only 1.8 x 10^{-13} offspring are dispersed beyond a distance of 5xRMSD. In practice, summation can often be restricted to a distance of less than 5xRMSD.

If all the propagules grew to maturity, they would occupy an area $a.M_{ij}(t)$. In the absence of self-thinning, only a proportion P_1 will grow to maturity. Thus at the next generation, in the absence of self-thinning, a proportion

$$Q_0 = \frac{a.P_1.M_{ij}(t)}{A} \tag{2.3}$$

of the area should be covered by mature individuals. It is assumed that the propagules fall randomly so that in practice, a proportion

$$Q_1 = 1 - \exp(-Q_0) \tag{2.4}$$

of the cell will be covered (Hill, 1992). From equation 2.4 it can be seen that even when the potential area occupied by all the propagules is greater than the area of the cell in which they arrive some of the cell will remain unoccupied. The total proportion of the cell available for colonisation by propagules, Q_2, is its relative carrying capacity less the area occupied by surviving mature individuals i.e.

$$Q_2 = K_{ij} - \frac{a.P_2.N_{ij}(t)}{A} \tag{2.5}$$

Hence at time $(t + T)$ the number of individuals in the cell is:

$$N_{ij}(t+T) = P_2.N_{ij}(t) + \frac{A}{a}.Q_1.Q_2 \tag{2.6}$$

2.1.4. Modelling Dispersal

The number of dispersal functions is specified by the user so it is possible to have as many dispersal functions as required. Multiple dispersal functions may be particularly appropriate in cases where different dispersal mechanisms are operating. For most purposes two dispersal functions are probably sufficient. One can be used to represent local dispersal and the other long-distance dispersal. This results in a compound distribution. For the purposes of dispersal all the individuals are notionally located at the centre of their square.

At the start of each simulation, MIGRATE creates a "look-up" table. This stores the probability values for the dispersal function(s) in a way that can be accessed when calculating the number of propagules arriving in cells within a given distance of a propagule source. This increases computational efficiency since it is quicker to access the stored values than to have to continually recalculate the probability values. The dispersal functions which are used in MIGRATE have tails which extend out to infinity. However, beyond a certain distance the probability values become so low as to be negligible. The area over which dispersal is allowed to occur is determined by the value given to the parameter "furthest_cell" which is specified by the user at the beginning of the simulation. A "window" is then effectively placed over each cell in the habitat grid and the cell at the centre of the window disperses its offspring to all the cells within the window according to the dispersal function. As a check that the values assigned to the dispersal parameters, the cell length and the furthest_cell have been set appropriately, MIGRATE calculates the sum of the dispersal probabilities over the area specified by the value of furthest_cell. The dispersal sum should be equal to the dispersal probability value associated with each dispersal functions. The total of the dispersal probability values should be equal to 1. Values which are less that 1 indicate that the value of furthest_cell may have been too small, whereas values which are greater than 1 indicate that the cell length was too large in relation to the length of the realistically achievable part of the dispersal curve.

Deterministic versus stochastic modelling

MIGRATE is essentially a deterministic model. Although some of the processes involve the use of random numbers (see section 2.1.5) this is done merely to ensure that whole numbers are being dealt with. In order to make MIGRATE stochastic it would be necessary to use the Poisson distribution in conjunction with the long-distance dispersal probability values to determine the actual number of propagules which arrive in a cell. The Poisson distribution is a simpler form of the Binomial distribution and can be used to calculate the number of successes (i.e. arriving propagules) when the number of trials (dispersing propagules) is very large but the probability of success on each trial is very small. The probability of *k* successes is given by:

$$P(k) = \frac{e^{-\mu}\mu^{k}}{k!k} \tag{2.7}$$

where *n* is the number of trials, *p* is the probability of success and $\mu = pn$. The incorporation of this extra equation into MIGRATE would, however, result in simulations taking much longer to run. In addition to this, simulations may have to be run several times over in order to get a picture of the average outcome. The area where chance plays its most important role in migration is in the dispersal and establishment of offspring. However, since our knowledge of long-distance dispersal is so poor there is no advantage in trying to improve MIGRATE by modelling this process stochastically. The analytical models of van den Bosch *et al.* (1992) and Marinissen and van den Bosch (1992) are deterministic but have been shown to be good predictors of observed migration rates. In modelling the metapopulation dynamics of butterflies, Hanski and Thomas (1994) found that a stochastic version of their spatially explicit model produced results which were qualitatively the same as their deterministic model. Hengeveld (1989) states that although processes such as diffusion are stochastic when viewed at a small scale, the overall process of particle flow can be described in deterministic terms. Therefore the assumption is made in MIGRATE that the essentially stochastic processes of dispersal and establishment can be successfully modelled in a deterministic way.

Choice of dispersal function

Various dispersal functions have been implemented in both the one-dimensional and two-dimensional versions of MIGRATE. These include the normal distribution, the negative exponential distribution and the Weibull distribution. The formulae for these dispersal functions are given in Appendix A. The one-dimensional dispersal functions take the form *f*(x) where x is the distance between offspring and parent. The two-dimensional dispersal functions are of the form *f*(r) where r is $\sqrt{x^2+y^2}$ and x and y are the distances in the east-west and north-south directions respectively. Dispersal is assumed to be a rotationally symmetrical process occurring equally in all directions from each cell.

One of the unique features of the normal distribution which made it a particularly attractive distribution to include in MIGRATE is that its two-dimensional form can be integrated with respect to y to give the one-dimensional form. As a consequence of this, the migration rate produced by normal dispersal functions is the same in both one and two-dimensions. The integral of a two-dimensional function with respect to y gives the marginal distribution of dispersal distances i.e. the relationship between the density of individuals and the distance between the origin and the projection of the place of arrival onto the x axis of the Cartesian grid. It is the marginal distribution of a two-dimensional dispersal function which should be used in order to derive the same migration rate in one-dimension as in two (Van den Bosch *et al.*, 1992).

For the negative exponential and Weibull distributions, it is not possible to obtain a two-dimensional equation which can be integrated with respect to y to produce the one-dimensional equations given in Appendix A. It can be shown by plotting the numerical solution of the two-dimensional integral with respect to y (i.e. the marginal distribution) and the corresponding one-dimensional function given in Appendix A that the two distributions are not quite the same. For example, for the negative exponential distribution, the marginal distribution has a slightly higher tail than the one-dimensional formula given by equation A3. This explains why the negative exponential distribution produces a slightly slower migration rate in one-dimension compared with two-dimensions.

The negative exponential distribution has been included as a possible dispersal function since this is a distribution which has been commonly observed in the field. The Weibull distribution was added at a later date since this was found to give a good fit for the dispersal of *Senecio vulgaris* (Bergelson *et al.*, 1993). This is a two parameter distribution which may take on a variety of shapes including the negative exponential and is therefore a potentially good dispersal function to use if the dispersal densities can be determined quite accurately. As a consequence of this, the Weibull distribution is probably more suitable for modelling the dispersal of seeds which are dispersed over only a few metres and can be successfully trapped over this distance. This was the case for *Senecio vulgaris* where sticky traps were used to catch the wind dispersed plumed seeds.

The one-dimensional version of MIGRATE also has the facility for the empirically measured dispersal densities to be entered directly, thus avoiding the need to fit any dispersal curve. As most data in the literature are on distances only and lack any directional information it was inappropriate to develop this for the two-dimensional version of MIGRATE. In order for the empirical observations of dispersal densities to be used, the distance values must first be converted into marginal dispersal distances. This was done using a computer program which converted observed dispersal distances into marginal dispersal distances. For the purposes of this calculation, it was assumed that dispersal occurred symmetrically in all directions. For each dispersal observation, 20 marginal dispersal distance values were calculated and 1/20th of the propagule density at the observed distance assigned to the distance category within which the marginal dispersal distance occurred. The distance categories are user-defined, but should be equal to the cell length to be used in the MIGRATE simulations. The marginal dispersal distances were calculated using the formula:

$$\text{Marginal dispersal distance} = x\cos\theta_i$$

$$\text{where } \theta_i = \tfrac{\pi}{2}\cdot\tfrac{1}{20}\cdot(i-0.5) \qquad (2.8)$$

where i is all integers ≥ 1 and ≤ 20 i.e. the marginal dispersal distances were calculated by taking a 90° ($\pi/2$ radians) sector and dividing it into 20 equal sectors. The marginal dispersal distance was then calculated as the cosine of the angle made between the x axis and the line bisecting each sector.

In addition to these dispersal functions, the two-dimensional version of MIGRATE also has the option of placing most of the offspring into the parent's cell. This allows for the possibility of population increase without dispersal. This option is appropriate where the local dispersal function is very short in relation to the length of the cell. At the start of the simulation, MIGRATE creates a grid composed of one cell divided into 400 equal squares. Dispersal is calculated from the centre of the grid according to a local bivariate normal dispersal function and the proportion of propagules which escape the grid i.e. are capable of escaping from the parents cell is determined. Since these individuals would be placed in the centre of one of the adjacent cells, the dispersal probability values associated with the adjacent and corner cells have to be reduced in small equal proportions until the RMSD of the original local dispersal function is obtained. In the one-dimensional version of MIGRATE a less accurate version of this option was implemented whereby all the locally dispersed offspring were placed in the parent's cell. Sensitivity analyses using the one-dimensional model have shown that this is a good approximation when the tail of the long-distance dispersal function is long (section 4.1.3). As the number of computations is much less in the one-dimensional model, it is easy to test this approximation by repeating the simulation with a small cell length appropriate to the length of the local dispersal function.

The problem of scale

In order to allow for a dispersal function where successful dispersal occurs over distances of much more than ten times the cell length a system of amalgamating cells has been developed in the two-dimensional version of MIGRATE in order to increase computational efficiency. This facility was not needed in the one-dimensional version of MIGRATE because the number of computations involved here is so much less. The degree of amalgamation is specified by the user at the beginning of the simulation. The way in which the process of amalgamation works is best illustrated by an example. With a cell length of 1 km and a long-distance bivariate normal dispersal function with an RMSD of 10 km an amalgamation of 5 cells could be set without any significant loss in accuracy. Dispersal probability values at a 5 km resolution are calculated i.e. for the purposes of long-distance dispersal the cell length has been effectively increased to half the value of the RMSD. As there are 25 1 km squares within each 5 km square, the probability of arrival in each 1 km square is simply approximated as being 1/25th of the probability of arriving in the 5 km square within which the 1 km square falls. This approximation is a simple extension of what is already happening in the modelling of dispersal, since a continuous process is being modelled as a discrete process.

Logging of dispersal distances

From the values given to the dispersal parameters and the product of S and P_1 it is possible to predict the furthest distance over which successful establishment may occur. However, in order to gain a better idea of what is happening, a procedure has been implemented in the two-dimensional version of MIGRATE to count the number of potential recruits dispersing into various distance categories. The recruits are referred to as potential recruits because whether or not they actually establish depends upon the availability of suitable habitat within the cell where they arrive. The sampling interval for the distance categories is equal to the cell length. As the logging of dispersal distances significantly reduces the run-time of MIGRATE the procedure was implemented as an option which could be compiled and therefore included as part of the simulation if required. The one-dimensional version of MIGRATE simply outputs the value of the furthest distance over which a prospective recruit is dispersed. It should be noted however, that the value of the longest dispersal distance is partly determined by the number of generations which are simulated. This is because for simulations of a longer time span there is more opportunity for long-distance dispersal events to occur.

2.1.5. The "rounding" Option and Stochastic Events

MIGRATE has been created as a deterministic model for purposes of clarity and simplicity , however, both the one-dimensional and the two-dimensional versions of MIGRATE include the facility to round the number of individuals to a whole number according to a random number between 0 and 1. This introduces a small area of stochasticity, but serves mainly to prevent the occurrence of fractions of individuals. Fractions of individuals are generated as a direct consequence of the survival and dispersal probabilities and the random nature in which individuals fall in a cell (equation 2.4). Sensitivity analyses using the one-dimensional version of MIGRATE have shown that rounding does not have a significant effect on the migration rate although in some cases it may lead to a slight reduction in the rate. Its main effect is to cause the shape of the migration front to become less smooth. This effect is usually only observed in cases where there are a small number of individuals being dispersed over a long distance. In the case of the two-dimensional version of MIGRATE, rounding is always carried out. If this were not done, then the very small fractions of individuals at the migration front would appear as yellow shaded areas on the output plots making the extent of spread appear larger than it would be in reality. In the one-dimensional plots, the low values at the front of the distribution are so small as to be indistinguishable from zero.

The random number generator "ran1" from the C programming library (Press *et al.*, 1992) was used to generate random numbers between 0 and 1. The fractional part of each real number is compared with a random number generated by ran1. If the random number is less than the fractional part of the real number against which it is being compared then the real number is rounded up to the nearest whole number. If the random number is greater than the fractional part of the real number then the real number is rounded down.

2.1.6. Summary of Assumptions Made in MIGRATE

1. All individuals in a cohort are identical with respect to fecundity and survival etc. The parameter values used are the average values for the cohort.

2. The fecundity and survival parameter values are dependent on the age of an individual and not its size.

3. For the purposes of dispersal, all individuals are considered to be at the centre of the 1 km square which they occupy.

4. Dispersal occurs in a radially symmetrical fashion.

5. The organism settles down for life after dispersing from its place of origin.

6. All individuals occupy the same area therefore intraspecific competition for space occurs once only i.e. during recruitment to the first cohort.

7. The stochastic processes of dispersal and establishment can be effectively simulated in a deterministic way...

8. The probability of a propagule reaching the age of first reproduction is random and does not depend on the distance from its parent.

2.1.7. Miscellaneous Technical Details Regarding MIGRATE

The number of cells which can be used in a simulation is limited by the amount of memory available on the computer. MIGRATE has been successfully used to model the dispersal of rhododendron over an area 10 km by 12 km at a 10 m resolution i.e. 1000 x 1200 cells were used to represent the habitat (Griffin, 1994). As eight cohorts were used, a further 8 x 1000 x 1200 cells were used to hold the number of individuals in each age class in each cell of the habitat map. This research represented the limits of what is possible on the Sun SPARC station IPX used to carry out the simulations.

Execution times depend on the number of generations over which a simulation is run, the number of cells used to represent the environment and how extensive the spread of the species being modelled is. They vary from less than a minute for simple one-dimensional simulations to up to a few hours for more complex two-dimensional simulations.

Double precision arithmetic was used where appropriate, for example in calculating the dispersal probabilities and the number of propagules arriving in each cell. Double precision was used here because it was considered that the small values which may arise should be calculated accurately. In order to conserve memory space, single precision variables were used to store the number of individuals in each cohort, the relative carrying capacity values and the climate suitability map. The larger values of these variables meant that precision here was not so important.

2.2. Estimating Parameter Values for Tree Species

One of the reasons that much of the modelling work on migration has been concentrated on short-lived species is because quantitative data on their ecology can be more readily obtained, either through field work or from the literature. The great longevity of trees has meant that there is very little direct evidence on their population dynamics (Crawley, 1990).

The following parameter values may usually be obtained from the literature:

1. age to reproductive maturity (T);
2. number of propagules produced per year;
3. frequency of mast years where appropriate;
4. typical age of death.

From 2 and 3 it is possible to estimate the number of propagules (S) produced per generation. There are very limited amounts of quantitative data on the probability of survival for long-lived species such as trees. One possible means of deriving survivorship and fecundity data is to carry out long-term studies of the kind carried out by Pinero *et al.* (1984) where the fate of individual seedlings was followed over time. Survivorship curves also could be obtained by analysing the current age structure of a population (Crawley, 1983). The assumption made with such a study is that if recruitment is constant and age-specific mortality is neither time dependent nor density dependent, then the fraction of individuals in an age class is a good estimate of survivorship to that age. However, in most cases, the age structure of a forest will have been determined by past disturbance events such as storms, fires and pest outbreaks and will not therefore reflect progressive age-specific mortality. If it is assumed that following initial establishment survivorship is constant, then the probability of adult survival (P_2) may be estimated from the equation:

$$P_2 = \exp\left(-\frac{T}{T_d - T}\right) \tag{2.9}$$

Whittaker (1975) suggests that the death rate of *Quercus alba* is roughly constant over its 300 year life span, so constant survivorship may not be such an unrealistic assumption to make. In the absence of more accurate data, equation 2.9 probably represents the most satisfactory means of estimating the probability of adult survival.

It is known that the probability of a tree seed reaching the age of first reproduction is very low, for example, Crawley (1983) assumes a probability of survival to the age of first reproduction of $5x10^{-5}$ when estimating the range within which the intrinsic rate of population increase for a tree which first reproduces at 40 years lies. Clarke (1992) lists the many reasons why sitka spruce seedlings fail to establish. From the mortality data which Clarke has gathered from various sources it is possible to deduce that the probability of a seed surviving until its second winter is $1.4x10^{-4}$. Watt (1919) discusses why so few acorns become mature trees.

The field studies that have been done on dispersal distances were discussed in section 1.5. These studies have generally measured only local dispersal due to the difficulties in obtaining quantitative data on long-distance dispersal events. Results from these studies have lead to the conclusion that most seeds fall with a few hundred metres of the canopy The data on long-distance dispersal events are mostly anecdotal. However, it is possible to use the one-dimensional version of MIGRATE to obtain values for the probability of survival to reproductive maturity and the long-distance dispersal parameters. This may be done by varying the values of these parameters in order to determine the area of parameter space in which the required migration rate (as determined from palaeoecological studies) occurs.

2.3. Setting up the Environmental Conditions

2.3.1. Initial Distribution of Individuals

MIGRATE has been developed so that there are various ways in which the initial distribution of the species being modelled may be entered. For the two-dimensional version of MIGRATE these include:

1. As an ASCII file consisting of a grid reference followed by the number of trees in the square defined by the grid reference. The number of figures in the grid reference should correspond with the cell size used in the model simulations. For example, a six figure grid reference is require for a simulation with a 1 km square resolution. Missing grid references are interpreted as meaning that there are no individuals present at that location. The grid references are checked to ensure that they fall within the boundary of the area being modelled.

2. As an ordered list of tree numbers starting with the south west corner and finishing with the north east corner.

Distribution data files are read in for all cohort classes and the total number of individuals present in each cell checked to ensure that it does not exceed the maximum value determined by the relative carrying capacity. If the maximum value has been exceeded then the number of individuals in each cohort class is reduced in equal proportions so that the total number of individuals is equal to the maximum value.

For the one-dimensional version of MIGRATE, the initial distribution is read in as an ordered list of either actual numbers or the fraction of the cell which is occupied. The initial distribution is checked against the relative carrying capacity values in the same way as for the two-dimensional model.

2.3.2. Creation of Habitat Suitability Maps

For the one-dimensional version of MIGRATE the value of the relative carrying capacity which is constant for all cells is specified by the user. It would not be appropriate to use heterogeneous relative carrying capacity values in the one-dimensional version of MIGRATE since the one-dimensional migration process can not allow for a species to spread around areas of unsuitable habitat. For the two-dimensional version of MIGRATE, the area covered by the habitat map and its resolution is determined by the array size (number of cells in the habitat map) and the cell length. The array size is defined by the constants *i_max* and *j_max* which are defined at the beginning of the program. For technical reasons, these values have to be explicitly set to the exact number of cells required to represent the study area. The cell length should be set to correspond with the resolution of the habitat data.

Format of the input file

The data can be entered in the following formats:

1.
```
nrows 140
xllcorner 250000
yllcorner 460000
cell size 1000
NO DATA value -9999
6.56 0.68 0.43 8.21..........
```

Line 1 is the number of rows i.e. number of cells in the northerly direction. Lines 2 and 3 give the 6 figure grid reference for the southwest corner of the habitat grid. Line 4 gives the cell length in metres and line 5 the data value which indicates the presence of the sea. The actual data values expressed as percentages follow in order starting with the northwest corner and finishing with the southeast corner.

2.

```
276.0 544.0 348.0 654.0
561 321 16.1
561 322 8.3
...........
```

The first line lists the lower northerly, lower easterly, upper northerly and upper easterly grid references expressed as real numbers. The data then follow in any order as an easting, northing and % value. Missing data values indicate the presence of the sea.

3.

```
0A31400025
749201AA6
```

This is an ordered list starting with the southwest corner and finishing with the northeast corner. The relative carrying capacities are converted into numbers according to the rule 0 = 0.0, 1 = 0.1, ... A = 1.0.

In order to create a habitat suitability map which can be considered to be representative of the modern day landscape, data from the 1 km resolution Institute of Terrestrial Ecology land cover of Great Britain database can be used to create files of either of the first two formats. These data consist of percentage coverage values for twenty five different land cover types. MIGRATE currently allows the percentage cover of one land cover type to be read in and used to assign the relative carrying capacity value. However, it would be very easy to use more than one land cover type and generate the relative carrying capacity values based on these. The third format was used by Griffin (1994) where a conversion program was used which took input from several GIS coverage maps (holding data on for example, the presence/absence of roads, rivers, forests and grazing regime) and produced output in the required format. By using this approach a more versatile relative carrying capacity map can be created.

Once the data have been read in and expressed as a fraction of the cell available for occupancy (in the range 0.0 to 1.0) then they may be modified further if required by multiplying by some fraction which determines the final relative carrying capacity value. This option is most useful where the relative carrying capacity values have been set using the percentage cover of one of the land cover types as it effectively determines how much of that land cover type the migrating species can come to occupy.

With the third option the facility for allowing the relative carrying capacity values to change during the simulation, for example in response to changes in land management practices, has been implemented. This option was used by Griffin (1994) to investigate the potential spread of rhododendron in Glen Etive and possible control strategies. It would be straight forward to include this facility with the other options if the need were to arise.

A final option for setting up the relative carrying capacity map is to set up a random habitat map. In this case the relative carrying capacity is either 0 or some constant specified by the user. The fraction of cells which are non-zero is specified by the user. This option allows simple investigations to be made into the effects of habitat availability on migration rates in the same way as has been done by Schwartz (1992).

In order to set up a homogeneous environment, the option to set all land cells to a constant value has been implemented.

The use of probability of occurrence values for investigating the response to climate

The relative carrying capacities may be modified by using a probability of occurrence file. This file is read into MIGRATE in the form of an easting and a northing value followed by a probability of occurrence value. The probability values were calculated by fitting the current presence/absence data for a species in Europe (obtained from the *Atlas Florae Europea*) to three bioclimatic variables at a 50 km resolution (Huntley *et al.*, 1995). The resulting response surface consisted of probability of occurrence values at a 10 km scale with respect to the mean temperature of the coldest month, the temperature sum above a 5°C threshold and the ratio of the actual to the potential evapotranspiration rate. In order to use the response surface to generate a current distribution of a species which resembles its observed distribution, it was found that a probability threshold had to be set. If this threshold probability is exceeded then the species is predicted to occur otherwise it is predicted to be absent. The response surface can be used to generate probability of occurrence values for each 10 km square in the British Isles using climate data obtained from the Climatic Research Unit (Huntley, unpublished results). These data can then be read into the MIGRATE model and used to modify the values of the relative carrying capacities. Where the probability of occurrence threshold is exceeded, the relative carrying capacity values are modified by multiplying by the probability of occurrence value for that square. However, if the threshold is not exceeded then the relative carrying capacity is set to zero. By using a climate scenario for a doubling in the concentration of carbon dioxide, it would be possible to derive probability of occurrence values for the species being modelled under future climatic conditions. A climate response surface for the invasive weed *Fallopia japonica* (Japanese knotweed) derived from European climate and distribution data has been successfully used to predict its native distribution in Southeast Asia (Beerling *et al.*, 1995). The close agreement between the simulated distribution and the observed distribution indicates the robustness of this static correlative modelling approach.

Smoothing the relative carrying capacity values

In order to investigate the effect of the distribution of habitat availability, the option to smooth the relative carrying capacity values has been implemented. Each cell is taken in turn and a new relative carrying capacity value assigned by taking the average relative carrying capacity value of all non-sea cells within a specified distance. The new carrying capacity values are stored separately until all the cells have been assigned a new value. The old values are then replaced by the new smoothed values.

2.3.3. Climate Suitability Map

The facility to read in a temperature dataset as a means of determining whether or not reproduction can occur in a particular grid square has been implemented. Temperature was chosen as a means of deciding whether or not reproduction can occur because much of this research project has concentrated on the response of *Tilia cordata* to future climatic change since the factors which determine its range limit in northern England are well understood (Pigott, 1992 and references therein). From this research, it has been established that the northern limit of *T. cordata* in the British Isles is correlated with the mean August daily maximum temperature. The MIGRATE model could be refined to take into account any variable which correlates with or is known to influence the distribution of the species being modelled (for example, precipitation). In the absence of detailed data on the relationship between temperature and propagule output it was decided to simply use a threshold temperature below which no reproduction can occur.

The climate data relating to temperature were obtained from the Climatic Research Unit (University of East Anglia) and are in the form of nine ASCII files which hold the minimum, mean and maximum temperatures for each month at the lowest, modal and highest elevations for each 10 km square of the British Isles. A separate program was written to extract the relevant temperature values and output them as an ordered list. The input required for this data extraction program are the grid references of the south west and north east corner of the area being modelled, the number of the month for which the temperature data are required and the name of the chosen temperature data file.

In order to produce a 1 km resolution climate map from the 10 km resolution data, altitude data from the Bartholomew's 1993 contour data were used. As the relationship between climate and altitude is linear, a computer program was written which read in the data from the three climate files corresponding with the three elevation categories. Linear regression was then performed on the relationship between temperature and altitude for each 10 km square. The temperature value for each 1 km square was output by inserting its elevation as given by the Bartholomew's contour data into the linear solution.

As temperature is not constant from year to year, a final refinement to the model was to include a mechanism for allowing the climate to fluctuate. Statistical analysis of the mean August daily maximum temperatures for Durham for the period 1960 to 1990 revealed that this variable had a good fit to a normal distribution (correlation coefficient 0.8) with a standard deviation of 1.57°C. The same dataset for Morecambe yielded a standard deviation of 1.47°C. In order to use these data to determine an estimate of temperature variability it was assumed that there was no trend during this period and that temperature variability remained constant. During a simulation in which climate is acting as a limiting factor, MIGRATE reads in the climate data as described above and then uses random numbers to vary the temperatures about their mean values. This is done by multiplying the standard deviation (which is specified by the user) by a random number from a standard normal distribution and then adding this value to the actual temperature value. The routine "gasdev" in conjunction with ran1 from the C programming library (Press, 1992) was used to generate the normally distributed random numbers. So that climate may vary on an annual time scale, a temperature value is generated for each year, i.e. if the generation time is 25 years then 25 temperature values are generated for each square during each time step of the simulation. The fecundity of the species is then modified by multiplying it by the number of times the temperature threshold has been exceeded expressed as a fraction of the number of years in a generation.

CHAPTER 3

Field Work: An Investigation into Seed Dispersal

Much of the data required for MIGRATE can be obtained or estimated from the literature. However, there are very few data on seed dispersal distances. The data which do exist are mostly anecdotal observations of long-distance dispersal. There are also a few detailed studies on local dispersal done mainly by commercial foresters. This chapter describes the field work which was carried out in order to obtain a seed dispersal curve i.e. the change in seed density with respect to the distance from the seed source. The results are compared with those obtained in other studies. As for most other studies, dispersal was measured from a forest edge rather than from an isolated tree. Computer simulations were done in order to look at how the dispersal curve at a forest edge relates to the dispersal curve from an individual tree since it is this which is used in the MIGRATE model.

3.1. Choice of Species

The choice of species was restricted by the availability of a suitable site for that species. Wind dispersed seeds are more easy to study since seed traps can be used, although these may also be appropriate for some bird dispersed propagules (for example, Smith, 1975). Where animals are the main agent of dispersal it is usually more appropriate to examine seedling recruitment.

3.2. Choice of Site

The following conditions were needed in order for a site to be considered suitable:

- an isolated tree or block of trees acting as a good seed source;

- a large area adjacent to the seed source over which dispersal and preferably also establishment is occurring;
- no reproductively mature trees of the same species as that being studied in the area where dispersal is being measured.

Although other published work on seed dispersal does not explicitly state the criteria used in the selection of a study site, the above criteria are generally met. The reasons for the first two criteria are fairly obvious. It is necessary to have a good seed source so as to increase the number of seeds which will be trapped and therefore increase the reliability of the fit of the field data to a dispersal curve. A large seed source effectively allows dispersal to be measured over a longer distance. Most studies have been from forest edges (Willson, 1993) because these are more often to be found with large expanses of land adjacent to them into which dispersal can occur. A solitary tree, however, is much more difficult to find. The size of the area into which dispersal is occurring should be as large as possible. Ideally, the study site should be large enough to permit the recording of the longest dispersal event which is likely to occur. This distance may be estimated by multiplying the post-glacial maximum migration rate by the minimum age to seed production. For example, if the maximum migration rate of *Pinus* in England is taken as 700 m yr^{-1} (Birks, 1989) with 15 years as the minimum age to first reproduction (Miles, 1988), then the required dispersal distance per generation is 10.5 km. This long-distance dispersal event needs to occur only once every 15 years in order for the post-glacial migration rate of 700 m yr^{-1} to be achieved. As it is so rare it is very unlikely to be detected by field studies.

The maximum distance over which dispersal has been measured by other workers varies considerably, from about 100 m (for example, Boyer, 1958; Hughes and Fahey, 1988) to up to 4 km (for example, Welch *et al.*, 1990). The tail of the dispersal distribution is notoriously difficult to measure because of the low frequency at which the long-distance dispersal events occur Willson (1993). However, by extrapolating the proximal part of the dispersal curve it may be possible to make predictions about the frequency at which the long-distance dispersal events may occur.

The last criterion is necessary so that one can be certain of the origin of the seeds. Statistical techniques such as maximum likelihood analysis could have been used to determine which tree a seed was most likely to have originated from. However, this would require the mapping of all the conspecific trees in the study area. This would be a very substantial task in a large study area with a large number of seed producing conspecifics spread throughout. In addition, the amount of computation required in the use of maximum likelihood analysis would become unmanageably large where dispersal occurs over a large area. Ribbens *et al.* (1994) used maximum likelihood analysis to fit parameter values to a dispersal model. These values were then successfully used in their stand model SORTIE. However, they were effectively concerning themselves only with local dispersal as they found that mapping all adult trees within a 20 m radius was more than adequate for all species except those with a mean dispersal distance greater than 15 m. The wider confidence interval found for those species with a mean dispersal distance greater than 15 m was thought to be due to the uncertain effects of recruits derived from trees located outside the mapped area. This would be a major problem where long-distance dispersal events are the main area of interest. It is therefore possible to conclude from their work that maximum likelihood analysis is suitable for fitting a curve to the locally dispersed seeds, but not for the more widely dispersed seeds. For forest stand models such as SORTIE which operate at a small spatial scale, it is the local dispersal distribution which is most important in determining recruitment patterns and so the use of maximum likelihood analysis is appropriate. However, at a larger scale when the subject of interest is migration, the long-distance dispersal events play a more important role than the local dispersal events so maximum likelihood analysis is less appropriate.

There are several ways in which dispersal could be investigated. Those approaches which involve looking at established seedlings require that the area under study is as homogeneous as possible so that establishment is not complicated by factors other than distance from the seed source (for example, soil type, altitude, aspect, existing vegetation cover etc.). These conditions are particulary well met where dispersal is occuring into abandoned agricultural fields (for example, Johnson, 1988; Myster, 1993). The alternative approach which involves the trapping of seeds does not demand such stringent criteria.

If a site has a series of aerial photographs available spanning a period of several decades then these may be useful in obtaining a measure of the rate of spread. From this, together with a knowledge of the generation time of the species, it is possible to estimate the maximum successful dispersal distance but not the shape of the whole dispersal curve.

3.3. Sites Visited

A considerable amount of time was spent looking for a suitable study site. Various people were contacted for suggestions and visits were carried out where appropriate.

North Yorkshire Moors

Various sites were visited within Cropton and Dalby forests in the North Yorkshire Moors National Park with the help of the forest district manager. A site in Givendale (Grid Reference 879845) was considered to be suitable for investigating sycamore (*Acer pseodoplatanus*) dispersal. The site had recently been clear felled to leave 15 metre wide strips of sycamore trees separated by about 120 metres of newly planted spruce (see Fig. 3.1). Another site near Keldy Castle in Cropton Forest (Grid Reference 778921) was chosen for studying Scots pine (*Pinus sylvestris*) and larch (*Larix decidua* Mill.) dispersal. This site consisted of recently replanted clear felled land which was enclosed on four sides by plantation. Scots pine was restricted to the northerly and southerly plantations (see Fig. 3.2).

Hamsterley Forest (County Durham)

As for the sites in the North Yorkshire Moors there were various possible sites within Hamsterley Forest (Grid Reference 040290) for looking at the dispersal of seeds into clear felled land adjacent to plantations of Scots pine, Norway spruce and larch etc.

Farmland adjacent to Houghall Woods (County Durham)

The fields adjacent to Houghall Woods (Grid Reference 280278) were examined for recruitment in spring 1993. However, due to grazing by sheep and cattle very few tree seedlings were found.

Hartside Nursery near Alston (Cumbria)

This site (Grid Reference 708468) consisted of mixed deciduous woodland alongside a stream. Adjacent to the woodland was some rough grassland which was ungrazed although mown in early summer. No seedlings were found where the grass was growing densely, however, plenty of sycamore seedlings were found on a steep bank where the vegetation cover was less dense. Unfortunately, this area of recruitment was too small for a meaningful survey to be carried out. There also was evidence that grazing rabbits were stunting the growth of the seedlings.

Cockle Park (Northumberland)

This site (Grid Reference 201913) consisted of some mature sycamore trees adjacent to currently ungrazed pasture. Sycamore seedlings were very obvious in the disturbed area by the field gate. However, in the less disturbed area where the grass was over 6 inches high no seedlings could be found.

Castle Eden Dene National Nature Reserve (Cleveland)

The woodland at Castle Eden Dene (Grid Reference 425390) occurs in fairly discrete blocks of different National Vegetation Classification types. However, the small size of the blocks coupled with the fact that many otherwise suitable sites occurred on rather steeply sloping ground meant that no really suitable site was found. The only site which may have been suitable for seed trapping studies was considered to be liable to vandalism due to its close proximity to the town of Peterlee.

Carrbridge Fire Site (Speyside)

A large area of Scots pine forest (Grid Reference 890230) was destroyed by fire in 1978 so it was thought that this may offer an opportunity to study invasion. An aerial photograph exists of the site ten years after the fire. However, as for many of the potential sites in Scotland the land has been subject to grazing by deer thus inhibiting re-establishment. Since the aerial photograph was taken the land has been ploughed up and planted with Scots pine.

Muir of Dinnet National Nature Reserve (Deeside)

There is an area within the Dinnet National Nature Reserve where birch and pine are re-invading due to a reduction in grazing pressure. From the 1976 1:50,000 Ordnance Survey map, it is possible to see that the original plantation was restricted to a small area at Lochhead to the west of the A97 (Grid Reference 435006). However, there is now substantial re-colonisation of pine and birch all the way up to the summit of Culblean Hill (approximately 500 metres in altitude and 2 kilometres from the original plantation edge). Some of these trees are now reproductively mature, as a result the site is no longer suitable for carrying out seed trap studies or seedling surveys.

Tulloch Moor (Speyside)

A series of aerial photographs for the years 1948, 1966, 1978 and 1988 are available for Tulloch Moor (Grid Reference 960170). From these it is possible to see the spread of trees into the moor from the woodland to the north. Between 1966 and 1978 when re-invasion occurred most rapidly the rate of spread can be measured as approximately 16 m yr^{-1}. This is an order of magnitude slower than that determined by palaeoecologists for post-glacial migration. This slow migration rate is most likely to be a result of grazing by sheep and deer. Within more recent years, regeneration has been removed from parts of the moor so as to ensure it retains its moorland character which is an important habitat for birds. The moor itself is not more than two kilometres wide and so would not be suitable for looking at dispersal distances greater than one kilometre.

Northern Corries, Cairngorms National Nature Reserve (Speyside)

The moorland area to the north of Cairn Gorm and the south of The Queens Forest (Grid Reference 970050) is developing into subalpine scrub. The re-invasion of pine has already been studied by the Institute of Terrestrial Ecology who did a detailed survey of the area in September 1985 (Welch *et al.* 1990). It was considered inappropriate to attempt to repeat their work especially as it took 72 man days of field work to collect the data from which the Scots pine dispersal curve was produced.

3.4. Method

Two of the approaches for investigating dispersal which were reviewed in section 1.4 were tried. The first involves counting the number of saplings along transects running from the seed source (for example, Smith, 1900; Van Wilgen and Siegfried, 1986; Johnson, 1988). The other approach was one which has been used by Hughes and Fahey (1988) and commercial foresters (for example, Isaac, 1930; MacKinney and Korstian, 1938; Boyer, 1958; Roe, 1967) and involves the use of seed traps to catch seeds. For this method it was preferable to choose species which produced good seed crops most years. Trees with mast years separated by several years of very low seed production were avoided, as only two seasons were available for studying dispersal. This problem is not likely to occur when it is the distribution of seedlings which is being recorded.

3.4.1. Sampling Seedlings

At the Givendale site in the summer of 1993 sycamore seedlings were counted along transects running perpendicular to the seed source (Fig. 3.1). Contiguous 2 metre square quadrats were marked out along the line of the transect and the number of 1, 2 and 3 year old sycamore seedlings counted. A brief note was also made of the vegetation cover in each quadrat so that it would be possible to see if this was affecting recruitment in any way.

3.4.2. Seed Trapping

This method was used for sycamore seeds at the Givendale site in autumn 1993 and for Scots pine and larch seeds at the Keldy Castle site in the springs of 1994 and 1995. The seed traps had a catchment area of 0.25 m^2 and were constructed as shown in Fig 3.3. The collecting bag was made out of nylon net curtain fabric which was stapled to a wire frame. The frame was attached to the cane legs with electrical insulation tape. A large stone was placed in the bottom of the bag and some string tied above it and across to a pair of diagonally opposite legs. This was to prevent the trap from blowing inside out. Hughes *et al.* (1987) used a similar design for their seed traps. They did not consider the predation of seeds to be a problem because the seeds were funnelled down into the bottom of the trap where they were not clearly visible. There was also no evidence of rodents gnawing at the collecting bags. It seems reasonable therefore to assume that the seeds within the traps were not exposed to predation. There was no evidence to suggest that this was not a valid assumption. The traps themselves took only a few minutes each to erect in the field. The collecting bags had to be replaced after about one year in the field since exposure to weather and sun light caused the material to rot.

The traps were set out in a 10 m square grid arrangement. At Givendale there were 10 traps running along 9 transect lines (A to I) perpendicular to the seed source (Fig. 3.4). The first trap was within a few metres of the canopy of the sycamore trees. At Keldy Castle there were 7 transect lines with 11 traps in each (Fig. 3.2). The first trap was positioned 5 m from the canopy of pine and larch. The sites were visited at intervals of approximately six weeks in order for the seeds to be collected and any necessary repairs carried out to the traps.

Plate 1 shows a photograph of a seed trap in position at the Givendale site. Plate 2 shows photographs of the seed traps in position at Givendale (top) and Keldy Castle (bottom).

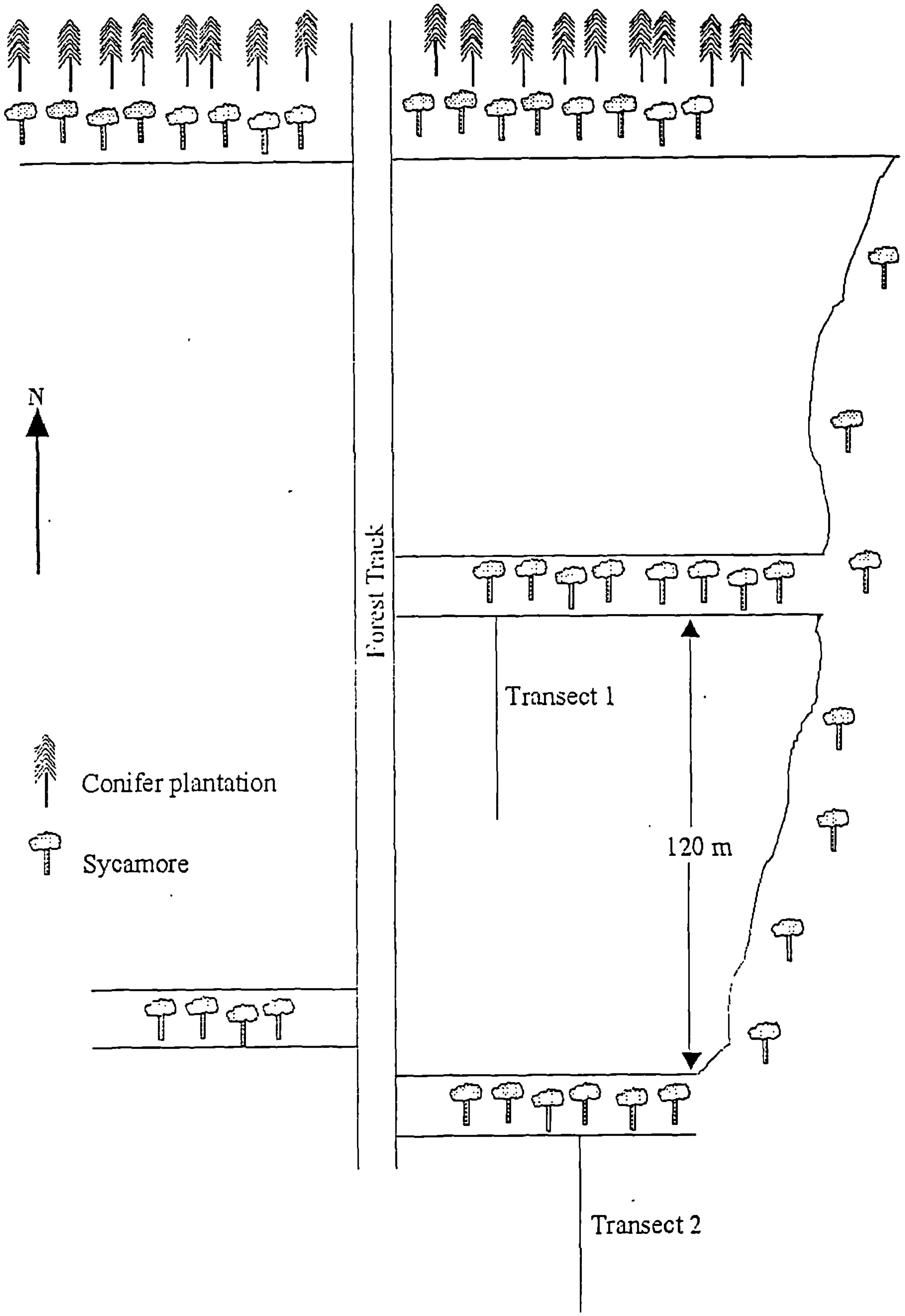

Figure 3.1 Schematic diagram of the Givendale site showing the locations of the transects used for taking seedling counts.

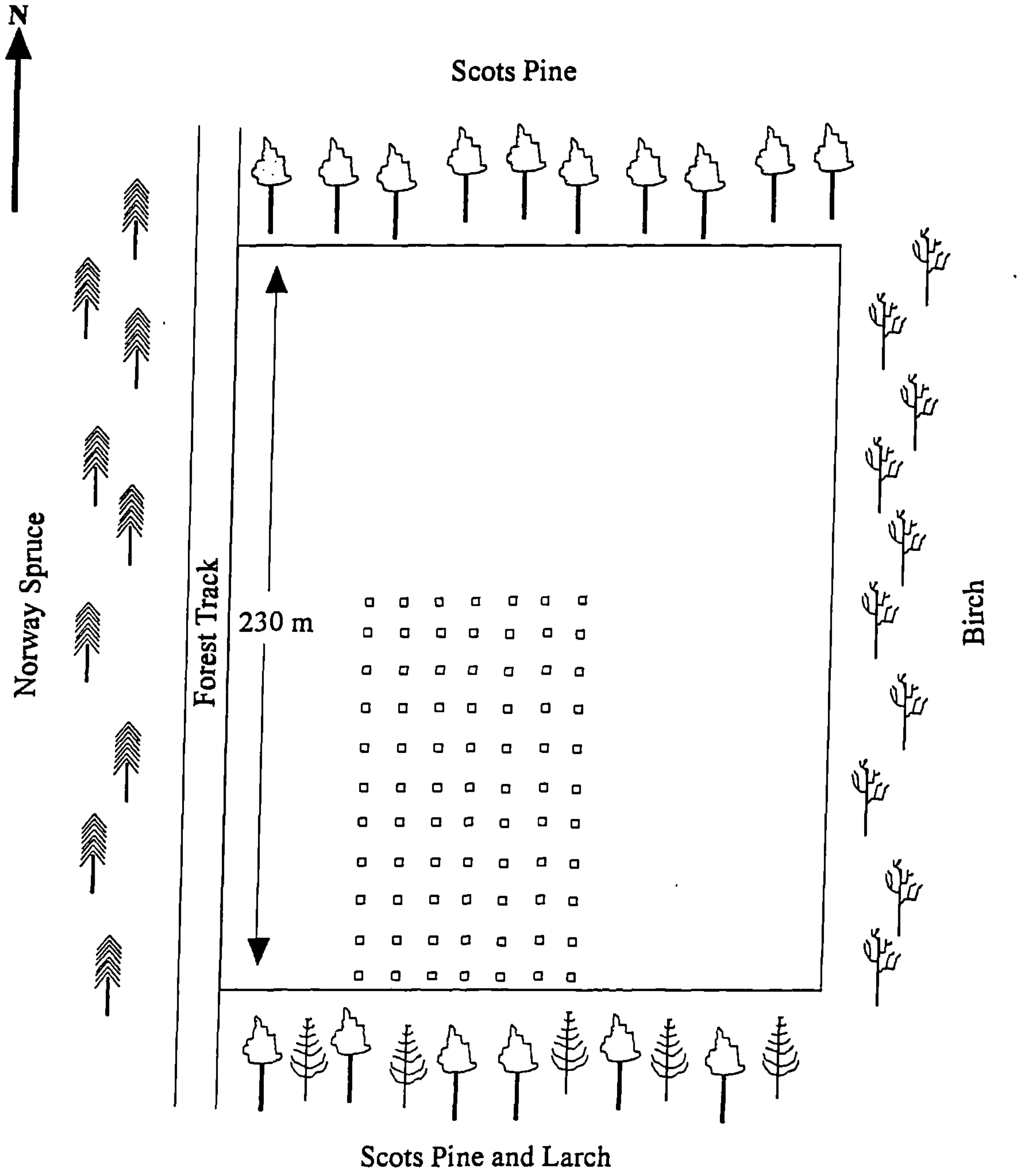

Fig. 3.2 Schematic diagram of the Keldy Castle site showing the arrangement of seed traps.

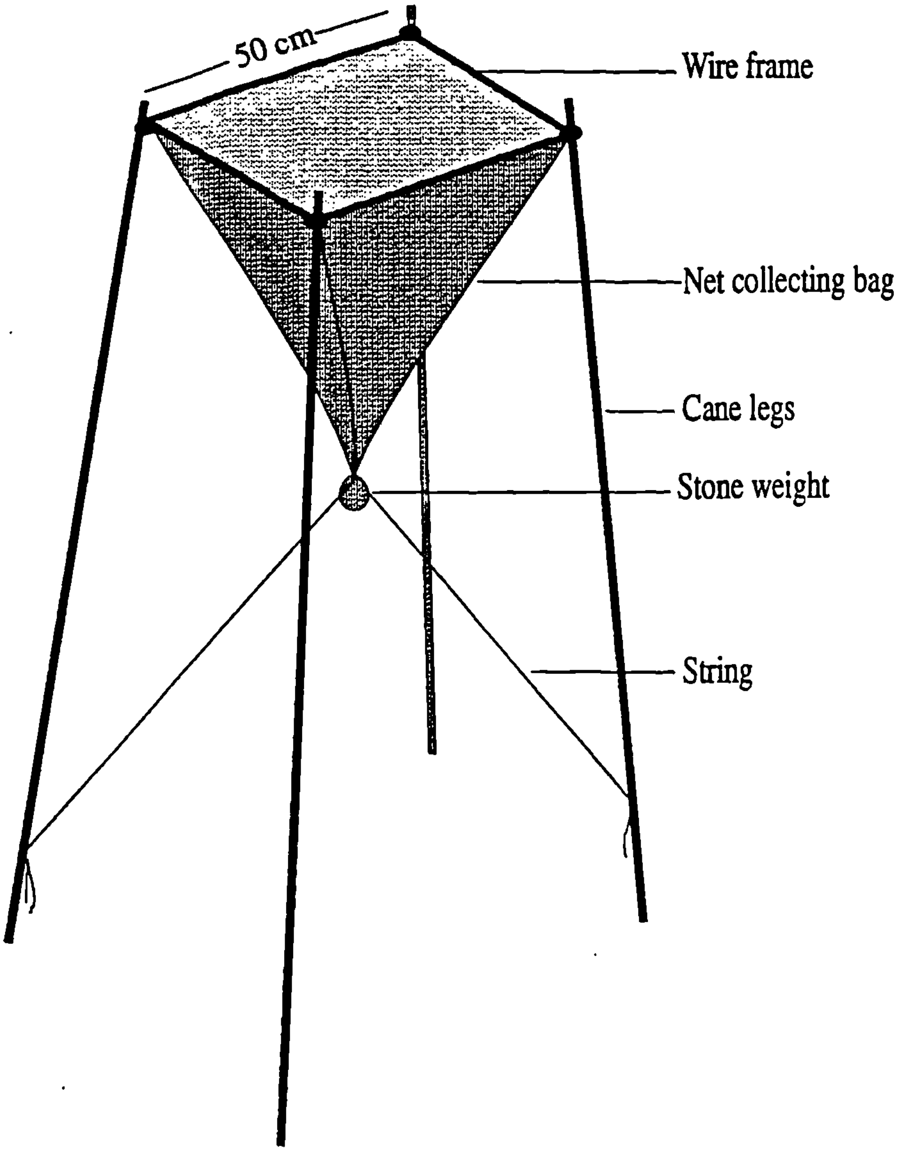

Figure 3.3 Diagram showing the construction of a seed trap.

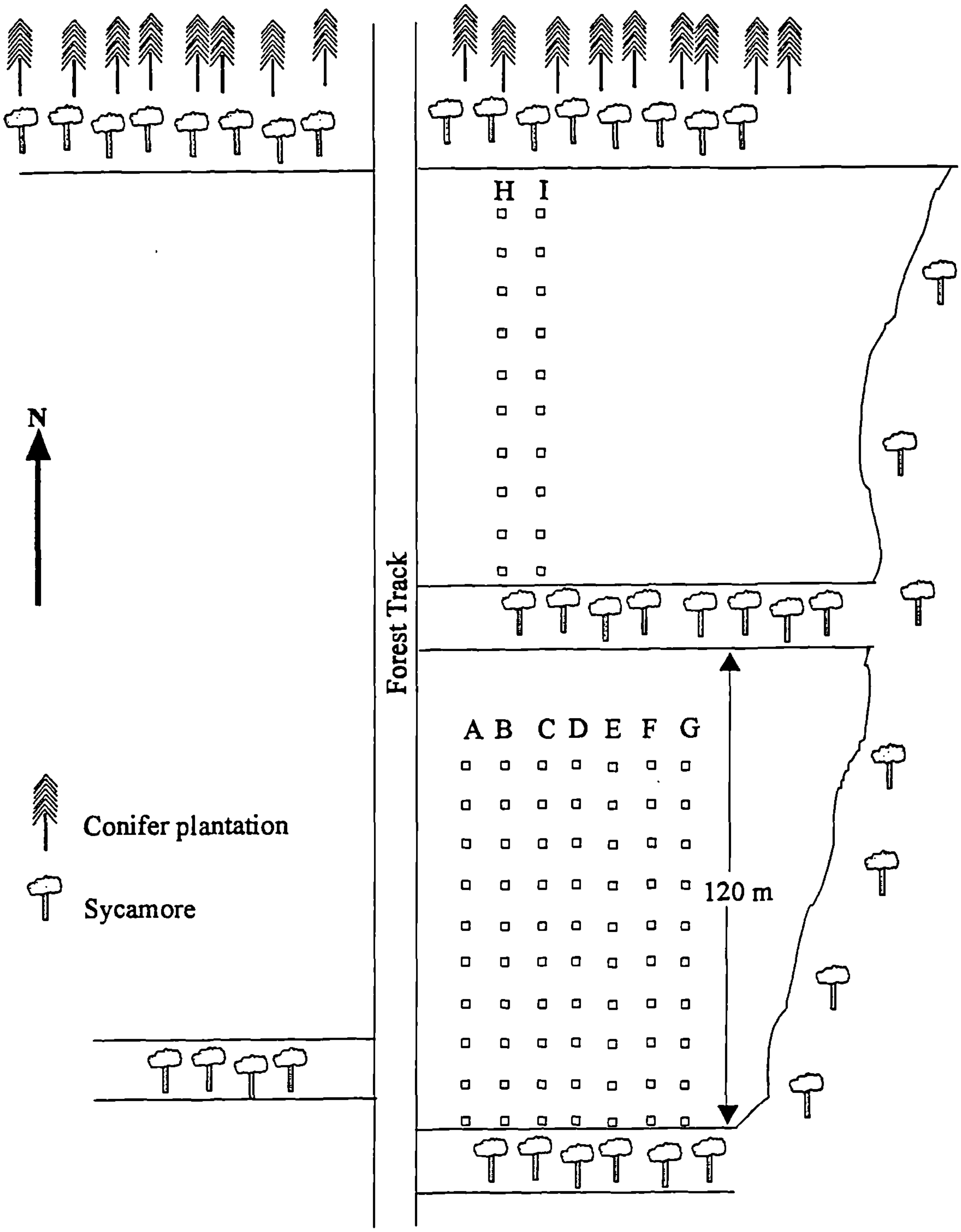

Fig. 3.4 Schematic diagram of the Givendale site with the position of the seed traps shown.

Plate 1 A seed trap in position at the Givendale site.

Plate 2 Seed traps in position at the Givendale site (top) and the Keldy Castle site (bottom).

3.5. Results

3.5.1. Givendale Seedling Survey - Summer 1993

The results from the two transects are given in Tables 3.1 and 3.2. For transect 1, further quadrats seemed pointless beyond 20 m. A brief examination was made along the remainder of the transect and although no sycamore seedlings were found the remains of seeds were seen. Transect 2 started further away due to the dense vegetation which was immediately adjacent the seed source.

The results from these two transects are obviously insufficient for obtaining a dispersal curve. The very patchy distribution of seedlings probably reflects the heterogeneous nature of the ground cover.

The dense vegetation cover also seems to inhibit the establishment of seedlings. In the woodland adjacent to the northern strip of sycamore, the bracken and brambles were much reduced. The density of sycamore seedlings here was much greater than found along the transects. Approximately 10 to 15 seedlings were counted in a 2 m square quadrat.

3.5.2. Givendale Seed Trap Results - Autumn 1993

An attempt was made at estimating the size of the seed source by using binoculars to make rough counts of the seed stalks remaining on the parent trees. The largest trees probably produced around 1,000 seeds whilst the smaller trees probably produced only a few hundred seeds. This very low seed output is most likely to be due to the spindly growth form of the trees. This is a consequence of them growing close together and until recently amongst a stand of mature coniferous plantation.

The seed trap data are given in Table 3.3. Only 17 seeds were trapped in total which was very disappointing. This could have been a result of the low seed output or damage to the seed traps rendering them ineffective. At this site, the traps seemed to be quite vulnerable to damage, probably by wind and deer.

3.5.3. Keldy Castle Seed Trap Results - Spring 1994

The traps were emptied three times during the dispersal season. In addition to Scots pine seeds, birch and larch seeds were frequently found. However, counts were only made for Scots pine and larch.

The larch seed counts for 3rd March, 25th April and 9th June are given in Tables 3.4, 3.5 and 3.6 respectively. The data are then amalgamated in Table 3.7 to show the average number of seeds found at each sampling distance from the edge of the seed source. A total of 390 larch seeds were collected.

The computer program "Curvefit" was used to fit both a normal and a negative exponential distribution to the mean number of seeds trapped (expressed as a proportion of the total) at each distance interval. The normal distribution had a correlation coefficient of 0.92 with the fitted equation having the formula:

$$\varphi = 1.62 \exp\left\{\frac{-(x+143)^2}{11887}\right\}$$

where x is the distance from the seed source. The RMSD for this distribution is 109 m ($\sqrt{11887}$) with the peak occurring at a distance of 143 m into the forest.

The negative exponential distribution had a correlation coefficient of 0.91 with the fitted equation having the formula:

$$\varphi = 0.3403 \exp(-0.0334x)$$

The half distance of dispersal (i.e. the distance over which the seed density falls by a half) is given by:

$$D_H = \frac{\ln(2)}{k} = \frac{\ln(2)}{0.0334} = 21\,\mathrm{m}$$

This corresponds with an RMSD of 73 m (see Appendix A) which is of the same order of magnitude as that obtained for the normal distribution. These curves together with the dispersal data from which they were derived are shown graphically in Fig. 3.5.

The total seed trap data for Scots pine are given in Table 3.8. Unfortunately only 59 Scots pine seeds were collected during this period. The apparent increase in seed density beyond 75 m resulted in Curvefit fitting a "normal distribution" with a positive exponent which is obviously wrong. However, the fit for the negative exponential distribution was more realistic with a correlation coefficient of 0.64 and the formula:

$$\varphi = 0.2068\exp(-0.0216x)$$

The half distance of dispersal in this case is 32 m. These results are displayed in Fig 3.6.

The apparent increase in seed density beyond 75 m could have been due to an input of seeds from the northerly plantation of Scots pine. Alternatively it could simply be an artefact resulting from chance effects due to the low numbers of seeds trapped.

In many cases the seed had become detached from the wing and it was often only the wing which was recovered. The seed itself was sometimes found amongst the litter in the seed trap. However, where only a wing was recovered, it was not clear what had happened to the seed. It could have been eaten by a bird or mammal, or have become detached from the wing before landing in the trap, or have become hidden in one of the folds in the bottom of the seed trap and been missed when the trap was emptied. Where only a wing was found, it was assumed that the seed had become detached after landing in the trap but for some reason had not been recovered.

3.5.4. Keldy Castle Seed Trap Results - Spring 1995

As the net collecting bags needed replacing following a year in the field, the number of seed trap transects was reduced to five during this period since this was considered to be sufficient for catching enough seeds to obtain a dispersal curve. Seed counts were made for larch and Scots pine on 19th April and 8th June 1995.

The larch seed counts are given in Tables 3.9 and 3.10 respectively with Table 3.11 showing the combined results. The line of best fit for the negative exponential had a correlation coefficient of 0.58 and the formula:

$$\varphi = 0.646\exp(-0.075x)$$

This corresponds with a half distance of 9 m. For the normal distribution the correlation coefficient was 0.61 with the formula:

$$\varphi = 0.0006\exp\left\{\frac{(x-117)^2}{1664}\right\}$$

However, this formula predicts an increase in seed density beyond 117 m and so is not a good model for seed dispersal.

The seed counts for Scots pine were again disappointingly low with over 90% of the seeds being collected on 8th June. The combined counts for Scots pine are displayed in Table 3.12. The line of best fit for the negative exponential had the formula:

$$\varphi = 0.230\exp(-0.023x)$$

with a correlation coefficient of 0.97 and a half distance of 30 m. The fitted normal distribution had the formula:

$$\varphi = 99.05\exp\left\{\frac{-(x+388)^2}{28492}\right\}$$

with a correlation coefficient of 0.35. This corresponds with an RMSD of 169 m and a peak which occurs 388 m into the forest.

Table 3.1 The number of 1, 2 and 3 year old sycamore seedlings observed in contiguous 2m square quadrats along transect 1 at the Givendale site in June 1993.

Quadrat No.	Distance from seed source	1 year	2 year	3 year	Existing Vegetation
1	3.6	1	0	0	Thick - grass, bracken and willow herb.
2	5.6	2	0	0	Not as thick as quadrat number 1.
3	7.6	0	0	0	Very thick - rowan, spruce, grass, bracken and bramble.
4	9.6	0	0	0	"
5	11.6	0	0	0	"
6	13.6	0	0	0	Thick grass, some bracken, brambles, one oak sapling. Remains of sycamore seeds.
7	15.6	0	0	0	Fallen tree, brambles, bracken, grass, one oak sapling. Sycamore seed remains.
8	17.6	0	0	0	Thick grass, one coppiced sycamore. Sycamore seed remains.
9	19.6	0	0	0	Thick grass, tree stump, bracken. Sycamore seed remains.

Table 3.2 The number of 1, 2 and 3 year old sycamore seedlings observed in contiguous 2m square quadrats along transect 2 at the Givendale site in June 1993.

Quadrat No.	Distance	1 year	2 year	3 year	Existing Vegetation
1	8	0	0	0	Willow herb, bracken and grass. One sycamore seedling observed just outside quadrat.
2	10	1	0	0	Thick vegetation. The seedling was growing at the base of bracken.
3	12	0	0	0	Heather and grass.
4	14	0	0	0	Thick vegetation.
5	16	1	0	0	Thick vegetation with seedling growing amongst grass.
6	18	0	0	0	Very thick vegetation - bracken, willow herb and brambles.
7	20	0	0	3	Grass. One seedling observed just outside the quadrat.
8	22	0	0	1	Mostly grass.
9	24	1	0	0	Grass and heather.
10	26	0	0	0	Dense vegetation - bracken and brambles.
11	28	1	0	0	Grass very tall and thick.
12	30	0	0	0	Very dense vegetation.
13	32	0	0	1	Very thick and tall vegetation.
14	34	0	1	0	Bracken and grass (sparse in places). Seedling found growing in grass.
15	36	0	1	1	Mostly fairly thick grass.
16	38	0	0	0	Thick vegetation - long grass.
17	40	0	0	0	Thick vegetation - brambles and gorse.
18	42	0	0	0	Thick vegetation - bracken, brambles and willow herb.
19	44	0	0	0	Thick vegetation.
20	46	0	0	0	Long grass, bracken and spruce.
21	48	0	0	0	Spruce, bramble, grass.
22	50	0	2	2	Gorse, birch, grass and bracken. Seedlings growing in grass.

Table 3.3 The total number of sycamore seeds collected from the seed traps at Givendale in autumn 1993. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned just beneath the canopy.

Trap No.	Transect									Average
	A	B	C	D	E	F	G	H	I	
1	0	0	0	0	0	0	1	0	0	0.11
2	0	1	0	0	0	0	0	0	0	0.11
3	1	0	0	0	0	0	0	0	0	0.11
4	0	0	0	0	0	0	0	0	0	0.00
5	0	0	0	1	0	0	0	0	2	0.33
6	0	0	0	0	0	0	0	0	0	0.00
7	1	0	0	0	0	0	0	1	0	0.22
8	0	0	0	0	0	0	0	0	2	0.22
9	0	0	0	1	1	0	0	0	0	0.22
10	0	2	0	0	0	0	0	3	0	0.55

Table 3.4 The number of larch seeds collected from the seed traps at Keldy Castle on 3rd March 1994. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	Transect							Total
	A	B	C	D	E	F	G	
1	2	1	2	3	3	1	0	12
2	1	0	1	0	3	1	1	7
3	0	0	2	0	0	1	0	3
4	1	1	0	0	0	1	1	4
5	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0
							Grand Total	26

Table 3.5 The number of larch seeds collected from the seed traps at Keldy Castle on 25th April 1994. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	Transect							Total
	A	B	C	D	E	F	G	
1	1	13	13	9	7	9	-	52
2	5	7	3	8	9	7	14	53
3	3	7	7	3	-	4	8	32
4	1	2	1	4	-	4	-	12
5	2	1	1	4	1	3	4	16
6	1	3	4	3	1	2	2	16
7	1	1	4	-	1	2	2	11
8	1	1	0	1	-	3	0	5
9	0	2	1	2	1	0	0	6
10	0	3	0	1	0	2	2	8
11	0	0	1	0	0	1	0	2
							Grand Total	213

Table 3.6 The number of larch seeds collected from the seed traps at Keldy Castle on 9th June 1994. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	Transect A	B	C	D	E	F	G	Total
1	4	3	15	3	16	10	7	58
2	1	0	3	2	3	6	4	19
3	3	1	2	2	3	6	5	22
4	0	2	2	0	0	0	4	8
5	2	0	2	3	5	2	5	19
6	1	0	0	2	0	2	0	5
7	0	0	1	1	1	4	1	8
8	0	1	1	2	0	0	1	5
9	1	1	0	2	1	1	0	6
10	0	0	0	0	0	0	1	1
11	0	0	0	0	0	0	0	0
							Grand Total	151

Table 3.7 Total number of larch seeds recovered from seed traps at the Keldy Castle site during spring 1994. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	3/3/94 No. seeds	24/4/94 No. seeds	9/6/94 No. seeds	Total no. of seeds	Total no. of traps sampled	Average no. of seeds per trap	Average as a proportion
1	12	52	58	122	20	6.10	0.318
2	7	53	19	79	21	3.76	0.196
3	3	32	22	57	20	2.85	0.149
4	4	12	8	24	19	1.26	0.066
5	0	16	19	35	21	1.67	0.087
6	0	16	5	21	21	1.00	0.052
7	0	11	8	19	20	0.95	0.050
8	0	5	5	10	20	0.50	0.026
9	0	6	6	12	21	0.57	0.030
10	0	8	1	9	21	0.43	0.022
11	0	2	0	2	21	0.10	0.005
Total	26	213	151	390	225	19.19	1.001

Table 3.8 Total number of Scots pine seed remains recovered from the seed traps at the Keldy Castle site during spring 1994. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy. These figures include cases where only a wing was found and no seed i.e. it was assumed that the seed had become detached from the wing after it had landed in the seed trap but was not recovered.

Trap No.	Transect							Total	No. of traps sampled	Average no. of seeds per trap	Average as a proportion
	A	B	C	D	E	F	G				
1	1	1	3	2	0	4	1	12	20	0.600	0.207
2	2	0	2	1	4	1	4	14	21	0.667	0.230
3	2	1	3	1	2	1	2	12	20	0.600	0.207
4	1	0	0	1	1	2	0	5	19	0.263	0.091
5	1	0	0	0	1	0	0	2	21	0.095	0.033
6	1	0	2	0	0	1	0	4	21	0.190	0.066
7	0	1	0	0	0	1	0	2	20	0.100	0.035
8	1	0	0	0	0	0	0	1	20	0.050	0.017
9	0	0	1	0	1	0	0	2	21	0.095	0.033
10	0	1	0	0	1	0	0	2	21	0.095	0.033
11	0	0	1	0	1	0	1	3	21	0.143	0.049
Grand Total								59	225	2.898	1.001

Table 3.9 The number of larch seeds collected from the seed traps at Keldy Castle on 19th April 1995. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	Transect					Total
	A	B	C	D	E	
1	0	0	1	1	4	6
2	2	0	0	5	2	9
3	0	0	2	2	4	8
4	0	1	3	2	3	9
5	0	0	0	0	3	3
6	1	0	-	0	0	1
7	0	0	0	0	0	0
8	1	0	0	-	-	1
9	0	0	0	0	0	0
10	0	0	0	0	0	0
11	0	0	0	0	0	0
					Grand Total	37

Table 3.10 The number of larch seeds collected from the seed traps at Keldy Castle on 8th June 1995. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	Transect					Total
	A	B	C	D	E	
1	2	3	3	5	9	22
2	3	4	0	3	1	11
3	1	6	4	1	1	13
4	1	2	1	1	1	6
5	0	0	1	0	1	2
6	0	0	0	-	1	0
7	0	0	0	0	-	0
8	0	0	0	0	0	0
9	0	0	0	0	0	0
10	0	0	0	0	0	0
11	0	0	0	1	0	1
					Grand Total	55

Table 3.11 Total number of larch seeds recovered from seed traps at the Keldy Castle site during spring 1995. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy.

Trap No.	19/4/95 No. seeds	8/6/95 No. seeds	Total no. of seeds	Total no. of traps sampled	Average no. of seeds per trap	Average as a proportion
1	6	22	28	22	1.273	0.304
2	9	11	20	22	0.909	0.217
3	8	13	21	22	0.955	0.228
4	9	6	15	22	0.682	0.163
5	3	2	5	22	0.227	0.054
6	1	0	1	20	0.050	0.012
7	0	0	0	21	0.000	0.000
8	1	0	1	20	0.050	0.012
9	0	0	0	22	0.000	0.000
10	0	0	0	22	0.000	0.000
11	0	1	1	22	0.045	0.011
Total	37	55	92	237	4.191	1.001

Table 3.12 Total number of Scots pine seed remains recovered from the seed traps at the Keldy Castle site during spring 1995. The traps were placed at 10 m intervals from the seed source starting with trap number 1 which was positioned 5 m from the edge of the canopy. These figures include cases where only a wing was found and no seed i.e. it was assumed that the seed had become detached from the wing after it had landed in the seed trap but was not been recovered.

Trap No.	Transect					Total	No. of traps sampled	Average no. of seeds per trap	Average as a proportion
	A	B	C	D	E				
1	4	3	8	4	2	21	22	0.955	0.251
2	1	4	4	2	2	13	22	0.591	0.155
3	1	4	6	4	0	15	22	0.682	0.179
4	1	4	2	1	1	9	22	0.409	0.107
5	1	1	2	1	2	7	22	0.318	0.084
6	0	2	1	0	0	3	20	0.150	0.039
7	1	1	1	2	0	5	21	0.238	0.063
8	1	1	0	0	0	2	20	0.100	0.026
9	0	0	0	0	1	1	22	0.045	0.012
10	1	0	1	1	0	3	22	0.136	0.036
11	1	1	1	1	0	4	22	0.182	0.048
Grand Total						83	237	3.806	1.000

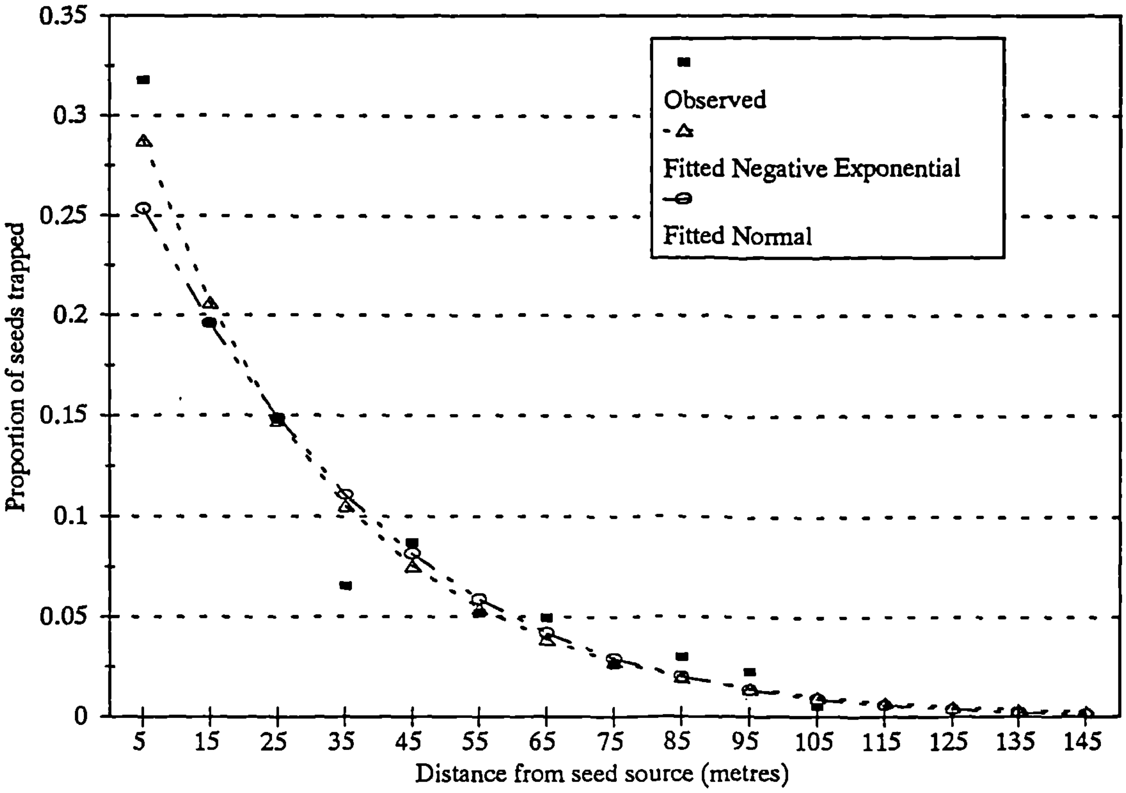

Fig. 3.5 The observed distribution of larch seeds at Keldy Castle in spring 1994. Lines of best fit for the negative exponential ($r^2 = 0.91$) and normal distribution ($r^2 = 0.92$) are shown.

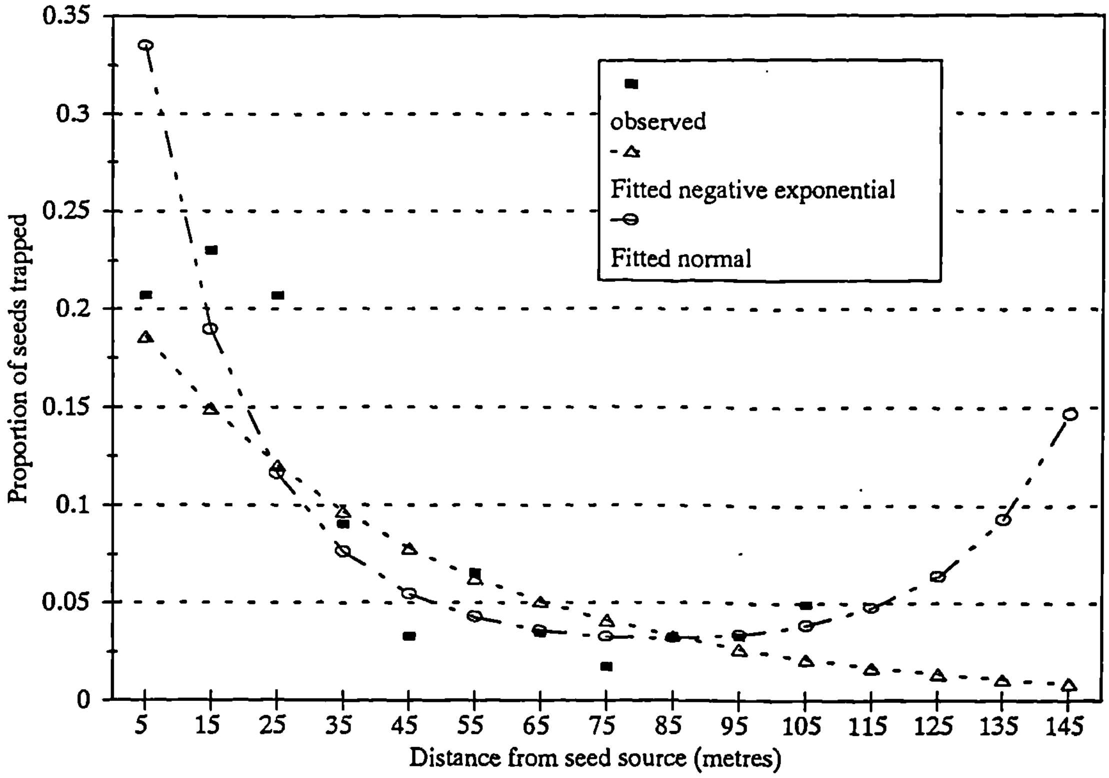

Fig. 3.6 The observed distribution of Scots pine seeds at Keldy Castle in spring 1994. Lines of best fit for the negative exponential ($r^2 = 0.64$) and normal distribution ($r^2 = 0.81$) are shown.

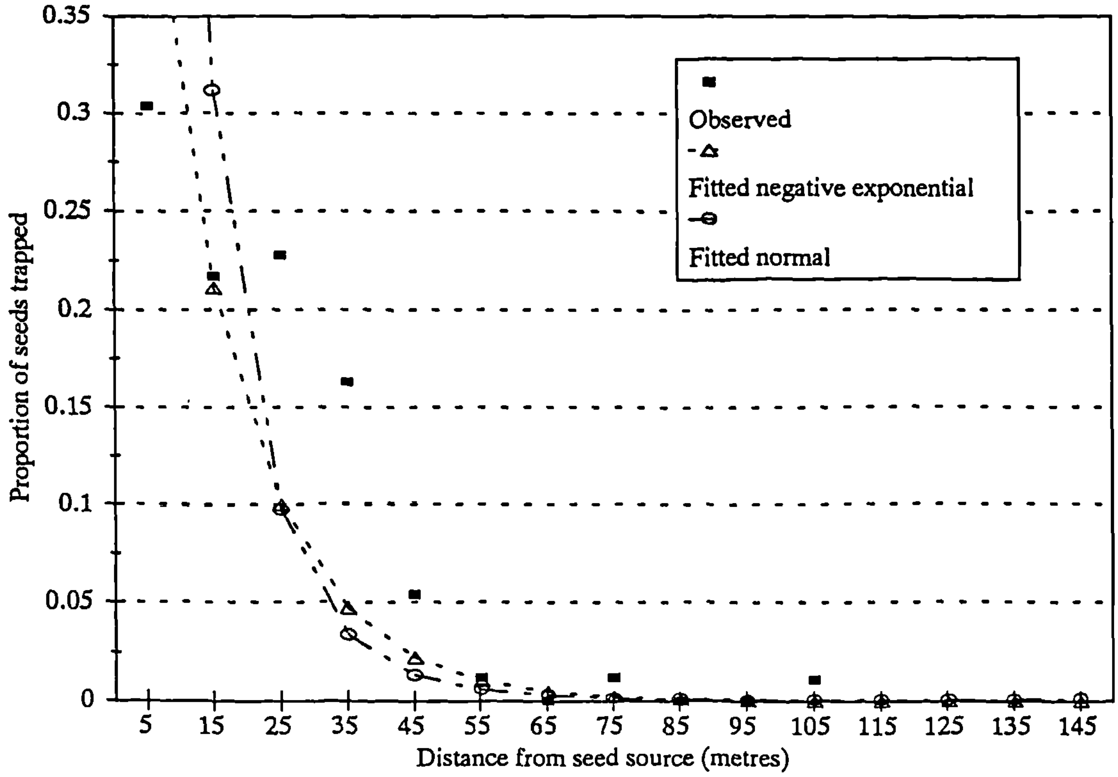

Fig 3.7 The observed distribution of larch seeds at Keldy Castle in spring 1995. Lines of best fit for the negative exponential (r^2 = 0.58) and normal distribution (r^2 = 0.61) are shown.

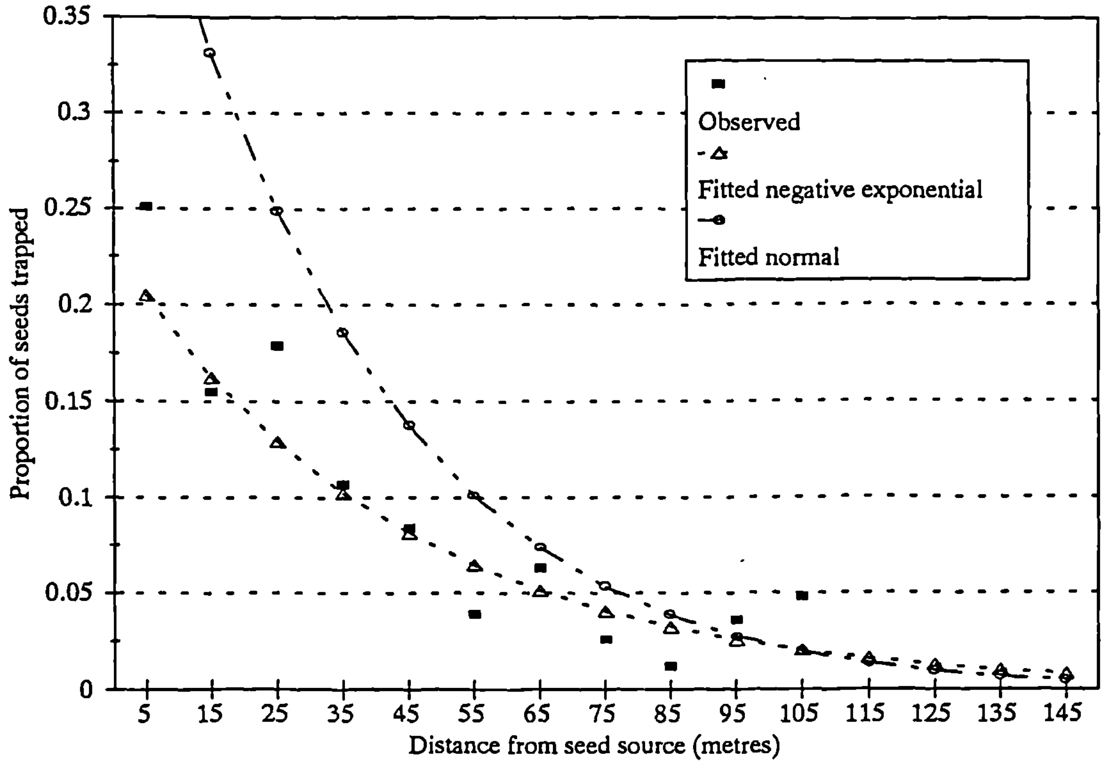

Fig 3.8 The observed distribution of Scots pine seeds at Keldy Castle in spring 1995. Lines of best fit for the negative exponential (r^2 = 0..97) and normal distribution (r^2 = 0.35) are shown.

3.6. Discussion

3.6.1. Comparison with Results from Other Studies

Johnson (1988) fitted negative exponential curves to the distribution of seedlings of American lime (*Tilia americana*), sugar maple (*Acer saccharum*) and red ash (*Fraxinus pennsylvanica*) and obtained half distances of 8 m, 27 m and 68 m respectively. A seed trap study done on the longleaf pine (*Pinus palustris*) produced a dispersal curve which had a negative exponential distribution with a half distance of 23 m (Boyer, 1958). A similar study done on the Engelmann spruce (*Picea engelmannii*) by Roe (1967) also obtained a negative exponential distribution with a half distance of between 30 m and 50 m depending on the study site. Although Hughes and Fahey (1988) do not quote the half distances they obtained for sugar maple and yellow birch (*Betula lutea*), it is possible to deduce from their seed dispersal graphs that these were of the same order of magnitude as the half distance values obtained in this study. They also found that the seed densities began to increase beyond about 100 m from the forest edge due to an input of seeds from the opposite side of the forest clearing. Bjorkbom (1971) obtained half distance values of between 15 m and 20 m for the paper birch (*Betula papyrifera*). It would therefore seem that the half distance values of 9 m and 21 m obtained for larch and 22 m and 32 m for Scots pine are in good agreement with other studies.

However, Welch *et al.* (1990) obtained a much larger value for the half distance of dispersal of Scots pine. Their value of approximately 700 m is an order of magnitude larger than those values given above. The reason for this is not clear, although it is likely that their study site in the Cairngorm mountains is more exposed to strong winds resulting in longer dispersal distances. It would be interesting to carry out seed trapping experiments in the Cairngorms using a similar trap layout to that at Keldy Castle to see if there is any evidence to support this. Alternatively it may be that the longer dispersal distances are more readily detected by seedling surveys than seed trap studies resulting in the latter method determining shorter dispersal curves.

3.6.2. Local versus Long-Distance Dispersal

The dispersal distances measured in this study were very small. Distances of up to 100 m from the seed source were measured but only with a low frequency ($5\text{x}10^{-3}$ for larch). Ideally, it should be possible to measure dispersal at distances up to 10 km from the seed source. Palaeoecological studies of past migrations indicate that dispersal distances of this order of magnitude must have occurred. However, even if a suitable study site could be found the number of seed traps required in order to detect seeds at such distances would be so large as to make the study impracticable. However, surveys of seedling distribution can potentially cover a much larger area because seedlings are more easy to detect.

Both this study and those of other workers (For example, Johnson,1988; Boyer, 1958 and Roe, 1967 etc.) have concentrated on local dispersal. The only study which could be considered to have looked at long-distance dispersal is that of Welch *et al.* (1990), however, even they only studied distances of up to 4 km. In order for the post-glacial migration rates of 100 to 1000 m yr^{-1} to have been achieved successful dispersal must have occurred over distances of at least 2 km (assuming a short generation time of 20 years and a slow migration rate of 100 m yr^{-1}). Such dispersal events would be virtually impossible to detect through the use of seed traps. A more appropriate method would be to do a survey of seedlings in the manner undertaken by Welch *et al.* (1990) However, this requires finding a large homogeneous site where invasion is occurring. In today's landscape which is heavily influenced by man it is extremely doubtful that such a site exists.

It can therefore be concluded that although it is possible to measure local dispersal in the field it is not feasible to measure long-distance dispersal. An alternative approach must be sought if one is to obtain probability values for dispersal distances above a few kilometres. One possibility would be to use a separate model to simulate seed dispersal. Such models were reviewed in Chapter 1, however, they are not currently detailed enough to model dispersal sufficiently accurately. A realistic seed dispersal model would need to incorporate detailed meteorological data, including the effects of turbulent air flow and the morphological adaptations of seeds for wind dispersal.

3.6.3. Relationship between the Dispersal Curve Observed from a Forest Edge and the Dispersal Curve Produced by an Individual Tree

The studies reported here have looked at dispersal from forest edges. However, MIGRATE simulates the dispersal of propagules according to a dispersal function for an individual tree. As there is a good deal of uncertainty in the fitting of a dispersal curve to the field observations there is little value in trying to make any accurate prediction as to the shape of the dispersal curve produced by an individual tree. The dispersal curve produced at the forest edge has therefore been used as an approximation to the actual dispersal curve produced by an individual.

In order to check that this approximation is reasonable, computer simulations have been carried out to see how the dispersal curve at the forest edge relates to the dispersal curve of the individual. A hypothetical environment was set up in which a block of trees released seeds according to either a bivariate normal distribution or a two-dimensional negative exponential distribution (see Appendix A). The environment consisted of a grid of 80 x 100 square cells with the first 35 columns being occupied by a single tree each producing 10 propagules for dispersal. The actual numbers used here are irrelevant as they affect only the height of the dispersal curve and not its shape. The number of seeds arriving in each column of cells was summed. The seed sums for each column beyond the forest edge were converted into proportions by dividing by the total number of seeds dispersed beyond the forest edge. Normal and negative exponential curves were then fitted to these values using the computer program "Curvefit".

In the first simulation, dispersal occurred according to a bivariate normal distribution with a RMSD of 0.1 km. The cell length was set at 0.01 km and the furthest cell to which dispersal was calculated was set at 50 (i.e. 0.5 km). Density values up to 0.5 km from the forest edge were used to fit the dispersal curves. The normal distribution

$$\varphi = 0.121\exp\left\{\frac{-(x+0.02)^2}{0.0096}\right\}$$

has a near perfect fit (correlation coefficient = 0.995) to the edge distribution. It has an RMSD of 0.098 km which is in very close agreement with that of the individual tree.

The negative exponential distribution

$$\varphi = 8.2\exp(-56.2x)$$

also has a very good fit (correlation coefficient = 0.938) to the edge dispersal curve. However, the fit is poor near the seed source where it severely over estimates the actual distribution. The RMSD of this distribution is given by

$$\text{RMSD} = \frac{\sqrt{6}}{k} = \frac{\sqrt{6}}{56.2} = 0.044 \text{ km}$$

which is a poor approximation to the RMSD of the individual dispersal function.

A comparable simulation was done in which individual trees disperse seeds according to a two-dimensional negative exponential dispersal function. The half distance was set at

$$D_H = \frac{\ln(2).\text{RMSD}}{\sqrt{6}} = 0.0283 \text{ km}$$

so that the RMSD was the same as for the bivariate normal distribution in the previous simulation. The cell length was kept at 0.01 km but the furthest cell was increased to 100 to allow for the longer tail of the negative exponential distribution. As for the normal distribution, seed density values up to a distance of 0.5 km from the forest edge were used to fit the dispersal curves.

The negative exponential distribution

$$\varphi = 0.23\exp(-22.7x)$$

had a correlation coefficient of 1.0 and a half distance of 0.031 km which is a 91% agreement with the half distance of the individual dispersal curve.

For the normal distribution there was a correlation coefficient of 1.0 with the formula

$$\varphi = 4.6 \times 10^{12} \exp\left\{\frac{-(x+2.95)^2}{0.28}\right\}$$

Although this is an excellent fit, it is not a realistic model since it predicts that the dispersal peak occurs at a distance of 2.95 km into the forest.

The results of these simulations are shown in Fig 3.9 and Fig. 3.10. The edge dispersal curves are similar although that produced by trees dispersing according to a negative exponential distribution has a longer tail than that produced when the trees disperse according to a bivariate normal distribution. These results will hold for all normal and negative exponential dispersal functions providing the cell length is not made too large in relation to the RMSD and dispersal distances of at least 5xRMSD are allowed.

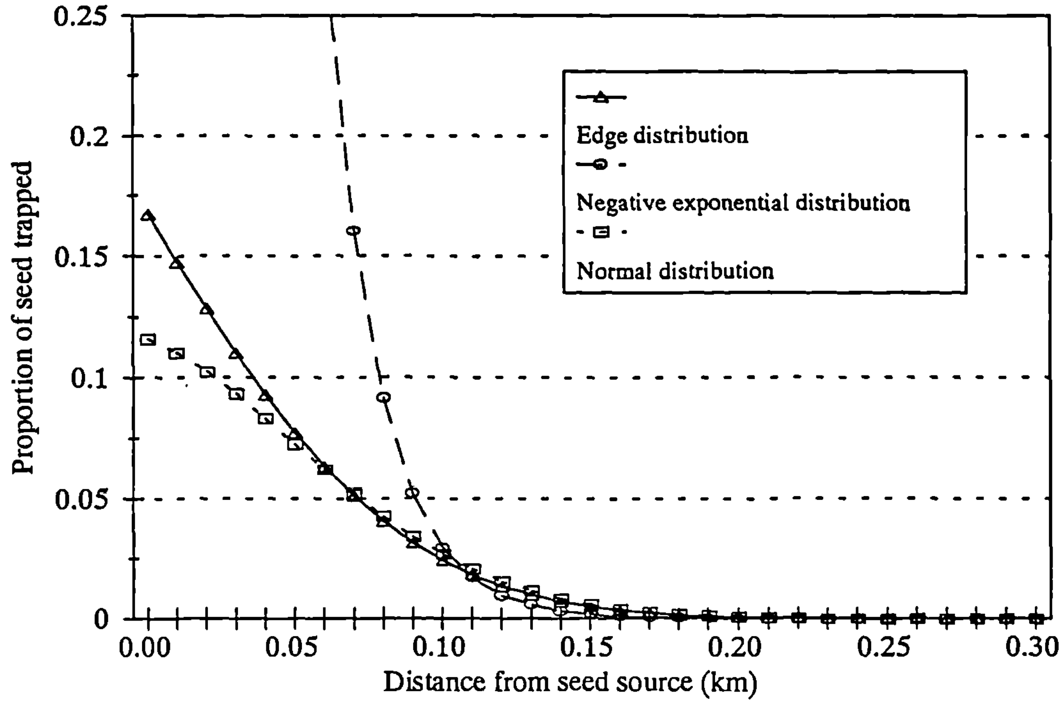

Fig. 3.9 Simulated seed dispersal from a forest edge. Seeds were dispersed from individual trees according to a bivariate normal distribution with an RMSD of 0.1 km. The computer program curvefit was used to fit a negative exponential distribution and a normal distribution.

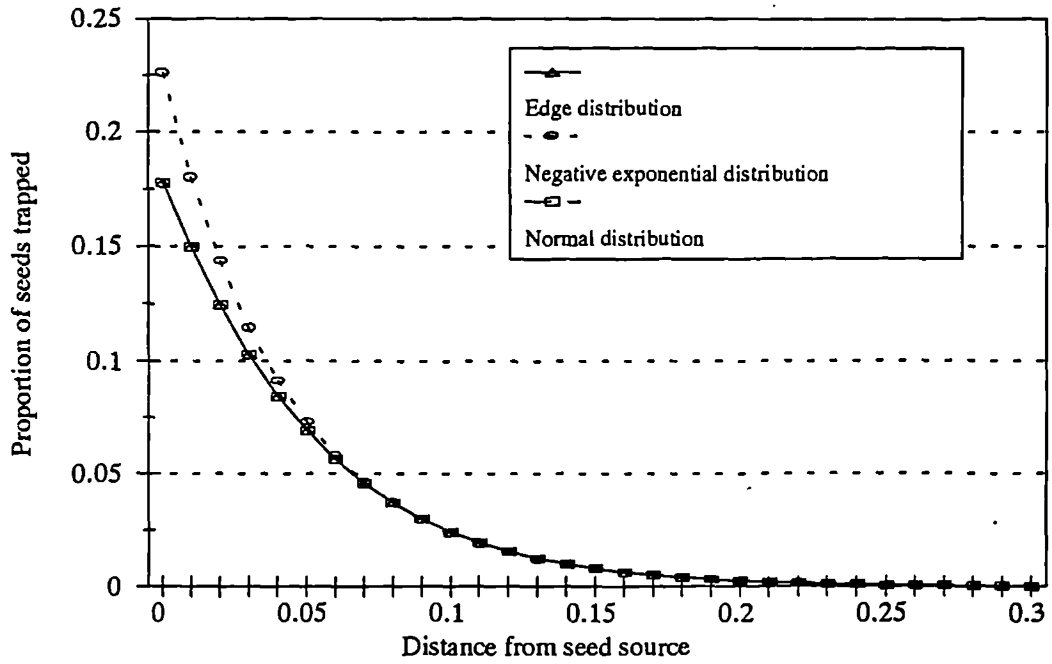

Fig. 3.10 Simulated seed dispersal from a forest edge. Seeds were dispersed from individual trees according to a negaive exponetial distribution with a half distance of 0.0283 km. The computer program curvefit was used to fit a negative exponential distribution and a normal distribution.

3.7. Conclusions

Seed trapping has been shown to be an effective means of sampling the seed shadow at distances of up to 100 m from the seed source.

In the cases where sufficient seeds were trapped, the dispersal curve showed a good fit to both the negative exponential distribution and the normal distribution (with the mean occurring at some distance within the stand). It would therefore seem that either one of these distributions could be used to simulate the local dispersal of seeds.

In order to measure dispersal distances greater than 100 m, seedling surveys are potentially more appropriate. However, it was not possible to find a site that was large and homogeneous enough to use seedling establishment as a means of obtaining a seed dispersal curve.

The seed trap results obtained in this study suggest that most seeds are dispersed only over relatively short distances by wind. However, it would be useful to conduct a similar experiment at a more exposed site to see if the dispersal distances there are significantly greater.

Computer simulations have shown that if trees disperse their seeds according to a bivariate normal distribution then the RMSD of a normal distribution fitted to the dispersal curve at the forest edge will be a good approximation to the RMSD of the dispersal curve produced by an individual tree. Similarly, if trees disperse their seeds according to a negative exponential distribution then the half distance of a negative exponential distribution fitted to the edge dispersal curve will be a good approximation to the half distance of the dispersal curve produced by an individual tree. Although a negative exponential distribution has a good fit (as indicated by the correlation coefficient) to the edge dispersal curve produced by normally dispersed seeds and vice versa, a closer examination of these fitted curves reveals that they do not make realistic sense.

CHAPTER 4

Model Behaviour and Simulation Results

The first part of this chapter describes the sensitivity of MIGRATE to the values used for its parameters. This is important firstly because it enables one to understand how the model behaves and secondly because it allows one to identify those parameters to which the model is most sensitive and therefore where it is important to have accurate parameter values. For the one-dimensional version of MIGRATE, it is sometimes possible to predict the migration rate using the analytical equations first developed by Skellam (1951) and later refined by Van den Bosch *et al.* (1990, 1992). The migration rates simulated by MIGRATE are compared with those predicted by Skellam's model and that of Van den Bosch *et al.* Next, the two-dimensional version of MIGRATE is used as this is able to simulate the spread of an organism through a heterogeneous environment. It is in this context that the MIGRATE model has a real advantage over the analytical models since these assume the environment to be homogeneous. Van den Bosch and Hengeveld (submitted) have made further refinements to their model to take into account habitat heterogeneity. However, unlike MIGRATE their model is not spatially explicit and therefore can not show the pattern of spread through a heterogeneous environment. The two-dimensional version of MIGRATE is used to investigate the spread of *Tilia cordata* (small-leaved lime) through northern Britain. In particular, the effects of habitat availability and climate are investigated.

4.1. Sensitivity Analysis

Sensitivity analysis been defined by Conroy *et al.* (1995) as "...the controlled variation in parameter values in isolation and in combination, and the observed response of model output". The simulations described in this section are not intended to be exhaustive but have been chosen in order to give a good picture of the sensitivity of MIGRATE to its parameter values. The one-dimensional version of MIGRATE was used to investigate the sensitivity of the model to the values assigned to the reproductive and dispersal parameters since the environment can be assumed to be homogeneous.

The graphical results of the sensitivity analysis simulations are grouped together in Appendix B.

4.1.1. Single Dispersal Function and Single Cohort Case

The initial simulations were done with just one cohort and one dispersal function since this is the most simple case and can therefore be investigated most easily. It is assumed that all individuals are produced at the beginning of a cohort period so that they are reproductively mature at the start of the next generation. The results are summarised in Table 4.1 at the end of this section.

The reproductive parameters given in Table 4.2 were set using values from the literature (for example, Pigott, 1991) which seemed reasonable for a tree such as *Tilia cordata.* As the exact nature of dispersal is so poorly understood it was decided that a normal distribution would be an acceptable choice for modelling this process (see Appendix A). There were no reasons for preferring any other dispersal function and as the normal distribution results in the same migration rate in both one and two-dimensions (see section 2.1.4) this seemed to be a sensible choice. The dispersal RMSD was chosen so as to achieve a migration rate of 0.2 km yr^{-1}. This is at the slow end of the range 0.05-0.5 km yr^{-1} recorded for *Tilia* during its post-glacial migration through the British Isles (Birks, 1989). The value of the RMSD can be determined from the following equation which is a reformulation of Skellam's (1951) model (equation 1.16):

$$C = \frac{\text{RMSD}}{T} . \sqrt{\ln R_0} \qquad (4.1)$$

where C is the migration rate, T the generation time and R_0 the net reproductive rate.

$$R_0 = b - d \qquad (4.2)$$

where b is the number of successful offspring produced per individual per generation and d the death rate per generation (Odum, 1971). In terms of the parameters used in the MIGRATE model, this equation may be expressed as:

$$\begin{aligned} R_0 &= S.P_0 - P_1 \\ &= F - P_1 \end{aligned}$$

It will be shown later in this section that when F is greater than 1.7 the effect of P_1 is negligible, i.e. R_0 may be considered to be equal to F.

The initial distribution was that the cells corresponding with the first 10 km were fully occupied. The estimation of the probability of a seed becoming a mature tree is based upon what is known in the ecological literature about the establishment and early survival of trees. It is known that most seed fail to become reproductively mature trees because of unfavourable germination conditions, predation and disease etc. (for example, Watt, 1919; Crawley, 1983 p29; Piñero *et al.*, 1984; Brubaker, 1986 and references therein; Clarke, 1992; Pigott, 1992; Crawley and Long, 1995).

Table 4.2 Default parameter values used in the sensitivity analysis

Parameter	Default value
Cell length	1 km
Area occupied by an individual	50 m^2
Generation length	25 years
Probability of a seed becoming a reproductively mature tree	5 x 10^{-5}
Probability of an adult surviving a further interval of one generation length	0.913
Number of offspring produced each generation	160000
RMSD	3.47
Carrying capacity	1.0 for all cell

Cell Length

Simulations B1, B2 and B3 show the effect of using a cell length of 1.0 km, 10 km and 0.1 km respectively. These simulations show quite clearly that if the cell length is made too large in relation to the length of a dispersal function then the model loses accuracy. It is easy to tell if the cell length is too large because this results in the dispersal sums being too large (i.e. greater than their associated probability value). The general effect of using a cell length that is too large is an underestimation of the migration rate and an overestimation of the intrinsic rate of population increase. In all of these simulations, the furthest cell was set at a value that corresponded with a distance of at least 5xRMSD. Beyond this distance, the probability of a propagule arriving is so small as to be negligible. For the purposes of computational efficiency it is best to choose a cell length which is as large as possible without any significant loss in accuracy. As a rule of thumb, the cell length should not exceed the RMSD.

Martin (1993) suggests the following 'migration criterion' for ensuring that the cell length is small enough to capture the migratory processes:

$L \leq T.m$

where L is the cell length, T the generation time and m the speed of the slowest vegetation movement of ecological significance. This implies that when $m = 0.2$ km yr^{-1} and $T = 25$ years the cell length should not exceed 5 km.

Area Occupied by an Individual

Simulations B4 and B5 show the effect of using a small area (5 m^2) and a large area (1000000 m^2) on the migration rate. It is clear from these simulations that the area occupied by an individual has no effect on the migration rate. It simply affects the density of established individuals.

If the rounding option is used (see section 2.1.5) and the maximum number of trees in a cell is less than 100, then the migration rate is less than the rate simulated without the rounding option. Simulation B6 shows that rounding is just beginning to have an effect when the maximum number of individuals in a cell is 100. In simulation B7 the rounding option was used together with the same parameter values as in simulation B5 where the maximum number of individuals per cell was 1. Rounding reduces the migration rate by eliminating the small 'fractions' of propagules which arrive at the front of the migrating wave. When the maximum density of individuals in a cell is less than 100 then these small fractions play a more significant role in determining the migration rate. This is a consequence of the reduced propagule input to the migration front due to the lower maximum density of individuals behind the advancing front. This same phenomenon is observed when a joint dispersal function is used and the long-distance component has a long tail.

Generation Time

In changing the generation time, it is also necessary to modify fecundity so that the annual reproductive output remains constant. The adult survival probability also has to be modified in accordance with equation 2.9. The migration rates from the simulations given in Table 4.3 confirm that species with a short generation time have a faster migration rate than those which take longer to reach maturity.

Table 4.3 The relationship between the generation time (age to first reproduction) and migration rate as determined with the MIGRATE model.

Generation Time (Years)	Migration Rate (km yr^{-1})	Simulation Number
10	0.38	B8
25	0.20	B1
50	0.12	B9

The results from these simulations agree with the rates predicted by Skellam's model (equation 4.1). The graph shown in Fig. 4.1 shows the relationship between the generation time and the migration rate (the migration rates were calculated using equation 4.1). The curve shows a good fit to a negative exponential distribution (correlation coefficient = 0.96).

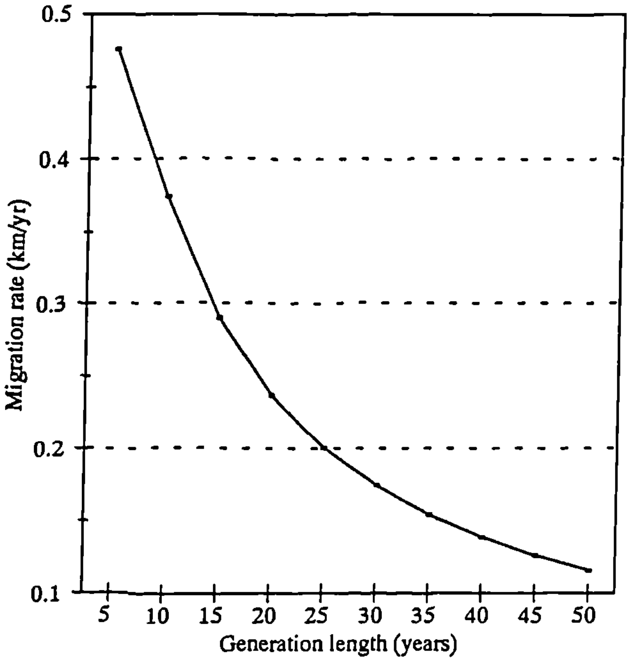

Fig. 4.1 The relationship between migration rate and generation time.

Fecundity

Fecundity (*F*) is defined as the number of successful offspring (i.e. number of propagules produced per generation x probability of a propagule reaching reproductive maturity). With the exception of very low fecundity values (<1.7) the migration rates simulated by MIGRATE are in exact agreement with equation 4.1. For fecundity values less than 1.7 the migration rate predicted by MIGRATE is higher than that predicted by equation 4.1. This is because in the MIGRATE model, individuals are able to breed in successive generations whereas equation 4.1 assumes that all the offspring are produced when an individual becomes mature and none are produced in the following generations. If the probability of adult survival is set to 0.0 then MIGRATE simulates the same migration rate as equation 4.1.

From this result it can be concluded that if the number of successful offspring produced per generation exceeds 1.7 and is constant for each cohort class then the adult survival probability has no effect on the migration rate i.e. individuals can die after having reproduced once without the migration rate being affected. The migration rate is simply determined by the number of offspring produced in the first generation interval.

From equation 4.1 it can be shown that in order to double the migration rate, the net rate of reproduction must be increased to the power 4:

$$\sqrt{\ln R_0'} = 2\sqrt{\ln R_0}$$

$$\therefore \ \ln R_0' = 4 \ln R_0$$

$$\therefore \quad R_0' = R_0^4$$

where R_0' is the net reproductive rate required to double the migration rate.

Adult Survival

As described above, the adult survival probability has a negligible effect on the migration rate except when the number of successful offspring is very low (<1.7).

RMSD

When MIGRATE is used with a single normal distribution it behaves as is expected from equation 4.1 i.e. in order to double the migration rate the RMSD must also be doubled.

The Joint Role of Fecundity and the RMSD in Determining the Extent of the Population Front

From the previous simulations it can be deduced that both the RMSD and fecundity determine the shape of the population front. A series of simulations were done in which the number of successful offspring and the RMSD were varied whilst maintaining a constant migration rate of 0.2 km yr^{-1}. The effect of the fecundity and RMSD parameter values on the extent of the population front is is shown in Figs 4.2 amd 4.3 respectively. These results show that for a population migrating at 0.2 km yr^{-1} very steep population fronts (<3.5 km) are produced when the number of successful offspring exceeds 1000 and the RMSD is less than 1.9 km. Fig. 4.4 shows that the extent of the population front is directly proportional to $^{RMSD}\!/\!_{\sqrt{\ln(F)}}$. The data points were calculated from the same simulations described above. These results imply that in order to get a migration front which extends over at least 5 km the ratio of the RMSD to sqrt(ln(*F*)) must exceed 1.0. A doubling of the RMSD results in both a doubling of the migration rate and an approximate doubling of the extent of the migration front. Similarly if *F* is increased to the power of 4 then the migration rate is doubled and the extent of the population front approximately halved

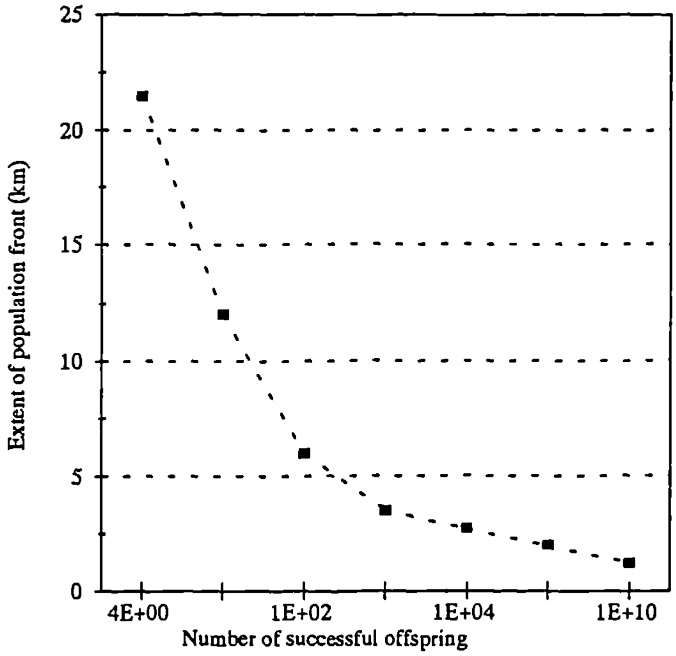

Fig. 4.2 The relationship between the number of successful offspring (*F*) and the extent of the population front.

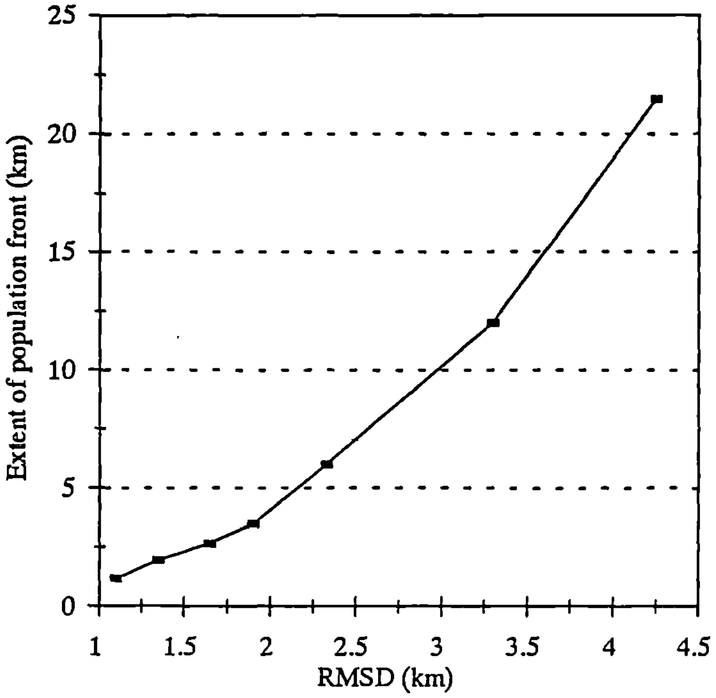

Fig. 4.3 The relationship between the RMSD and the extent of the population front.

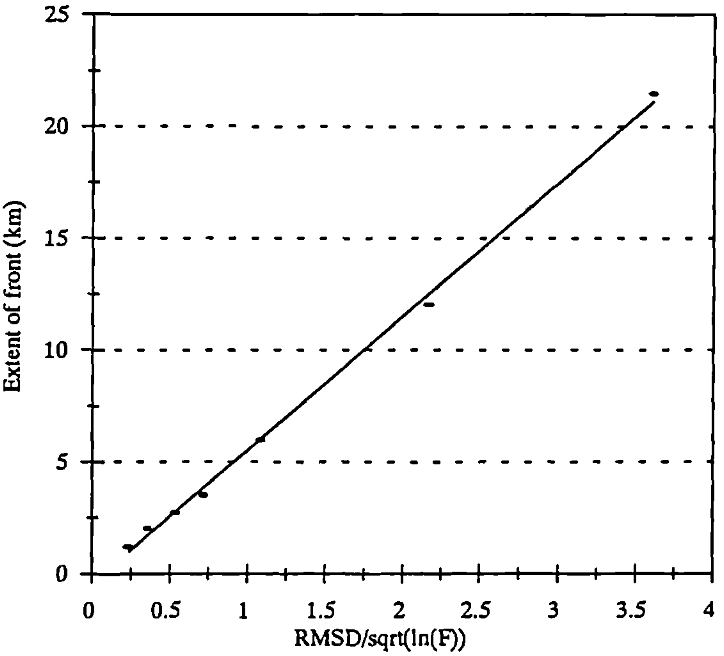

Fig. 4.4 The relationship between the extent of the population front and $\frac{\text{RMSD}}{\sqrt{\ln(F)}}$.

Normal Dispersal versus Negative Exponential Dispersal

The half distance of a negative exponential dispersal function can be set so that it has the same RMSD as a normal distribution (see Appendix A):

$$\begin{aligned} D_H &= \frac{\ln(2).\text{RMSD}}{\sqrt{6}} \\ &= 0.982\,\text{km} \end{aligned} \tag{4.3}$$

Simulation B10 shows a simulation using a negative exponential distribution with a half distance of 0.982 km. The resulting migration rate of 0.21 km yr^{-1} is slightly faster than the rate obtained for a normal distribution (0.20 km yr^{-1}). This is due to the slightly higher tail of the negative exponential distribution.

When using a cell length of 1.0 km the dispersal sum for the negative exponential distribution comes out at 1.04. In order to reduce it to a value which is closer to 1 it is necessary to make the cell length shorter and the value of the furthest cell larger. Simulation B11 shows a simulation where a cell length of 0.1 km was used with propagules being dispersed up to a possible maximum of 18 km from the parent tree. It can be seen that although the dispersal sum is now much closer to 1 there has been no significant effect on the migration rate.

Carrying Capacity

Mathematically, the effect of changing the carrying capacity is the same as making the same change to fecundity i.e. if the carrying capacity is reduced by a factor of 5 then fecundity must be increased by a factor of 5 to maintain the same migration rate (Simulation B12).

Simulation No.	Rounding Option (yes/no)	K	L (km)	a (m^2)	T (yr)	P_0	P_1	S	Dispersal Function	Dispersal Parameter (km)	C (km yr^{-1})	Front Width (km)	α
B1	no	*	*	*	*	*	*	*	*	*	0.20	15	0.15
B2	no	*	10	*	*	*	*	*	*	*	0.16	18.0	0.1
B3	no	*	0.1	*	*	*	*	*	*	*	0.20	15	0.15
B4	no	*	*	5	*	*	*	*	*	*	0.20	15	0.15
B5	no	*	*	10^6	*	*	*	*	*	*	0.20	15	0.01
B6	yes	*	*	10^4	*	*	*	*	*	*	0.19	15	0.1
B7	yes	*	*	10^6	*	*	*	*	*	*	0.13	0	-
B8	no	*	*	*	10	*	0.966	$6.4\text{x}10^4$	*	*	0.38	25	0.25
B9	no	*	*	*	50	*	0.819	$3.2\text{x}10^5$	*	*	0.12	12	0.1
B10	no	*	*	*	*	*	*	*	neg. exp.	0.982	0.21	20	0.1
B11	no	*	0.1	*	*	*	*	*	neg. exp.	0.982	0.22	20	0.1
B12	no	0.2	*	*	*	$2.5\text{x}10^{-4}$	*	*	*	*	0.20	15	0.15

Table 4.1 Summary of the results of the sensitivity analysis of the one-dimensional version of MIGRATE with one cohort class and one dispersal function. The rounding option refers to whether or not the number of individuals in each cell was rounded to a whole number (for a more detailed description of this feature see section 2.x). K = relative carrying capacity; L = cell length; a = area occupied by an individual; T = generation length; P_0 = probability that a seed reaches reproductive maturity; P_1 = probability that tree survuves a further interval of one generation; S = number of propagules produced by a reproductively mature tree; dispersal function is either a normal distribution or a negative exponential distribution; dispersal parameter is the value of the RMSD or half distance as appropriate to the dispersal function (sse Apendix A); C = migration rate; Front width is as shown in Fig. 4.1; α = rate of population increase; * = default value; $K = 1.0$; $L = 1$ km; $a = 50$ m^2; $T = 25$ yr; $P_0 = 5\text{x}10\text{-}5$; $P_1 = 0.913$; $F = 160000$; Dispersal function = normal; RMSD = 3.47 km. The migration rate, front width and rate of population increase were determined from the graphical output.

4.1.2. Single Dispersal Function and Multiple Cohort Case

The simulations described in section 4.1.1 used only one age class which consisted of the number of reproductively mature individuals. It was assumed that all offspring were produced at the beginning of a cohort period and therefore reproduced in the next generation cycle of the simulation. The use of additional cohorts makes the model more realistic since each cohort class can have different fecundity and survival values. In particular, the first cohort class may be used for juveniles which are not reproductively mature.

It can be seen that if the fecundity and survival probabilities are the same for each cohort in a multiple cohort simulation (Simulation B13) then the result is the same as that for a single cohort simulation (Simulation B1).

By repeating the previous simulation but with a zero fecundity value assigned to all cohort classes except the first it can be shown that it was the propagule input from the first cohort class that determined the migration rate (Simulation B14). Propagules produced by the older cohort classes therefore have a negligible effect on the migration rate. This phenomenom will be true for all simulations where the number of successful offspring per generation is both constant for each cohort class and greater than 1.7.

It is interesting to note that behind the population front the population density now fluctuates in a wave-like manner. The troughs are due to an insufficient input of propagules due to the presence of non-reproductive individuals in the immediate area.

If it is assumed that reproductively mature individuals produce offspring at a constant rate throughout a generation period then the average number of offspring produced by an individual in the first cohort class can be calculated as follows:

$$S(\text{cohort1}) = \frac{1+2+3+.........+T}{T} \cdot \frac{S(\text{cohort2})}{T} \tag{4.4}$$

Simulation B15 shows the migration rate obtained for a 10 cohort simulation where the first cohort class is given a fecundity value of 83200 (based on an adult fecundity of 1.6 x 10^5 per generation and a generation length of 25 years). The migration rate has been reduced from 0.20 km yr^{-1} (Simulation B12) to 0.17 km yr^{-1}. The slower migration rate predicted by simulation B15 is more realistic than that predicted by simulation B13 since it allows for a limited amount of reproduction to occur in the first cohort class as a consequence of only a fraction of them reaching maturity during a simulated time step. In

Simulation B16, an older cohort class produces significantly more offspring than the other reproductively mature cohort classes, however, the migration rate has been increased only very slightly.

In simulation B17 the probability of becoming a mature tree has been reduced by a factor of 10 and the RMSD increased to 11 km so as to maintain the migration rate at approximately 0.2 km yr^{-1}. The wave-like fluctuations behind the population front are a result of the low propagule output of the first cohort class. These fluctuations disappear if the number of propagules is increased to 1.6×10^5.

4.1.3. Joint Dispersal Function and Multiple Cohort Case

The RMSD for dispersal used in the above simulations is very large when compared with field observations. These indicate that most propagules fall very close to the parent tree with very few going beyond a few hundred metres. It therefore seems that there must be at least two dispersal processes operating. In the following simulations, two dispersal functions were used, one for local dispersal and one for the rare long-distance dispersal events.

Simulation B18 is the result of a simulation in which 90% of the propagules were dispersed according to a normal dispersal function with RMSD = 0.2 km. The RMSD of the normal dispersal function for the remaining 10% of propagules was varied until a migration rate of approximately 0.2 km yr^{1} was obtained. The cell length was reduced to 0.1 km so as to operate at the scale of the shortest dispersal function. This meant that the furthest cell had to be increased to 350 so as to accommodate the long-distance dispersal function. This increase in computation resulted in the simulation taking considerably longer to run. Although this is not a problem in the one-dimensional version of MIGRATE it would become a problem in two-dimensional simulations. In simulation B19 the previous simulation is repeated but with a cell length of 3 km and all the locally dispersed propagules simply being placed in the parent's cell. It is clear that this approximation has had no effect on the migration rate.

Simulations B20 and B21 are similar simulations but with the proportion of propagules being dispersed according to the distant dispersal function set at 0.99 and 0.999 respectively. In both cases, the RMSD of the distant dispersal function was increased so as to maintain the migration rate at approximately 0.2 km yr^{-1}. These results are summarised in Table 4.4.

Table 4.4 The relationship between the probability of dispersal by the long-distance dispersal function and the RMSD of the long-distance dispersal function. The RMSD of the long-distance dispersal function was varied so as to maintain a constant migration rate of 0.2 km yr^{-1}. All other parameter values were held constant.

Probability of distant dispersal	RMSD of distant dispersal (km)	Simulation number
0.1	6.7	B19
0.01	9.7	B20
0.001	12.3	B21

When simulation B21 is repeated with a cell length of 0.1 km then the migration rate is 8 m yr^{-1} slower. The slightly faster migration rate obtained with a cell length of 3 km is due to the fact that there can be more individuals in a cell and therefore the chance of long distant dispersal is increased.

Simulations B23 and B24 are the same as simulations B19 and B21 respectively, but with the use of the rounding option. It is clear from these simulations that the rounding option causes a loss in the smoothness of the migration front. It has the greatest effect when the probability of long-distance dispersal is small. There is also a small reduction of approximately 10 m yr^{-1} in the migration rate due to the 'loss' of the very small fractions of individuals at the migration front.

4.2. Comparison with Skellam's Model

Simulation B25 shows the migration of oak obtained when using the parameter values used by Skellam (1951). The simulated rate of 0.05 km yr^{-1} is in exact agreement with that predicted by equation 4.1. This simulation shows quite clearly that the population front is unrealistically steep, a consequence of the high fecundity.

4.3. Comparison with Van den Bosch *et al.s*' Models

The following describes a comparison between a simulation done using MIGRATE and the analytical approximation formulae developed by Van den Bosch *et al.* (1990, 1992). The number of successful offspring as used in the previous simulations was reduced so that the net number of successful offspring (R_0) did not exceed 7.0, the limit for an accurate prediction by equation 4.9 (Van den Bosch *et al.*,1992).

Following the notation of Van den Bosch *et al.* (1992) the hypothetical life table shown in Table 4.5 was constructed. In contrast to Van den Bosch *et al.* (1992) and in accordance with the MIGRATE model, *l* is taken to be the number of individuals alive at the beginning of the cohort period (Odum, 1971 page 175).

Table 4.5 A hypothetical life table for a long-lived species with 10 cohort classes.

Cohort No. i	Age interval (years)	Average age a_i	Number of successful offspring m_i	Survivorship l_i	$l_i.m_i$	$a_i.l_i.m_i$	$a_i^2.l_i.m_i$
1	0-25	12.5	0.416	1.0000	0.416	5.2000	65.00
2	25-50	37.5	0.8	0.9130	0.7304	27.3900	1027.13
3	50-75	62.5	0.8	0.8336	0.6669	41.6785	2604.90
4	75-100	87.5	0.8	0.7610	0.6088	53.2734	4661.42
5	100-125	112.5	0.8	0.6948	0.5559	62.5354	7035.23
6	125-150	137.5	0.8	0.6344	0.5075	69.7825	9595.09
7	150-175	162.5	0.8	0.5792	0.4634	75.2953	12235.49
8	175-200	187.5	0.8	0.5288	0.4230	79.3207	14872.64
9	200-225	212.5	0.8	0.4828	0.3862	82.0758	17441.11
10	225-250	237.5	0.8	0.4408	0.3526	83.7511	19890.89
	above 250	-	-	0.0000	0.0000	0.0000	0.00
Total					5.1107	580.3027	89428.90

The net reproductive rate was estimated as

$$R_0 \approx \sum_i l_i m_i = 5.11 \tag{4.5}$$

The mean age at child bearing (u) was estimated as

$$u \approx \frac{1}{R_0} \sum_i a_i l_i m_i = 113.55 \tag{4.6}$$

The variance of the age at child bearing (v^2) was estimated as

$$v^2 \approx \frac{1}{R_0} \sum_i a_i^2 l_i m_i - u^2 = 4605.7 \tag{4.7}$$

The following equations developed by Van den Bosch *et al.* (1990, 1992) were used to estimate the migrate rate:

$$C_1 \approx \frac{\sigma}{u} \sqrt{2.\ln R_0} \tag{4.8}$$

$$C_2 \approx C_1.\left\{1 + \left[\left(\frac{v}{u}\right)^2 + \frac{1}{12}.\gamma\right] \ln R_0\right\} \tag{4.9}$$

Where σ^2 is the variance of the marginal dispersal density and γ the kurtosis of the marginal dispersal density. If the distribution is normal then the variance is equal to ½.RMSD^2 and the kurtosis is equal to zero. The above calculations were performed on a spreadsheet which was set up to allow the data to be entered in the form of a life table. The migration rates were then calculated automatically using cells which had been programmed accordingly.

A value of 11 km was used for the RMSD which together with the reproductive characteristics estimated from the data in Table 4.5 using equations 4.5 to 4.7 gave migration rates of 0.124 km yr^{-1} (equation 4.8) and 0.196 km yr^{-1} (equation 4.9). These migration rates are approximations to the migration rates obtained using the reproduction and dispersal kernel formulae from which they were derived. C_1 is said to be accurate when $R_0 \leq 1.5$, whereas the more complicated formula for C_2 is reported to be accurate when $v/u \leq 0.6$ and $R_0 \leq 7.0$. It can therefore be assumed that in this example C_2 should be the better predictor of the migration rate. Equation 4.8 is the same as Skellam's (1951) model if it is assumed that all the offspring are produced when the individuals become reproductively mature i.e. $u = T$. However, it is also a refinement of Skellam's model in that it allows for multiple cohorts with variations in survivorship and fecundity. C_2 is a refinement of C_1 since by incorporating the kurtosis of the marginal dispersal density it does not assume that the dispersal function is normal.

Since the analytical models given by equations 4.8 and 4.9 assume the environment to be homogeneous it was appropriate to use the one-dimensional version of MIGRATE when comparing the migration rate simulated by MIGRATE with that predicted by the analytical models. 10 cohort classes were used corresponding with the 10 cohort classes in Table 4.5. The initial number of individuals in each cohort class is unimportant since the migration rate eventually stabilises to a constant rate. The product of the number of propagules (S) and the probability of surviving to maturity (P_0) for each cohort was set so as to equal the value of m in Table 4.5. The probability of surviving from cohort i to cohort i+1 was calculated as ${}^{l_{i+1}}\!/_{l_i}$. A normal dispersal function was used with an RMSD of 11 km. With these parameter values the simulated migration rate was 0.19 km yr^{-1} (simulation B16). This is a 65% agreement with C_1 and a 95% agreement with C_2.

The close agreement between the predictions of the analytical models of van den Bosch *et al.* and the MIGRATE simulations indicates that the models have a very similar formulation. However, this does not imply that the formulation is correct. Only by testing the models against observed migrations can the formulation be validated. Further refinements can then be carried out to the models as necessary. Van den Bosch *et al.* (1992) have attempted to validate their models using observed migration rates for the collared dove, muskrat, house sparrow, starling and cattle egret. They found that given the accuracy of the type of field data used the model predictions were in reasonable agreement with the observed rates of spread (Van den Bosch *et al.*, 1992; Hengeveld, 1994). The migration rates simulated by MIGRATE for the muskrat, house sparrow and collared dove are compared with those predicted by the models of Van den Bosch *et al.* (1992) in Table 4.6. Van den Bosch *et al.* (1992) do not give sufficient data for MIGRATE to be used to simulate the migration of the starling and cattle egret. An example showing how the MIGRATE simulations were carried out is given by simulation B26 which shows the migration of the collared dove according to a normal dispersal function. Some of the discrepancy between the rates predicted by MIGRATE and those predicted by the formulae developed by Van den Bosch *et al.* is probably due to the fact that Van den Bosch *et al.* assume that survivorship (l_i) is the number of individuals alive at the end of the time interval and not at the beginning.

Table 4.5. Comparison between the observed migration rate (km/yr) as given by Van den Bosch et al. (1992) and the rates obtained from MIGRATE and the analytical models of Van den Bosch et al. (1992).

		Migration rate (km yr^{-1})			
Species	Observed	MIGRATE[1]		Van den Bosch *et al.* model	
		Gaussian Dispersal	Empirical Dispersal	C_1	C_2
Muskrat 1900-1930	10.9	5.4		4.8	7.0
Muskrat 1930-1960	5.1	4.9		3.3	3.9
House sparrow (U.S.A.)	16.8	8.9	12.0	6.0	10.2
House sparrow (Europe)	27.9	9.5	13.9	8.2	23.0
Collared dove	43.7[2]	81.0	80.0	56.3	65.6

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[1] Approximate migration rate as determined from the graphical output of the MIGRATE simulation (see section 2.1)

[2] It is interesting to note that the observed migration rate determined by Hengeveld and Van den Bosch (1991) is much less than the rates predicted by any of the models. In all the other cases the observed migration rate is greater than the predicted migration rates. Hengeveld and Van den Bosch (1991) determined the rate of spread of the collared dove from a graph of the square root of the area occupied against time. However, the rate determined by this process is only half of that recorded in the ornithological literature (for example, Fisher, 1953; Welty, 1962; Sharrock, 1976) where the migration rate was simply calculated as the distance travelled divided by the time taken. Without access to the original calculations carried out by Hengeveld and Van den Bosch (1991) it is not possible to establish the reason for this discrepancy.

4.4. Comparison with Bennett's Model

Following the suggestion of Watts (1973), Bennett (1983, 1986, 1988a) has used pollen accumulation rates to estimate the intrinsic rate of population increase. This is based upon observations that graphs of the natural logarithm of the pollen accumulation rate with respect to time are linear. This linear relationship is believed to be the direct result of the exponential rate of population increase. However, Davis and Sugita (submitted) argue that the shape of front has more to do with the dispersal properties of pollen and the migration rate of the taxon. Bennett (1988a) also suggests that *Fagus grandifolia* did not spread as a continuous front but as a series of outlying populations which gradually increased in density before merging with the main population. As the very low densities at the front of the expanding range are below the threshold required for detection by pollen analysis, Bennett (1986) suggests that the real rates of migration may be greater or lesser than those determined from pollen analysis. The following sections examine how simulations from the one-dimensional version of MIGRATE fit in with Bennett's model of migration.

4.4.1. Intrinsic Rate of Population Increase

The rates of population increase for the simulations done so far using MIGRATE (as determined from the gradient of the lower graphs) are much larger than those determined by Bennett (1983) for the post-glacial migration of trees in Norfolk. Simulation B17 has the lowest rate of population increase (0.03). In order to achieve values which fall within the range 0.022 to 0.002 given by Bennett (1983) and achieve a migration rate of 0.2 km yr^{-1}, not only does fecundity have to be low, but there must be a small number of individuals dispersing over a long-distance. Simulation B27 is the same as simulation B17 but with two dispersal functions rather than one. A small fraction of the propagules are dispersed according to a long-distance dispersal function with the remainder simply being placed in the parent's cell. The intrinsic rate of population increase has now been reduced to 0.022. This is still rather high for a tree such as *Tilia cordata* where Bennett (1983) gives the intrinsic rate of population increase as 0.0100-0.0039.

In order to further reduce the intrinsic rate of population increase the probability of seed survival was reduced to 2×10^{-6}. The RMSD of the long-distance dispersal function was increased from 35 km to 75 km in order to compensate for the reduction in seed survival and maintain the migration rate at 0.2 km yr^{-1} (simulation B28). The intrinsic rate of population increase is now 0.009. An alternative way to maintain a migration rate of 0.2

km yr^{-1} is to increase the probability of long-distance dispersal by a factor of 10 to 0.1. The required RMSD of the long-distance dispersal function is now only 45 km which intuitively seems more feasible (simulation B29). The consequence of this more concentrated dispersal function was a small increase in the intrinsic rate of population increase from 0.009 to 0.01. There was virtually no change in the extent of the population front.

These results imply that if the rates of population increase as determined by Bennett (1983) from fossil pollen analysis are realistic approximations of the intrinsic rate of population increase then the number of successful offspring must have been very low. Therefore in order for the post-glacial migration rates to have been achived dispersal must have occurred at low frequencies over very long-distances (exceeding 100 km).

4.4.2. The Role of Long-Distance Dispersal Events

In order to obtain a value for the intrinsic rate of population increase which is in agreement with Bennett (1983) it was necessary to couple a low reproductive success rate with a high RMSD for the long-distance dispersal function. With the same parameter values as used in simulation B28 and the number of individuals rounded to a whole number according to a random number generator (see section 2.1.4), a maximum dispersal event of around 240 km was recorded (average of 5 simulations) as occurring during the 100 generations over which the simulation was run. For simulation B29 the maximum recorded dispersal distance over the same time period was 170 km. It is likely that such very long-distance dispersal events would have originated from the area where the tree density was already high so they may not have had a significant effect on migration.

MIGRATE currently assumes that the probability of a propagule becoming a reproductively mature individual is constant. However, it is possible that those propagules which are dispersed further will have a greater chance of survival. This hypothesis is known as the escape hypothesis (Howe and Smallwood, 1982). They will escape density dependent factors such as herbivory and intraspecific competition. MIGRATE accounts for intraspecific competition through a self-thinning mechanism (see section 2.2 equation 2.3) but does not take into account herbivory which is likely to be greatest where the seed/seedling density is highest.

In order to assess the implication of a different survival probability associated with each dispersal function simulation B28 was repeated but with the probability of a propagule which is dispersed according to the long-distance dispersal function surviving to the age of first reproduction increased by a factor of 6 (simulation B30). This was done by assigning a probability value of 0.06 instead of 0.01 to the long-distance dispersal function rather than by making explicit changes to MIGRATE, therefore the dispersal sum does not equal zero. The simulated migration rate is now 90 m yr^{-1} faster than that simulated in B28. However, the rate of population increase shows only a small increase from 0.009 to 0.01. In order to bring the migration rate back down to 0.2 km yr^{-1} the RMSD of the long-distance dispersal function can be reduced to almost 50 km yr^{-1} (simulation B31). The extent of the migration front is very similar to that observed in simulation B28 with the rounding option. The maximum recorded dispersal distance during the 100 generation simulation is now 185 km (average of 5 simulations).

These simulations show that the model is very sensitive to the number of successful long-distance dispersal events. Given the very long-distances involved and their rarity it is unlikely that such events could ever be measured in the field. However, it is known that dispersal is capable of occurring over very long-distances (see Chapter 1). These simulations show that a value for the intrinsic rate of population increase as observed at a specific location over which the migrating species passes may help to determine the correct parameter values for the long-distance dispersal function, but only if it can be very accurately measured.

4.4.3. The Shape of the Migration Front

Bennett (1986) suggests that as pollen analysis can not detect tree population densities of much less than one per hectare it is not possible to determine whether spread is actually occurring at lower densities. Below the threshold for detection, the rate of migration may be slower or faster than that detected by pollen analysis. MIGRATE offers some evidence in support of this theory since in the examples where the number of successful offspring are low and the dispersal function has a long tail there is a period at the beginning of the simulation where the wave form of the migration front has yet to reach its equilibrium shape. For example, in simulation B27 for generations 5 to 20, the average migration rate measured at 10 trees ha^{-1} is 0.22 km yr^{-1}. However, if the migration rate is measured as the distance between the points where generations 5 and 20 meet the x axis then the migration rate for that period is 0.19 km yr^{-1}. So, for the period up to generation 20, the rate of migration depends on the position of the threshold line for detection. This phenomenon is only likely to occur when the initial distribution prior to migration has a shape different to that of the migrating front and when the number of successful offspring is low so that it takes many generations for the equilibrium to be achieved. Changes in dispersal distances and number of successful offspring during migration will result in changes in the shape of the wave front. During this period of change, the migration rates will again depend on the threshold level of detection.

4.5. Comparison Between the Intrinsic Rate of Population Increase Determined from MIGRATE Simulations with that Predicted by the Euler Equation

The intrinsic rate of population increase determined from the MIGRATE simualtions is in good agreement with that predicted by the approximation formula for the Euler equation (Van den Bosch *et al.*, 1992). For example, for the simulation shown in B27 the Euler equation predicts a rate of:

$$\alpha = \frac{\ln(R_0)}{\mu}\left[1+\frac{1}{2}.\left(\frac{v}{u}\right)^2.\ln(R_0)\right] \tag{4.10}$$

$\alpha = 0.019.$

The rate determined from MIGRATE was 0.022.

Van den Bosch *et al.* (1992) have shown that for small values of R_0 (≤ 1.5) the rate predicted by the Euler equation is approximately half that observed at a certain place during an invasion. A simulation done with $R_0 = 1.43$ had an intrinsic rate of increase of 0.0052 (simulation B32) and 0.0036 (from Euler equation). This is in agreement with Van den Bosch *et al.* (1992).

4.6. How May the Variation in the Observed Migration Rates of a Taxon be Explained?

The simulations done so far have used parameter values with the aim of achieving a migration rate of 0.2 km yr^{-1}. However, the palaeoecological record has shown that taxa migrated at different rates during their post-glacial migrational history. For example, Huntley and Birks (1983) give the migration rate of Tilia as 0.3 to 0.5 km yr^{-1} on the European mainland. The three most likely ways through which such a large change in the migration rate could be effected are:

- a change in the number of successful offspring produced per individual;
- a change in long-distance dispersal function (through its probability of occurrence or its distance parameter);
- a change in the age of first reproduction.

For simulation B28 a small increase in the number of successful offspring (brought about by increasing the probability of reaching the age of first reproduction from 2×10^{-6} to 6×10^{-6}) resulted in a large increase in the migration rate from 0.20 km yr^{-1} to 0.50 km yr^{-1} (simulation B33). The intrinsic rate of population increase also increased from approximately 0.009 to approximately 0.02, however, this is still just within the range given by Bennett (1983). Note that the rule regarding the relationship between fecundity and migration rate described in section 4.1.1 now no longer applies since the introduction of a second dispersal function and the use of two age classes has increased the complexity of the model. A much larger increase in the probability of reaching the age of first reproduction is needed for the migration rate simulated in B20 to reach 0.5 km yr^{-1}. In this case the probability of reaching the age of first reproduction has to be increased by a factor of 30 to 1.5×10^{-3} (simulation B34). This has also resulted in a large increase in the intrinsic rate of population increase from 0.07 to 0.20.

It is unlikely that there would have been any significant change in the long-distance dispersal function during post-glacial migration. Large changes in dispersal frequencies and distances would have to be accompanied by significant changes in the agents of dispersal, for example wind speed, frequency of storms, activity of animal dispersal agents etc. In order to increase further the migration rates simulated so far, the value of the RMSD of dispersal would have to be made even larger. It seems very unlikely that this could occur as it is already difficult to adequately explain the occurrence of the very long dispersal distances in the simulations carried out so far.

A decrease in the age of first reproduction could be a consequence of a faster growth rate due to more favourable climatic conditions. However, there is a limit as to how much this could be reduced. Table 4.1 shows that a decrease in the age of first reproduction can have a significant effect on the migration rate. Simulations B20 and B28 were repeated but with the age of first reproduction reduced to 10 years and the fecundity and survival probabilities modified as described in section 4.1.1. (simulations B35 and B36 respectively). In the case of simulation B35, there has been an increase in the migration rate from 0.20 km yr^{-1} to 0.34 km yr^{-1}. However, in the case of simulation B36 there has been virtually no increase in the rate of spread.

The results described in this section are to some extent surprising and could probably not have been guessed from the sensitivity analyses carried out for the simple one dispersal function one age class model described in section 4.1.1. In particular it is important to note how sensitive the model was to small changes in very low fecundity values in conjunction with a long-distance dispersal function with a large RMSD. The rates predicted by the models of Van den Bosch *et al.* (equations 4.8 and 4.9) for simulations B33 and B34 are in poor agreement with the rates simulated by MIGRATE (0.50 km yr^{-1} for B33 and 0.49 km yr^{-1} for B34). For simulation B33, the migration rates predicted by the models of Van den Bosch *et al.* were 0.095 km yr^{-1} (equation 4.8) and 4.2 km yr^{-1} (equation 4.9). For simulation B34 the migration rates were 0.026 km yr^{-1} (equation 4.8) and 4.3 km yr^{-1} (equation 4.9). The disagreement can be largely attributed to the very large value of R_0 for simulation B34 and the fact that the large value of the kurtosis of dispersal (270 and 300) does not seem to accurately represent a dispersal function in which a small number of individuals are dispersed over very long distances. The sensitivity of equation 4.9 to the kurtosis of the marginal dispersal density was confirmed by varying its value within the spreadsheet set up to calculate migration rates using Van den Bosch *et al.*s' models. For example, simulation B33 predicts the same migration rate as MIGRATE if the value of the kurtosis is set at 25.

4.7. Two-Dimensional Simulations Showing the Migration of *Tilia cordata* Through Northern Britain.

The main advantage the two-dimensional version of MIGRATE has over its one-dimensional counterpart is that it can be used to investigate the spread of a species across a heterogeneous environment. In order to assess the effect of environmental heterogeneity it was first necessary to carry out simulations in a uniform environment. The rate and pattern of spread in a homogeneous environment can then be compared with one more representative of the modern landscape of the British Isles in which areas of suitable habitat have both declined and become fragmented. These simulations were then followed by an investigation into the effects of climate. The habitat and climate maps were created as described in Chapter 2 using data from the Institute of Terrestrial Ecology's land cover database and the Climatic Research Unit's climate databases. Finally, some simulations were done in which the present day relative carrying capacity values are modified by using probability of occurrence values. In these simulations, no additional climatic restrictions are imposed as the three bioclimatic variables used in generating the probability of occurrence values are already acting by reducing the relative carrying capacity values. The simulations were all carried out for *Tilia cordata* since much is known about its ecology and its response to climate is particularly well understood.

4.7.1. Choice of Parameter Values

As described in section 2.2, some of the parameter values can be obtained or estimated from the literature. The values which were obtained by this means for *T. cordata* were given in section 4.1.1. Other parameters, however, have to be estimated by using the one-dimensional model to determine the area of "parameter space" within which the required migration rate is achieved. Two cohort classes were used as the reproductive data available in the literature were not sufficiently accurate to make the use of additional cohorts worthwhile. The most realistic approximation was therefore to use one cohort class to represent the young trees yet to reach reproductive maturity and another for trees older than the age of first reproduction. Two dispersal functions were used, since as described in section 4.1.3 this appears to be the most realistic representation of what happens in nature.

The simulations described in section 4.1 have enabled possible values for the parameters involved in long-distance dispersal to be determined. There are three parameters which determine the distance and frequency of long-distance dispersal events. These are the number of propagules reaching the age of first reproduction, the probability of long-distance dispersal and the RMSD of the long-distance dispersal function. If fecundity and the probability of dispersal by the long-distance function are low then the RMSD of the long-distance dispersal function must be compensatingly large. Each two-dimensional simulation was carried out twice using a different set of parameter values. In case I, the parameter values used in simulation B20 were used but with the probability of reaching reproductive maturity increased by x 5 to allow for a reduction in the relative carrying capacity to 0.2 (see section 4.7.2). In case II, the parameter values used in simulation B29 were used, again with the probability of reaching reproductive maturity increased by x 5. The parameter values are summarised in Table 4.6. The one-dimensional simulations using case I and case II parameter values are shown in Figs 4.5 and 4.6 respectively. In both cases the rounding option was used since this is always applied in the two-dimensional simulations (see section 2.1.5). The initial population was set as a strip of *T. cordata* 10 km deep with 50 mature trees per square km. Both sets of parameter values produced a simulated migration rate of approximately 0.18 km yr^{-1} in a homogeneous environment. However, they reflect two possible extremes, case I couples a high reproductive success with a relatively short long-distance dispersal function whereas case II couples a lower reproductive success with a much longer long-distance dispersal function. The simulation with case I parameter values has a steep continuous migration front as is thought to have occurred by Davis (for example, Davis 1983b; Davis and Sugita, submitted). Case II parameter values, however, result in a more extensive population front which is in agreement with Bennett's (1983, 1986, 1988a) view. The intrinsic rate of population increase for case II (0.01) is in agreement with Bennett's (1983) measurements which were determined from the pollen record. The low rate of population increase results in a delay lasting as much as several millennia before the equilibrium abundance levels are reached (Bennett, 1986). Case I parameter values result in an intrinsic rate of population increase which is approximately eight times greater than that resulting from case II parameter values.

The assumptions made throughout these simulations are that the reproductive and dispersal parameters are the same as for post-glacial migration. In addition it is assumed that the post-glacial migration rates were limited by dispersal since if, for example, climate was limiting migration then it would not have been appropriate to use the post-glacial migration rates as a means of estimating the RMSD of the long-distance dispersal function as this would have resulted in its value being underestimated. Attempts have been made to discover whether or not tree migration lagged climate change (Davis *et al.*, 1986). However, they were unable to draw any firm conclusions since as dispersal and climate are not mutually exclusive causes for colonisation delays it is impossible to determine whether the migration rate was climate limited or dispersal limited. However, the relative constancy of the maximum migration rates between geographical regions despite differences in the rates of climate change suggests that the post-glacial migration rates were limited by dispersal and colonisation and not by the rate of climate change (Huntley, 1989).

The initial distribution of *Tilia cordata* (Fig. 4.7) was derived from Pigott's (1992) presence absence map. This map had to be converted into the number of trees per square km. As Pigott (1992) states that many of the existing populations are small it seemed reasonable to assume that there were 50 reproductively mature trees in each 1 km square cell where *T. cordata* was recorded as being present. Refinements to this distribution were made by referring to Paice (1974) where sites with only one tree occurring were recorded separately. The number of trees in the juvenile age class was set to zero since although there had been some successful regeneration of *T. cordata* in the Lake District during the hot summers of 1976, 1983 and 1984 all the seedlings were consumed by wood mice and voles (Pigott, 1992). Simulations carried out with 50 seedlings as well as 50 mature trees in the initial distribution showed that the results were insensitive to this.

Table 4.6 Parameter values used in the two-dimensional simulations. Case I parameter values result in a higher intrinsic rate of population increase (0.08) than case II (0.01).

Parameter	Case I	Case II
Cell length	1 km	as case I
Area occupied by an individual	50 m^2	as case I
Generation length	25	as case I
Probability of becoming reproductively mature tree	2.5×10^{-4}	1×10^{-5}
Probability of adult surviving a further generation	0.913	as case I
Number of offspring produced per generation by juvenile cohort	83200	as case I
Number of offspring produced per generation by adult cohort	160000	as case I
Probability of dispersal by long-distance dispersal function	0.01	0.1
RMSD of long-distance dispersal function	9.7 km	45 km

4.7.2. Homogeneous Environment with no Climatic Restrictions

The relative carrying capacity was set at 0.2 i.e. up to 20 percent of the cell area may be occupied. These environmental conditions may be considered to be similar to those experienced by *T. cordata* during post-glacial migration if it is assumed that climate was not limiting its migration. During those times, *T. cordata* would have been migrating through land which was predominantly forested. Taxa such as *Betula*, *Corylus*, *Ulmus*, *Quercus* and *Pinus* had already spread throughout most of the British Isles before *T. cordata* arrived. *T. cordata* was probably a major constituent of forests during its migration (Birks, 1989) so a relative carrying capacity of 0.2 seems quite reasonable.

The simulation with case I parameter values shows that spread occurs by the circular expansion of populations which coalesce to form a continuous front (Fig. 4.8). The rate of spread of this front is approximately 0.18 km yr^{-1} which is in agreement with the rate simulated by the one-dimensional version of MIGRATE with the rounding option (Fig. 4.5). The simulation done with case II parameter values (Fig. 4.9) produces an outcome which is quite different to that produced with case I parameter values. Although *T. cordata* has spread just as far north it has done so at a much lower density and a continuous expansion front is not so obvious. The reason for the difference between the two simulations becomes apparent when the results from the one-dimensional simulations are examined (Figs 4.5 and 4.6). It can be seen that although both populations eventually attain the same rate of spread it takes much longer for the equilibrium abundance level to be reached with case II parameters. This is a consequence of the lower intrinsic rate of population increase with case II parameters. These results indicate that where the intrinsic rate of population increase is very low (less than about 0.02) it is important to know both the current distribution of the species being studied and the density at which it occurs. The simulation with case II parameters is in agreement with Bennett's view of the pattern of migration in that spread occurs at very low densities. Some of the outlying populations are sufficiently isolated so as to be possibly undetectable in the fossil record.

In order to gain some insight into the frequency of dispersal events occurring with case I and case II parameter values the number of dispersal events falling into various distances categories were counted using the dispersal logging option described in section 2.1.4. The numbers were converted into logarithms of the proportion of the total number of prospective individuals dispersed. The graphical display of these results is shown in Figs 4.10 and 4.11. These curves show that the majority of propagules are dispersed only a short distance from their parent. The slight increase in dispersal probability observed after the initial sharp fall off is a consequence of the relationship between the dispersal function itself and the fact that the area of each sampling annulus increases with increasing distance from the source.

4.7.3. Heterogeneous Environment with no Climatic Restrictions

In today's modern environment it is not appropriate to consider the habitat to be homogeneous. Habitat loss and fragmentation have resulted in a landscape which is very heterogeneous. In order to look at how this may affect the possible future migration of *T. cordata* a relative carrying capacity map was constructed as described in section 2.3.2 using the Institute of Terrestrial Ecology's land cover database. The values were the fraction of deciduous woodland in each 1 km square cell multiplied by 0.2 i.e. *Tilia* was able to occupy up to 20% of the deciduous woodland in each cell. None of the other habitat types were considered to be suitable for invasion. As *T. cordata* is a shade tolerant mid-successional tree species this land cover class seemed to be the most appropriate choice. In addition, it probably represents the only land cover category which could be invaded by *T. cordata.* As *T. cordata* will grow on a wide variety of soils (Paice, 1974) it was not thought necessary to include soils data in the creation of the habitat map shown in Fig. 4.12. Simulations were carried out using case I (Fig. 4.13) and case II (Fig. 4.14) parameter values and the current distribution of *T. cordata.*

It is clear that in the heterogeneous environment which is typical of the modern landscape the migration rate of *T. cordata* will be much reduced. The simulation with case II parameter values shows the greatest reduction in range expansion with very little spread being observed beyond the initial distribution sites. The rate of spread with a heterogeneous habitat is about three times less than that with a homogeneous habitat suggesting that the habitat loss and fragmentation typical of the modern landscape will significantly reduce the ability of a species to migrate.

In order to look at how the patchy nature of modern day habitat availability may affect the future spread of *T. cordata,* a simulation (Fig. 4.15) was carried out in which the relative carrying capacity of each cell was smoothed by assigning it the average relative carrying capacity of all land cells within a 3 km radius. The parameters used were the same as those used with case I parameter values and a heterogeneous environment with no climatic restrictions (Fig. 4.13). The resulting extent of spread is very similar in both simulations which indicates that the distribution of available habitat is not important at the scale of tree migration.

MIGRATE can also be used to investigate the effect of changes in both habitat availability (i.e. number of cells available for colonisation) and relative carrying capacity (i.e. proportion of each cell available for colonisation) in the same manner as has been done by Schwartz (1992). Such investigations enable the magnitude of the changes in the migration rate due to changes in habitat availability and suitability to be assessed. For example, using case I parameter values with a homogeneous environment and a relative carrying capacity of 0.2 the simulated migration rate was 0.18 km yr^{-1}. However, when the proportion of available cells was reduced from 1.0 to 0.1, the migration rate was reduced by a third to 0.12 km yr^{-1}. Although the magnitude of this response is less than that predicted by Schwartz (1992) who predicted that migration rates would decrease by a factor of ten as a consequence of a reduction in habitat availability from 80% to less than 30%, the reduction in the rate of spread is still great enough to indicate that habitat loss may contribute significantly to tree species failing to migrate fast enough to keep pace with future climate change. The quantitative differences between the results predicted by MIGRATE and Schwartz's model could be due to differences in the parameter values used in the simulations or differences in the formulation of the two models. However, simulations with MIGRATE using parameter values matching as far as possible those used by Schwartz predicted a two thirds reduction rather than a 10 fold decrease in the migration rate when habitat availability decreased from 80% to 10%. Schwartz observed that the migration rate predicted by his model depended upon the threshold level of detection. However, the one-dimensional simulations with MIGRATE show quite clearly that the migration rate is not dependent upon the level of detection once the population front has reached its equilibrium shape. If the population front was adapting to its equilibrium shape during the time period that Schwartz measured the migration rate then this may explain the discrepency between the results of the two models.

4.7.4. Effect of Climate

Under current climatic conditions, nowhere in northern Britain is hot enough during the summer for *T. cordata* to reproduce. Pigott and Huntley (1981) found that the frequent production of fertile seed is now almost bounded by the 20°C isotherm for the mean daily maximum temperature in August.

The climate map for a hypothetical year under current climatic conditions (Fig. 4.16) was constructed as described in section 2.3.3. In reality there are no 1 km squares which have a mean August daily maximum temperature greater than or equal to 20°C. However, these values are average values based on a thirty year period (1960 to 1990). The standard deviations of these data for Durham and Morecambe were 1.57°C and 1.47°C respectively. It therefore seemed reasonable to use a standard deviation of 1.6°C for the whole of the study area as a means of varying the current day values. When the temperature was varied according to a normal distribution with a standard deviation of 1.6°C then some of the grid squares have temperatures great enough for the successful reproduction of *T. cordata*. This is to be expected as Piggott (1992) has observed seedlings of *T. cordata* following the hot summers of 1976, 1983 and 1984.

The effect of modern day climate alone was examined by using a homogeneous environment but with the modern day climatic restrictions as described above. From these simulations, it can be seen that with case I parameters (Fig. 4.17) *T. cordata* could potentially extend its range much further north in the next 500 years. However, with case II parameters (Fig. 4.18) only a very limited amount of spread is predicted to occur.

When both the effects of modern day climate and land cover are investigated then the simulation with case I parameters (Fig. 4.19) shows a very much reduced pattern of spread, however, there is still a noticeable increase in tree density after 500 years. With case II parameters (Fig. 4.20), the density and distribution of *T. cordata* after 500 years is almost exactly the same as its initial distribution. This is more in tune with what is expected from current day observations.

These simulations showing the possible response of *T. cordata* to climate change assume that the mean August maximum daily temperature will continue to be the variable which determines its northern limit. However, this may be a false assumption since as climate changes other climatic variables, for example precipitation may become limiting. In order to obtain a better picture of how *T. cordata* may spread in the future a climate response surface was used to modify the present day carrying capacity values. The climate response surface consisted of probability of occurrence values for each 10 km square and was created as described in section 2.3.2. It was found that a threshold probability value of 0.5 was needed in order for the response surface to correctly predict the current distribution of *T. cordata* in Europe (Huntley *et al.*, 1995). Therefore, where this value was exceeded the relative carrying capacity was modified by multiplying by the probability of occurrence value for that square. If the threshold was not exceeded then the relative carrying capacity was set to zero.

Figs 4.21 and 4.22 show the potential range expansion of *T. cordata* with case I parameter values based on its current probability of occurrence at the modal altitude of each 10 km square under homogeneous and heterogeneous environmental conditions respectively. In both simulations the pattern of spread is similar although slightly greater than that predicted by the simulations in which the mean August maximum daily temperature was used as the limiting climatic factor (Figs 4.16 and 4.17). Possible reasons for the discrepancies between the simulations using probability of occurrence values and the simulations using the mean August maximum temperatures only are:

1. In Figs 4.21 and 4.22 the threshold for occurrence was set slightly too low therefore allowing *T. cordata* to spread more freely than in Figs 4.16 and 4.17.

2. The abrupt cut off threshold of 20°C for reproduction used in Figs 4.16 and 4.17 did not allow for some successful regeneration at slightly lower temperatures. When these simulations were repeated but with a cut off threshold of 19.5°C then the extent of spread was much more similar to the simulations using probability of occurrence values.

3. The response surface data are available only at a 10 km resolution and that by using the probability of occurrence at the modal altitude some of the 1 km cells will have been given probability of occurrence values which are too high or too low because their mean altitude differs from the modal altitude upon which the probability of occurrence was based.

These results indicate that if case I parameters are a reasonably accurate approximation to the actual parameter values for *T. cordata* then its current distribution is determined by a combination of the mean August daily maximum temperature and the availability of woodland in which it can potentially regenerate. If the area of woodland for *T. cordata* to spread into was more extensive, then its predicted current distribution with case I parameters would be further north than presently observed.

With case II parameter values and a uniform environment with a relative carrying capacity of 0.2 the restrictions imposed by the climate response surface resulted in spread occurring at very low densities. However, when a heterogeneous environment was used there was no detectable spread.

All the parallel simulations carried out with case I and case II parameter values have shown that simulations with case II parameter values are less able to respond to environmental change. The most likely reason for this is the lower intrinsic rate of population increase associated with case II parameter values.

A simulation was carried out using case I parameter values under uniform habitat conditions with a 2 degree increase in the mean August maximum temperature (Fig. 4.23). This simulation was done with the intention of comparing the difference between simulations in which the future distribution of *T. cordata* is simulated by the use of an increase in the mean August maximum temperature alone versus the use of probability of occurrence values generated from a climate response surface. It was decided to use case I parameter values with a uniform habitat since previous simulations have shown that these conditions resulted in the most extensive range expansion and highest population density, therefore any differences between the two means of effecting future climate change should be more marked. Unfortunately the required probability of occurrence values for a future climate scenario could not be generated in time for inclusion in this thesis. However, by examining the predicted European distribution of *T. cordata* based on its climate response surface it is possible to see that its distribution will shift northeast (Huntley *et al.*, 1995). Using the OSU scenario for a doubling in carbon dioxide concentration, the distribution of *T. cordata* in the British Isles is predicted to become restricted to a few localities in central Scotland. However, with the UKMO scenario *T. cordata* is not predicted to occur anywhere in the British Isles. These distributions are equilibrium distributions, therefore they do not take into account the dynamics of species' response to climatic change. Given the relatively short time scale over which climatic change is predicted to occur (the Intergovernmental Panel on Climate Change predict an increase of approximately 3°C by the end of the next century (Houghton *et al.*, 1990)) it is likely that the future distribution of *T. cordata* will be determined more by its ability to track suitable climate than by climate change itself.

4.8. Model Validation

The longevity of trees has meant that it has not been possible to use them as means of validating MIGRATE. In order to perform a validation exercise, it is necessary to have data on the distribution of a migrating species for at least two points in time. The time interval separating the two distributions should be long enough for there to be a significant difference between them. The minimum separation time will be determined by the rate at which the species is migrating and the spatial resolution at which the research is being carried out. For example, at the 1 km resolution used for modelling the two-dimensional spread of *T. cordata* a minimum distance of 25 km would probably suffice. Therefore, if a species is migrating at 250 m yr^{-1}, which is a typical migration rate observed during post-glacial migration then a time interval 10 years would be needed for a species which is capable of reproducing at 10 years, for example, birch and Scots pine

(Miles, 1988). For species such as oak which do not reproduce until they are much older, a proportionately longer time would be needed.

MIGRATE can, however, be used for other organisms which for modelling purposes can be considered to be sessile (i.e. they disperse as non-reproductive individuals and then settle down to breed within a relatively restricted range). Therefore it may be possible to attempt to validate the model formulation using another species. This has already be done for the one-dimensional version of MIGRATE in section 4.3 where the rates predicted by MIGRATE were compared with those predicted by Skellam's (1951) diffusion model, Van den Bosch *et al.*'s (1992) analytical model and the observed migration rates.

MIGRATE has been used to study the spread of rhododendron in Glen Etive (Griffin, 1994). Although the model was able to reproduce the present day distribution of rhododendron from an initial distribution consisting of the points of probable introduction in 1910 this work can not be considered to be a true validation since in order to obtain a value for the long-distance dispersal parameter the model was 'tuned' until the value used for this parameter gave a distribution which closely approximated to that observed for the present day. The model did, however, prove useful in looking at ways in which the spread of rhododendron in Glen Etive could be controlled. In order for a true validation to be carried out an independent measure of the long-distance dispersal parameter is required.

It had also been hoped to validate the model using data from another study carried out on the spread of rhododendron by Thomson *et al.* (1993). This study examined the spread of rhododendron from 1968 to 1986 using aerial photographs. However, it was decided that the change in the distribution of rhododendron observed during this study was unlikely to be sufficient for validating MIGRATE. In addition, the environmental data which would have been used to create the habitat map only covered three relatively small areas within the study area, the largest of which was approximately 6 km^2.

In the absence of any firm validation of the formulation of MIGRATE and the values used for some of its parameters it should not be used for making quantitative predictions. Despite this, it can still serve a useful purpose as both a management tools and for making qualitative predictions.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0002500, 0.91300;
F = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 8.70 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 16;
K = 0.20; Random number seed = 67; No climatic restraints;
Output interval = 10 generations; Last generation = 100

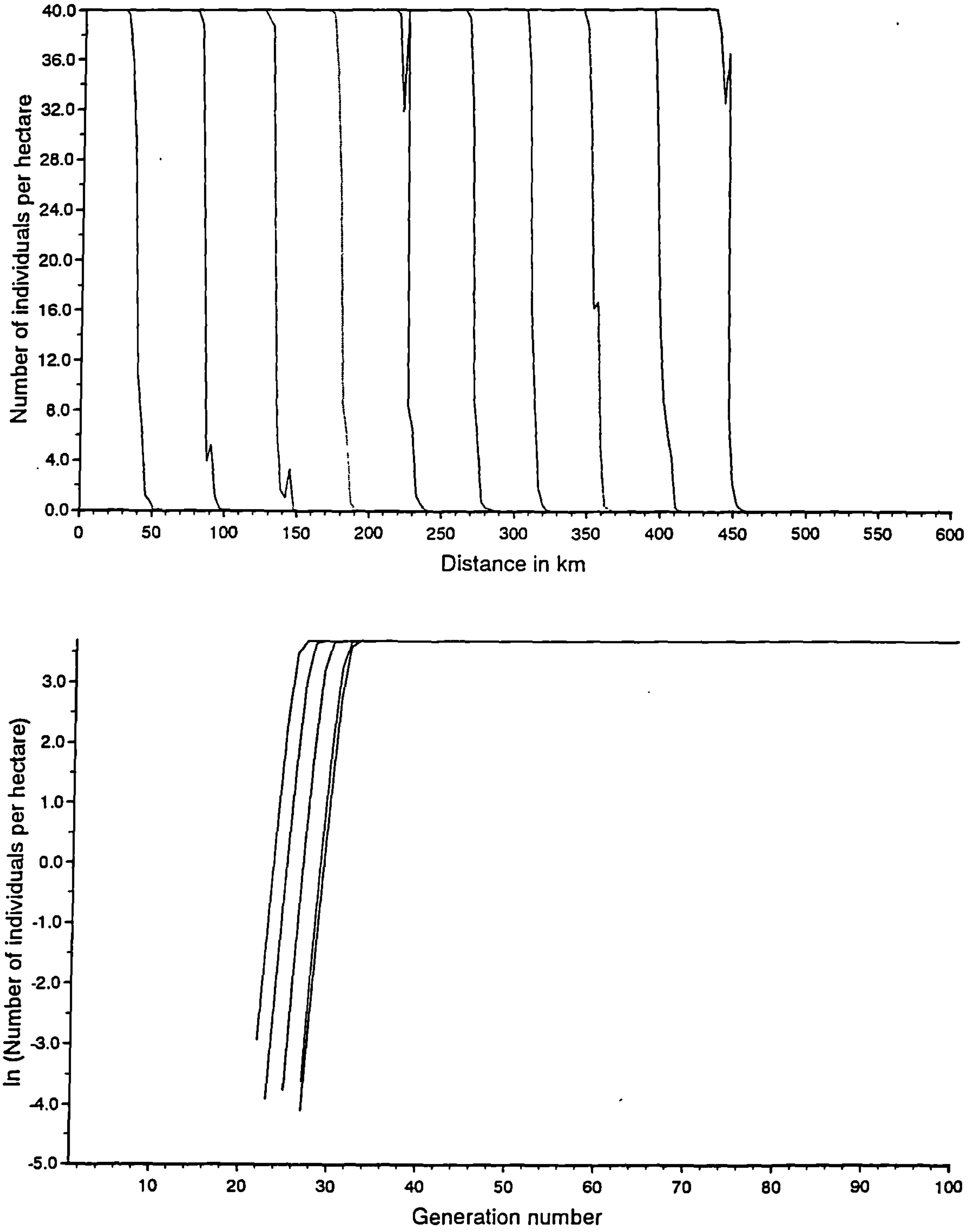


Fig. 4.5 The results of a simulation with case I parameter values (see Table 4.6). Migration rate = 0.18 km yr^{-1}, $\propto$ = 0.08.

```
L = 10.00 km; a = 50.00 m²; T = 25.00 years;
Survival probabilities = 0.0000100, 0.91300;
F = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.900000; RMSD2 = 45.00 km; P(RMSD2) = 0.100000;
Dispersal sums = 0.9000, 0.1000; Total = 1.0000; Furthest Cell = 30;
K = 0.20; Random number seed = 67; No climatic restraints;
Output interval = 10 generations; Last generation = 100
```

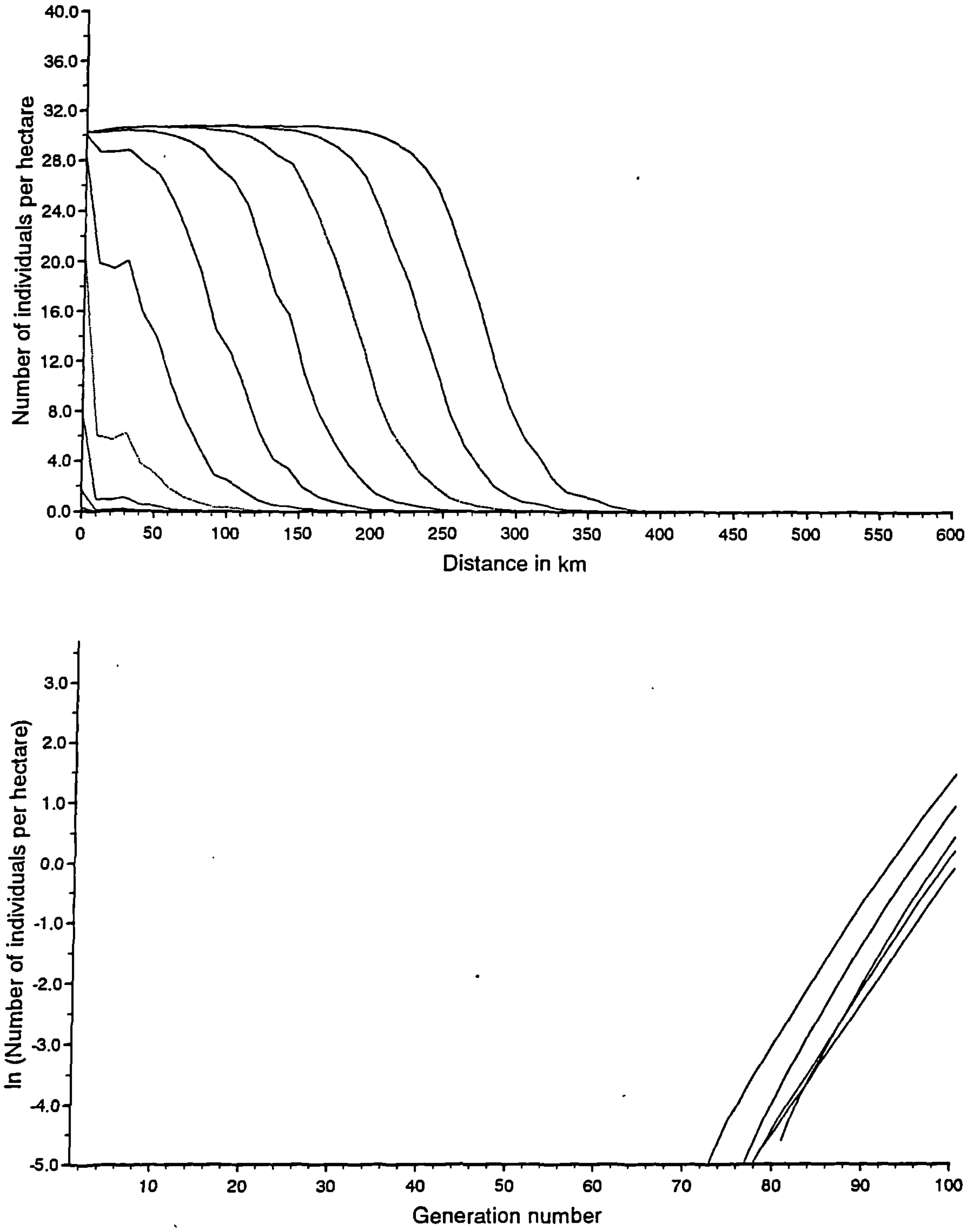


Fig. 4.6 The results of a simulation with case II parameter values (see Table 4.6). Migration rate = 0.18 km yr^{-1}, $\propto$ = 0.01.

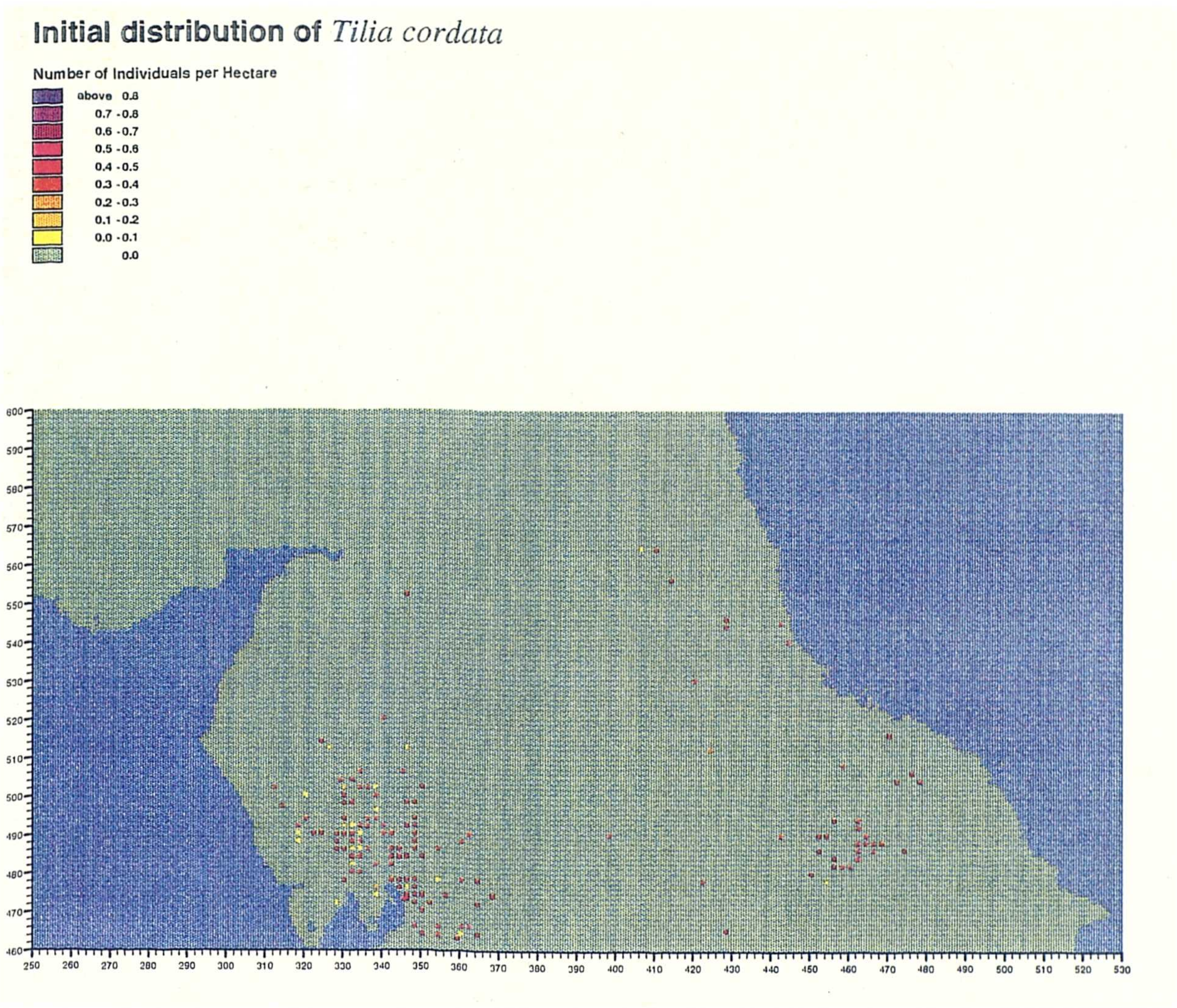


Fig. 4.7 The distribution of *Tilia cordata* as given by Pigott (1992) with refinements made by reference to Paice (1974).

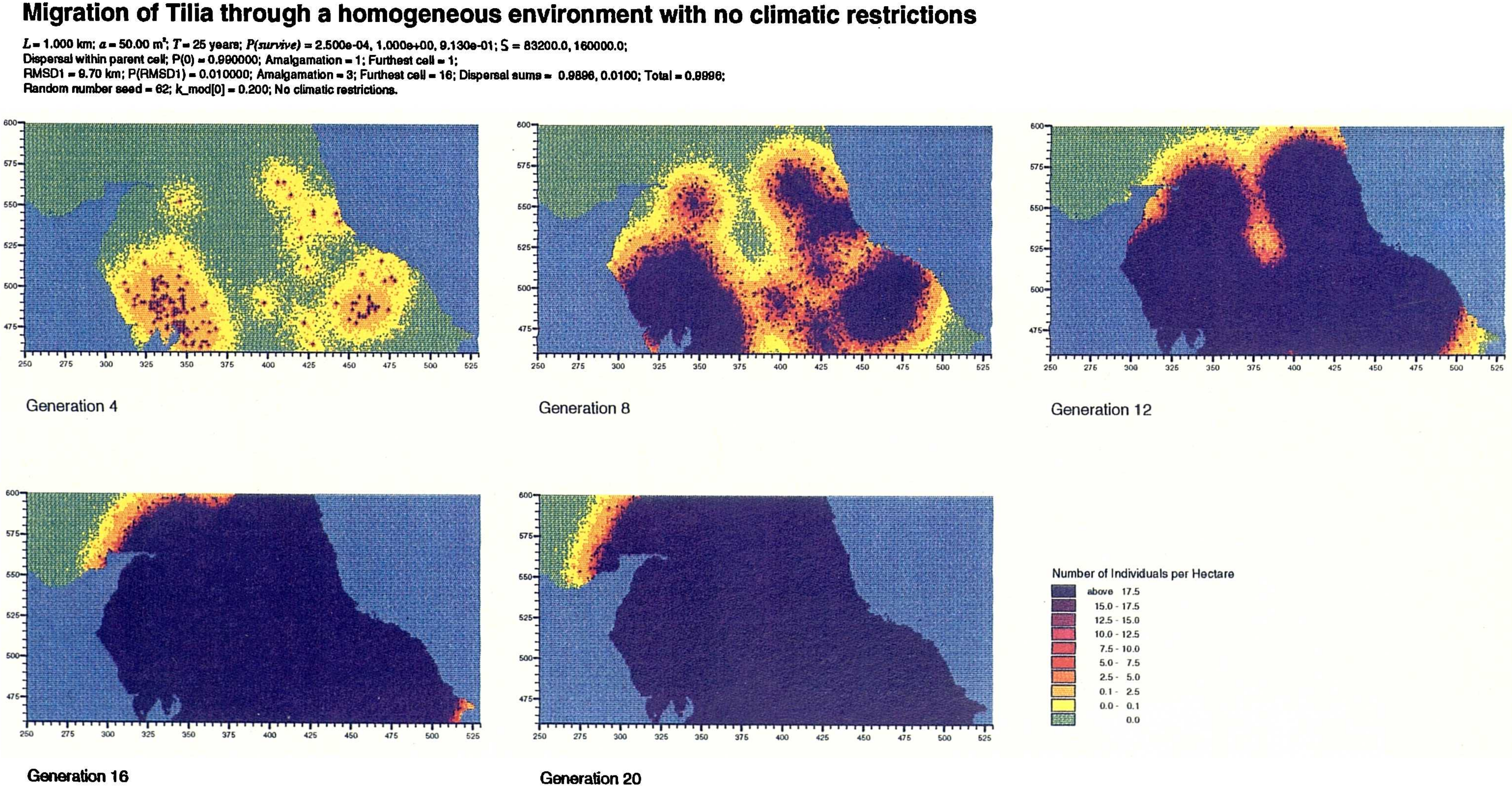


Fig. 4.8 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be homogeneous with a relative carrying capacity of 0.2. Climate was considered to be suitable for regeneration throughout the area covered by the simulation.

Migration of Tilia through a homogeneous environment with no climatic restrictions

L = 1.000 km; *a* = 50.00 m²; *T* = 25 years; *P(survive)* = 1.000e-05, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.900000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 45.00 km; P(RMSD1) = 0.100000; Amalgamation = 10; *Furthest cell* = 23; *Dispersal sums* = 0.8963, 0.1000; Total = 0.9963;
Random number seed = 62; *k_mod[0]* = 0.200; No climatic restrictions.

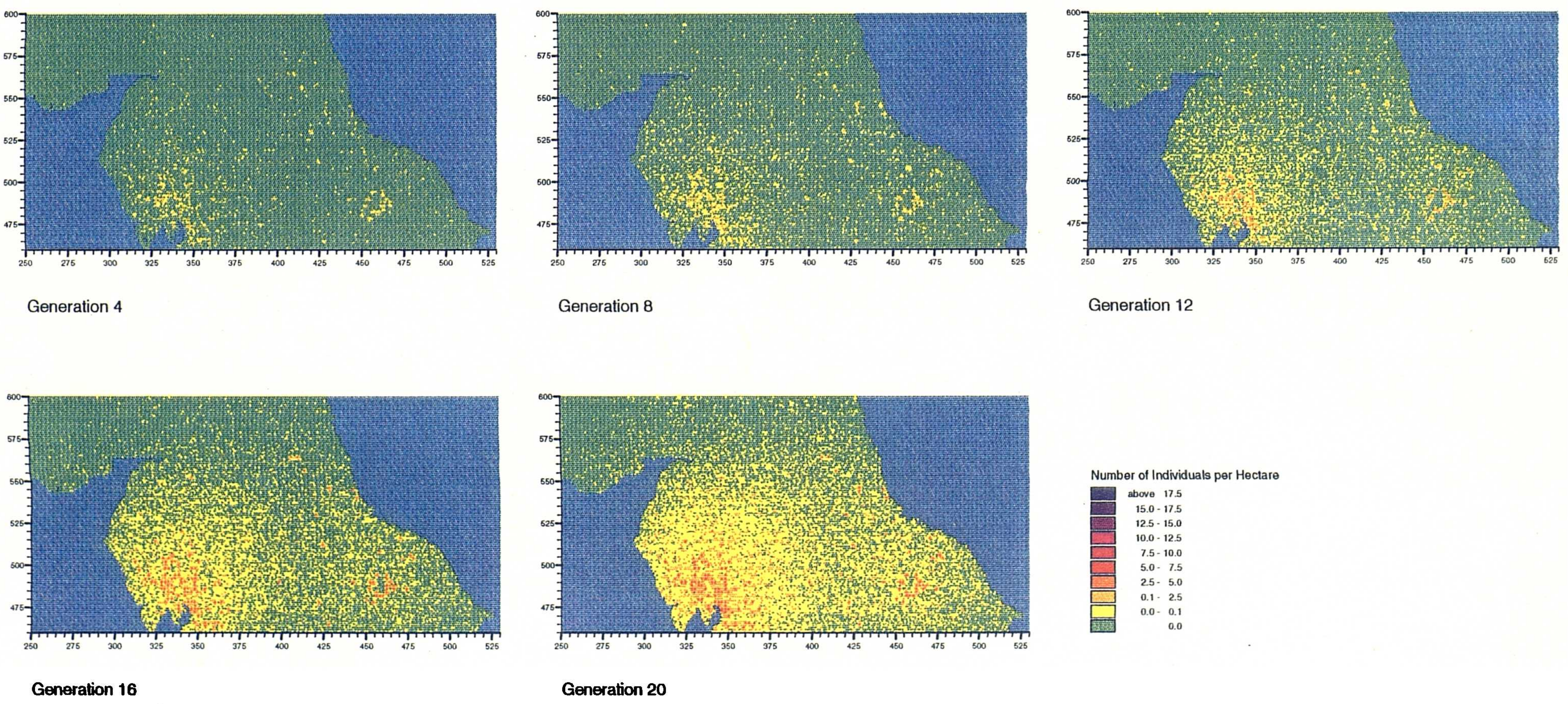


Fig. 4.9 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case II parameter values (see Table 4.6). The environment was assumed to be homogeneous with a relative carrying capacity of 0.2. Climate was considered to be suitable for regeneration throughout the area covered by the simulation.

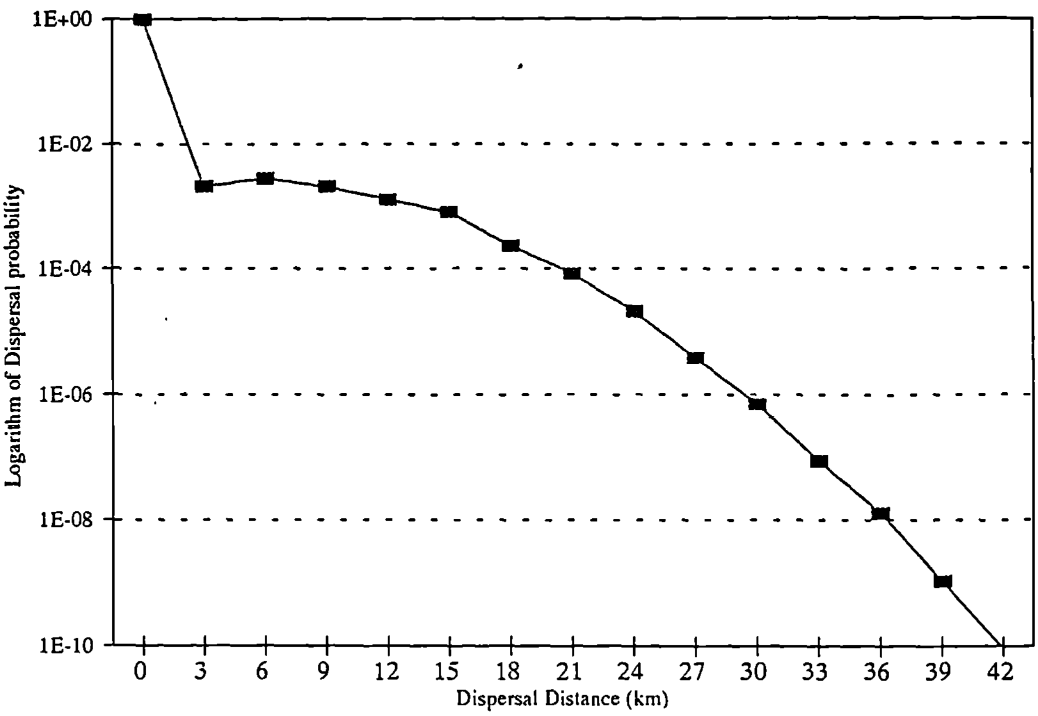


Fig. 4.10 Dispersal distances achieved during a simulation with case I parameter values and a homogeneous environment.

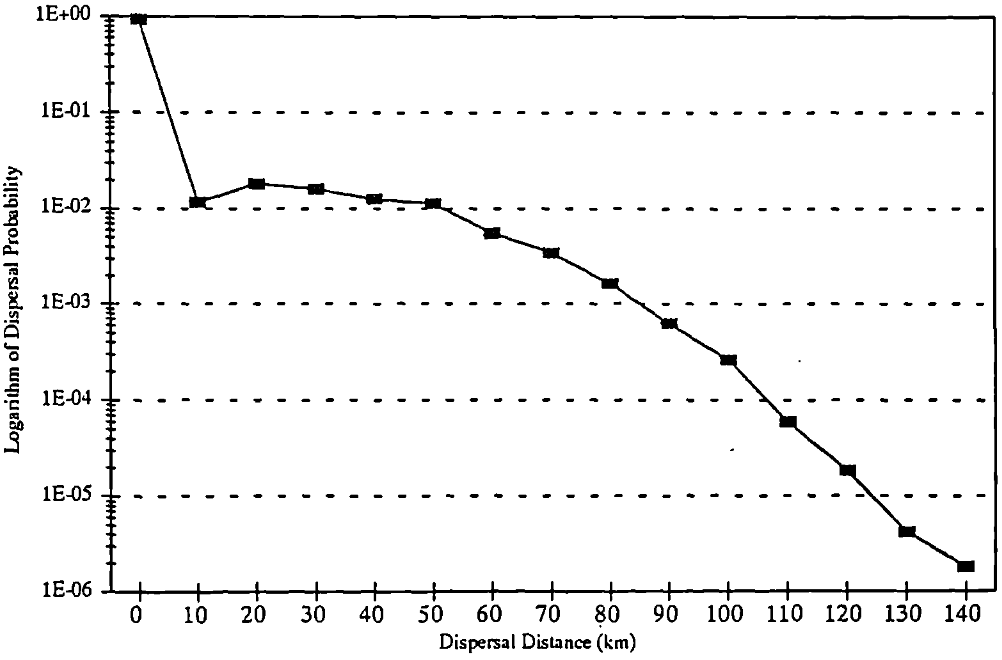


Fig. 4.11 Dispersal distances achieved during a simulation with case II parameter values and a homogeneous environment.

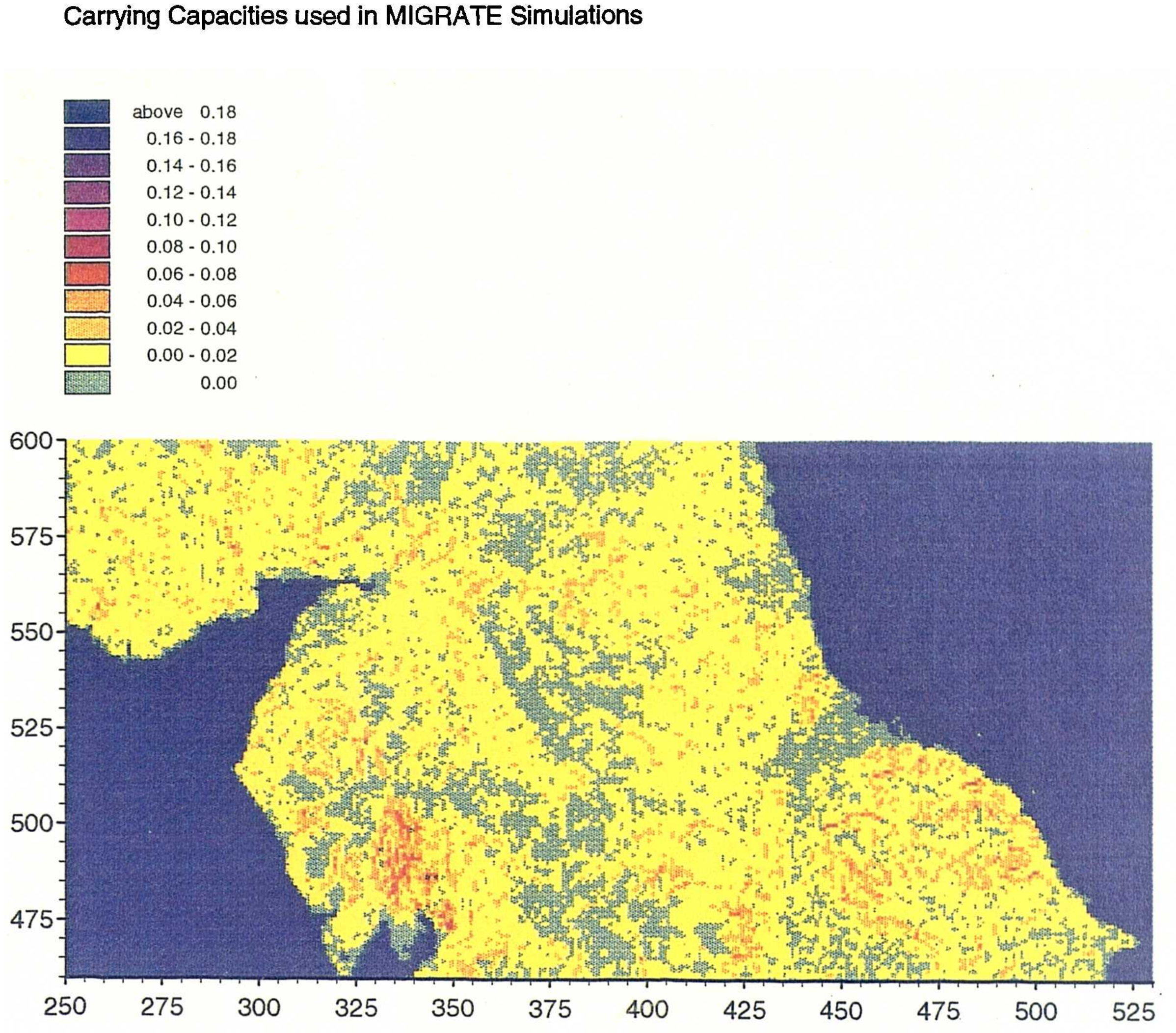


Fig. 4.12 The relative carrying capacity values used in simulations where the environment was assumed to be heterogeneous. These values were set using the assumption that *Tilia cordata* could come to occupy a maximum of 20% of the deciduous woodland cover. The land cover data were obtained from the Institute of Terrestrial Ecology's land cover database at a 1 km resolution.

Migration of Tilia through a heterogeneous environment with no climatic restrictions

L = 1.000 km; a = 50.00 m^2; T = 25 years; $P(survive)$ = 2.500e-04, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.990000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 9.70 km; P(RMSD1) = 0.010000; Amalgamation = 3; Furthest cell = 16; Dispersal sums = 0.9896, 0.0100; Total = 0.9996;
Random number seed = 62; k_mod[0] = 0.200; No climatic restrictions.

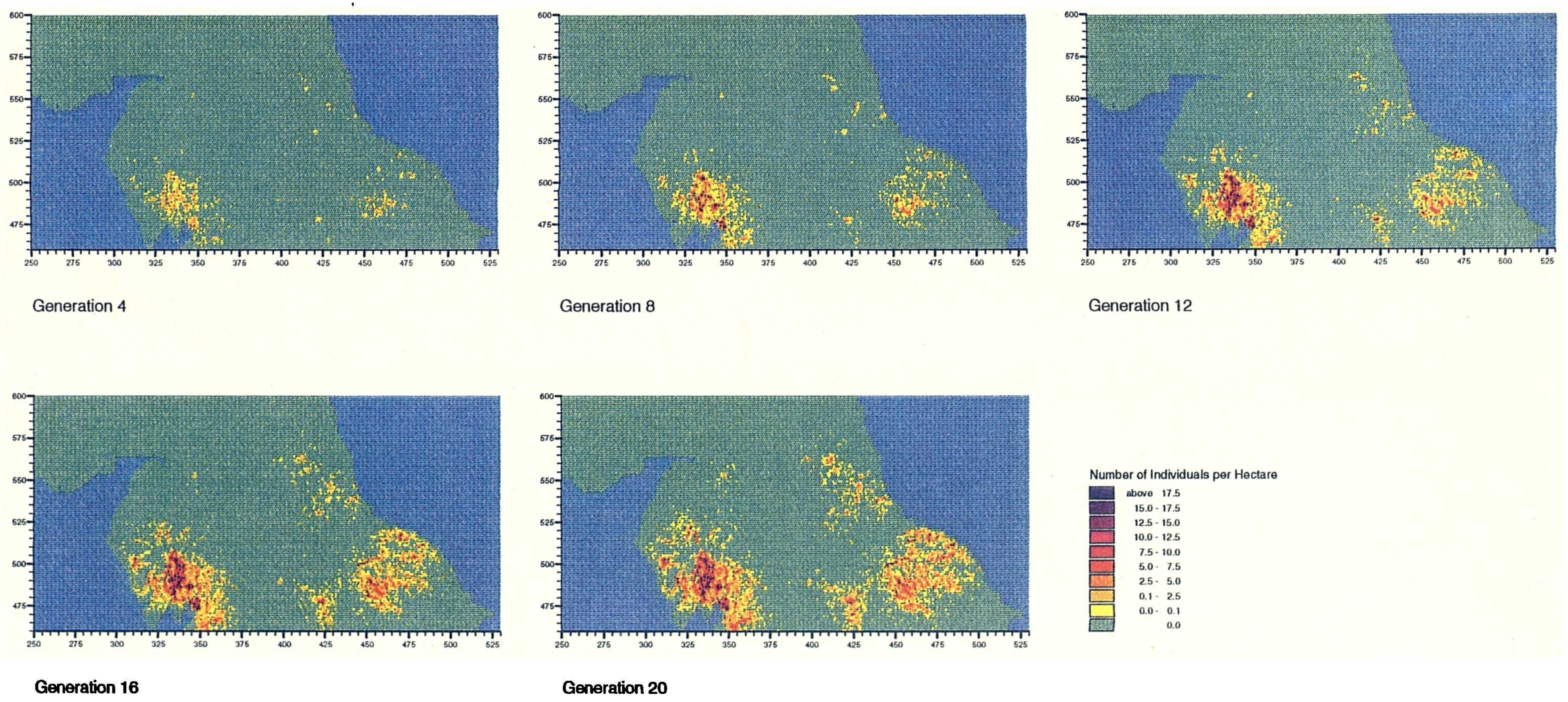
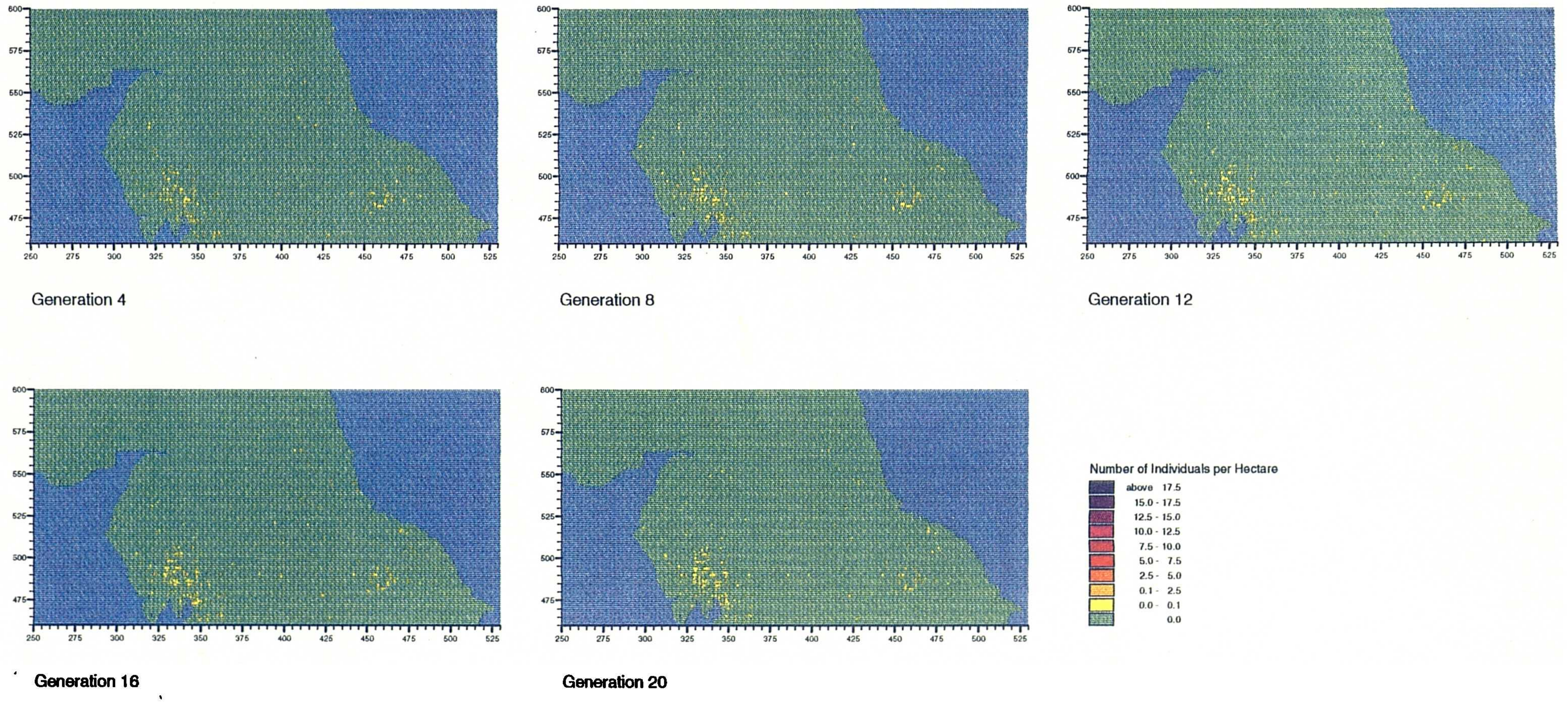


Fig. 4.13 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be heterogeneous with relative carrying capacity values as shown in Fig. 4.12. Climate was considered to be suitable for regeneration throughout the area covered by the simulation.

Migration of Tilia through a heterogeneous environment with no climatic restrictions

L = 1.000 km; *a* = 50.00 m^2; *T* = 25 years; *P(survive)* = 1.000e-05, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.900000; Amalgamation = 1; *Furthest cell* = 1;
RMSD1 = 45.00 km; P(RMSD1) = 0.100000; Amalgamation = 10; Furthest cell = 23; Dispersal sums = *0.8963, 0.1000; Total = 0.9963;*
Random number seed = 62; k_mod[0] = 0.200; No climatic restrictions.


Generation 4

Generation 8

Generation 12

Generation 16

Generation 20

Fig. 4.14 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case II parameter values (see Table 4.6). The environment was assumed to be heterogeneous with relative carrying capacity values as shown in Fig. 4.12. Climate was considered to be suitable for regeneration throughout the area covered by the simulation.

Migration of Tilia through a smoothed heterogeneous habitat with no climatic restrictions

L = 1.000 km; *a* = 50.00 m^2; *T* = 25 years; *P(survive)* = 2.500e-04, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.990000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 9.70 km; P(RMSD1) = 0.010000; Amalgamation = 3; Furthest cell = 16; Dispersal sums = 0.9896, 0.0100; Total = 0.9996;
Random number seed = 62; k_mod[0] = 0.200; No climatic restrictions.

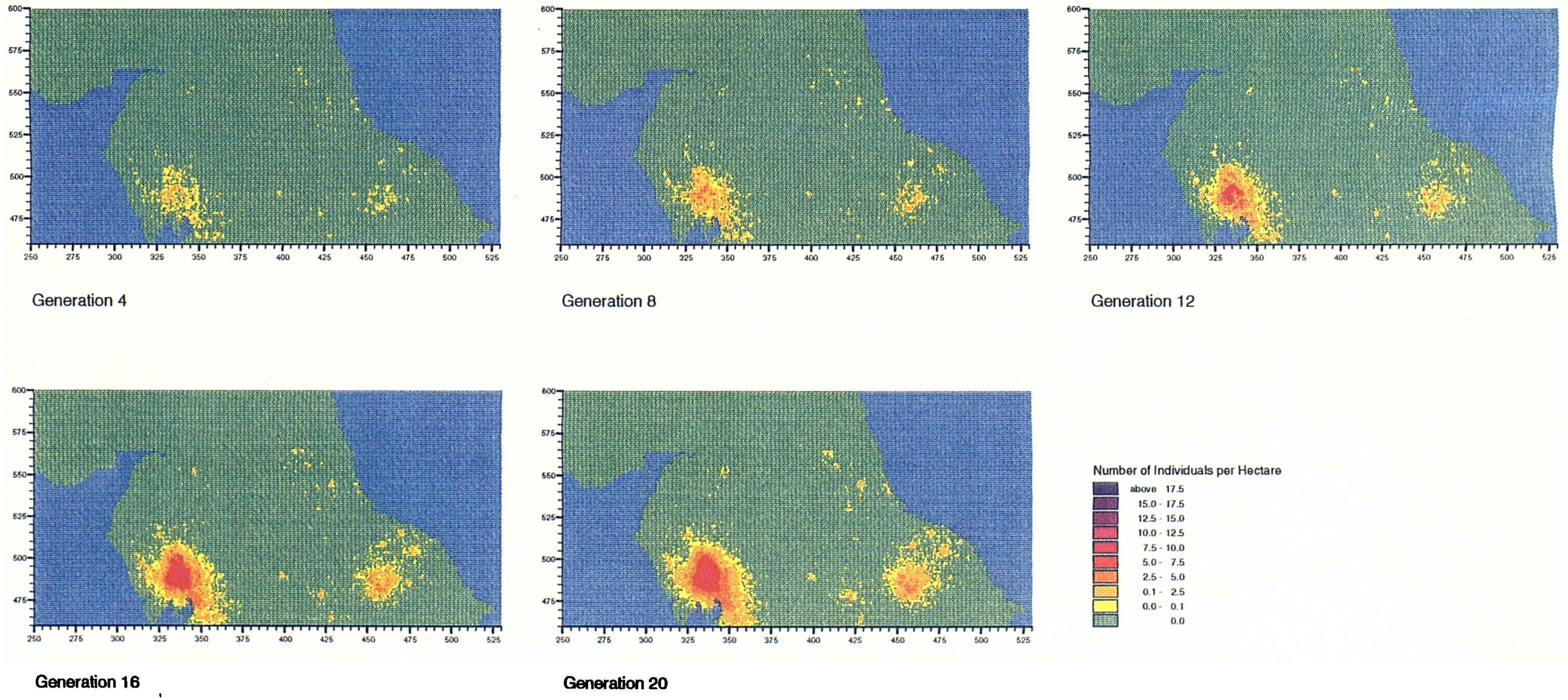


Fig. 4.15 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be heterogeneous, however, the relative carrying capacity values shown in Fig. 4.12 were smoothed by taking the average value of all 1 km squares within 3 km of each cell. Climate was considered to be suitable for regeneration throughout the area covered by the simulation.

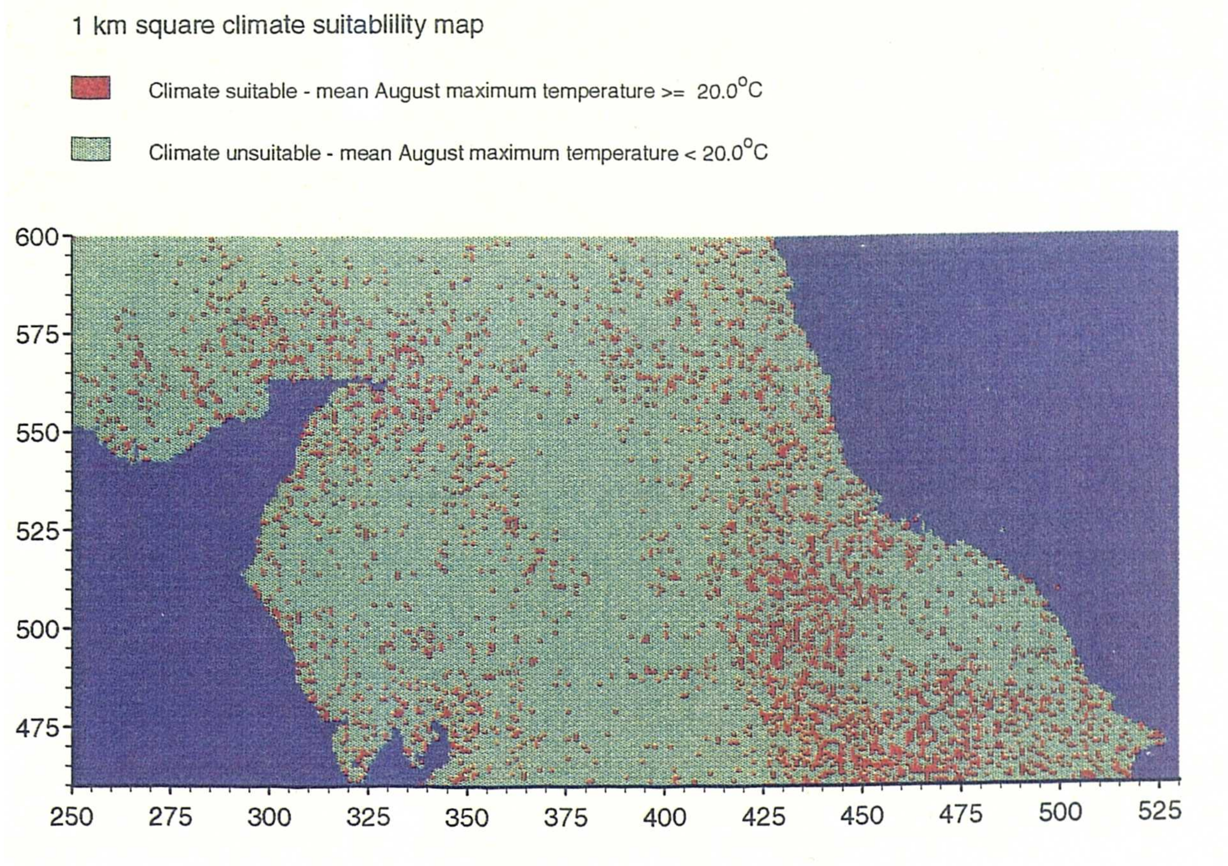


Fig. 4.16 A typical modern day climate suitability map for *Tilia cordata* based on the mean August daily maximum temperature for the period 1960 to 1990. Climate data obtained from the Institute of Terrestrial Ecology at the 10 km resolution was used in conjunction with Bartholomew's 1 km altitude data to produce a climate suitability map at the 1 km resolution (see section 2.3.3). It was assumed that reproduction could not occur if the temperature fell below a threshold value of 20°C. If the threshold was exceeded then reproduction could occur. During simulations, the climate data are made to vary about their actual values with a standard deviation of 1.6.

Migration of Tilia through a homogeneous environment with today's climatic restrictions

L = 1.000 km; a = 50.00 m^2; T = 25 years; *P(survive)* = 2.500e-04, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.990000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 9.70 km; P(RMSD1) = 0.010000; Amalgamation = 3; Furthest cell = 16; Dispersal sums = 0.9896, 0.0100; Total = 0.9996;
Random number seed = 62; k_mod[0] = 0.200; Climatic restrictions acting; Random number seed = 56.

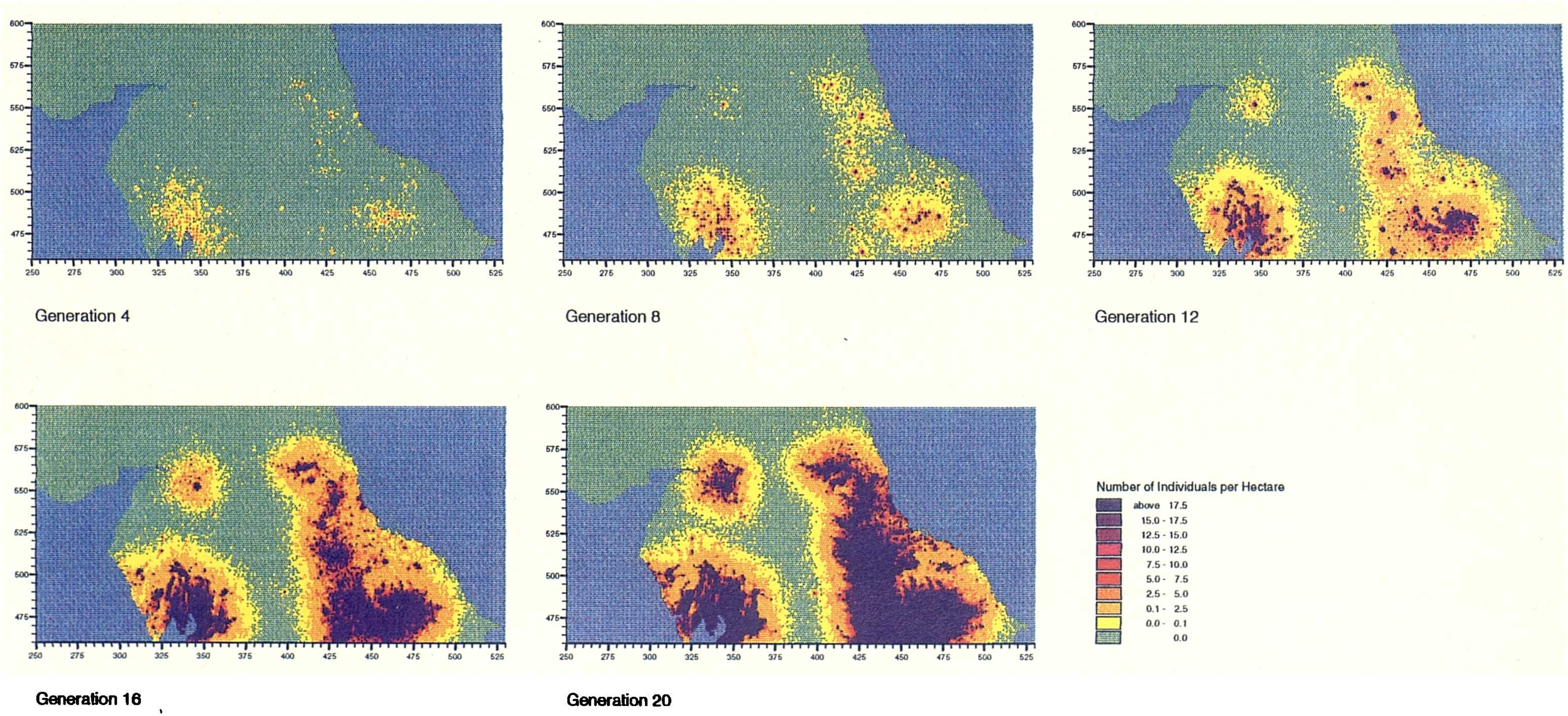


Fig. 4.17 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be homogeneous with a relative carrying capacity of 0.2. The reproduction of *T. cordata* was assumed to be limited by the current mean daily August maximum temperature which fluctuated on an annual basis according to a normal distribution with a standard deviation of 1.6 (see Fig. 4.16).

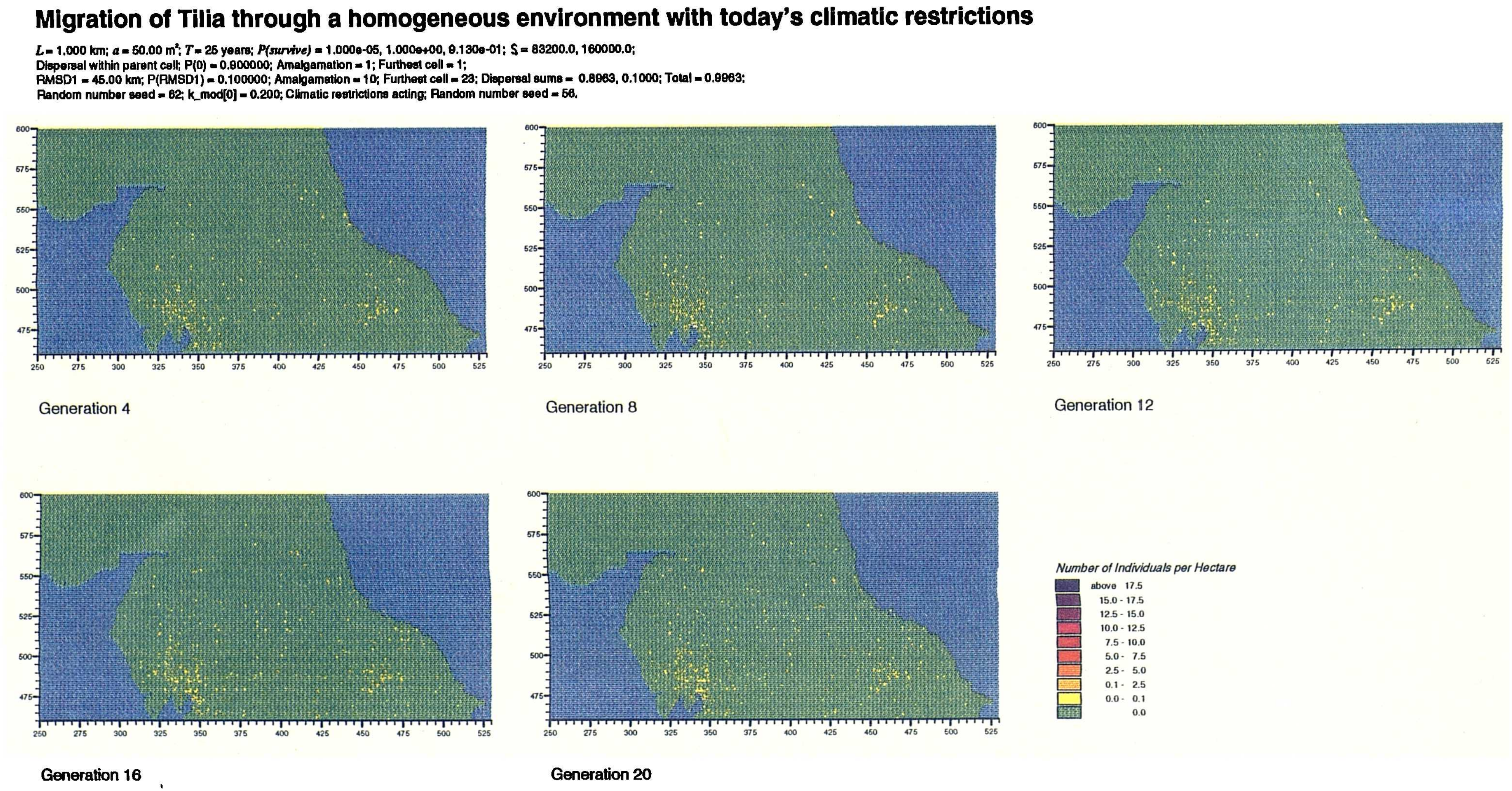


Fig. 4.18 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case II parameter values (see Table 4.6). The environment was assumed to be homogeneous with a relative carrying capacity of 0.2. The reproduction of *T. cordata* was assumed to be limited by the current mean daily August maximum temperature which fluctuated on an annual basis according to a normal distribution with a standard deviation of 1.6 (see Fig. 4.16).

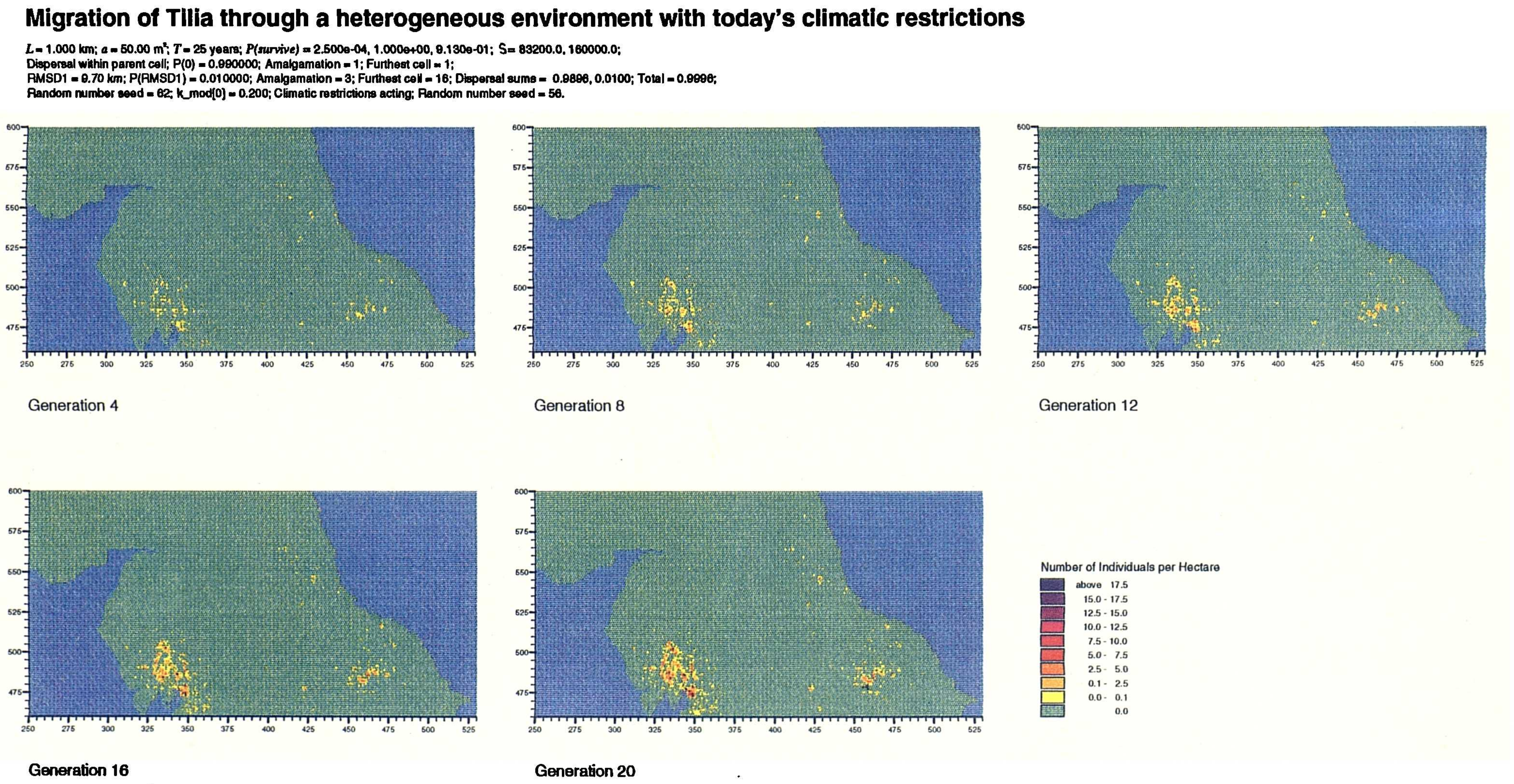


Fig. 4.19 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be heterogeneous with relative carrying capacity values as shown in Fig. 4.12. The reproduction of *T. cordata* was assumed to be limited by the current mean daily August maximum temperature which fluctuated on an annual basis according to a normal distribution with a standard deviation of 1.6 (see Fig. 4.16).

Migration of Tilia through a heterogeneous environment with today's climatic restrictions

L = 1.000 km; a = 50.00 m^2; T = 25 years; $P(survive)$ = 1.000e-05, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.900000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 45.00 km; P(RMSD1) = 0.100000; Amalgamation = 10; Furthest cell = 23; Dispersal sums = 0.8963, 0.1000; Total = 0.9963;
Random number seed = 62; k_mod[0] = 0.200; Climatic restrictions acting; Random number seed = 56.

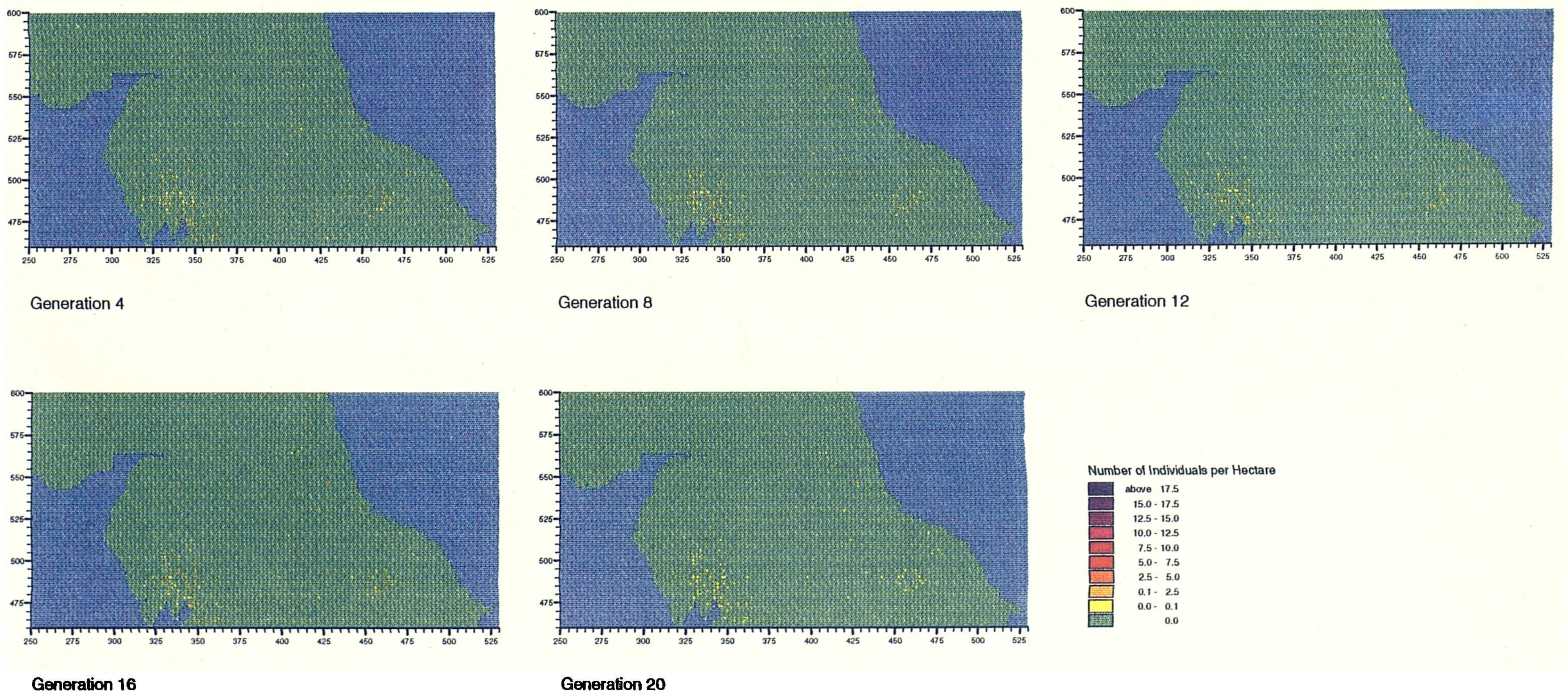


Fig. 4.20 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case II parameter values (see Table 4.6). The environment was assumed to be heterogeneous with relative carrying capacity values as shown in Fig. 4.12. The reproduction of *T. cordata* was assumed to be limited by the current mean daily August maximum temperature which fluctuated on an annual basis according to a normal distribution with a standard deviation of 1.6 (see Fig. 4.16).

Migration of Tilia through a homogeneous environment with climatic restrictions based on current probability of occurrence

L = 1.000 km; a = 50.00 m^2; T = 25 years; $P(survive)$ = 2.500e-04, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.990000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 9.70 km; P(RMSD1) = 0.010000; Amalgamation = 3; Furthest cell = 16; Dispersal sums = 0.9896, 0.0100; Total = 0.9996;
Random number seed = 62; k_mod[0] = 0.200; No climatic restrictions.

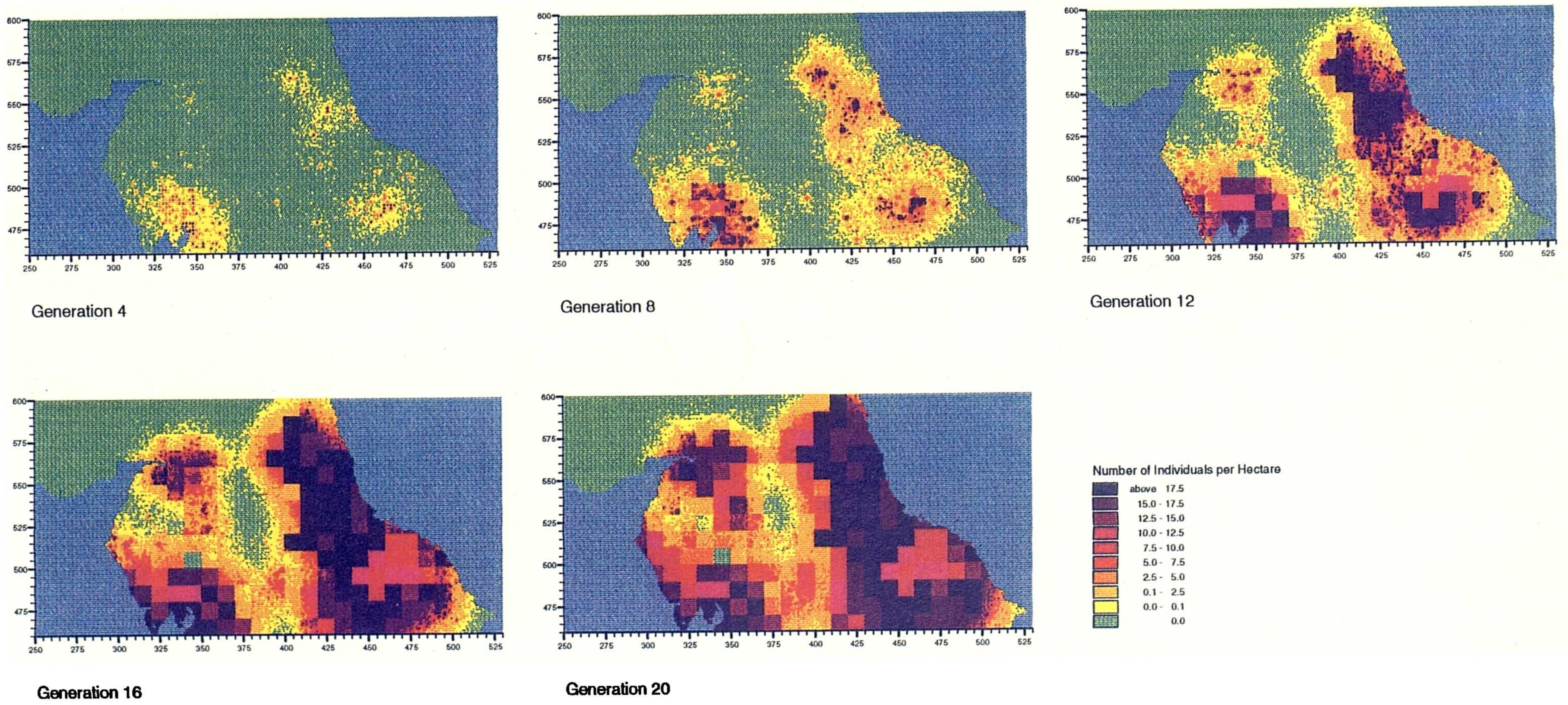
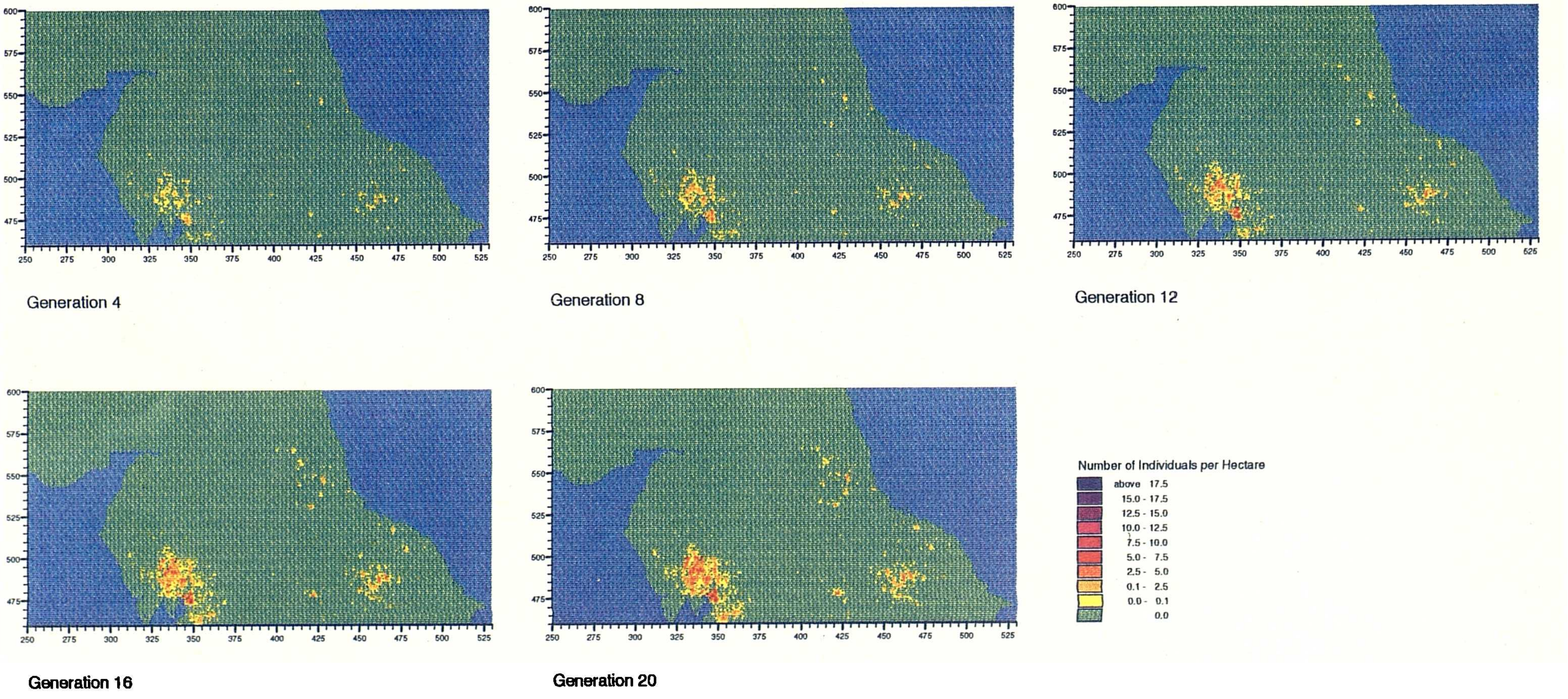


Fig. 4.21 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be homogeneous with a relative carrying capacity of 0.2. Climatic restrictions acted throughout the area covered by the simulation by reducing the relative carrying capacity values ccording to the modern day probability of occurrence of *T cordata* at the modal altitude of each 10 km square (see section 2.3.2). If the probability of occurrence was less than a threshold of 0.5 then the relative carrying capacities in that 10 km square were set to zero, otherwise they were modified by multiplying by the probability of occurrence.

Migration of Tilia through a heterogeneous environment with restrictions based on current probability of occurrence

L = 1.000 km; a = 50.00 m²; T = 25 years; *P(survive)* = 2.500e-04, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.990000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 9.70 km; P(RMSD1) = 0.010000; Amalgamation = 3; Furthest cell = 16; Dispersal sums = 0.9896, 0.0100; Total = 0.9996;
Random number seed = 62; k_mod[0] = 0.200; No climatic restrictions.



Generation 4

Generation 8

Generation 12

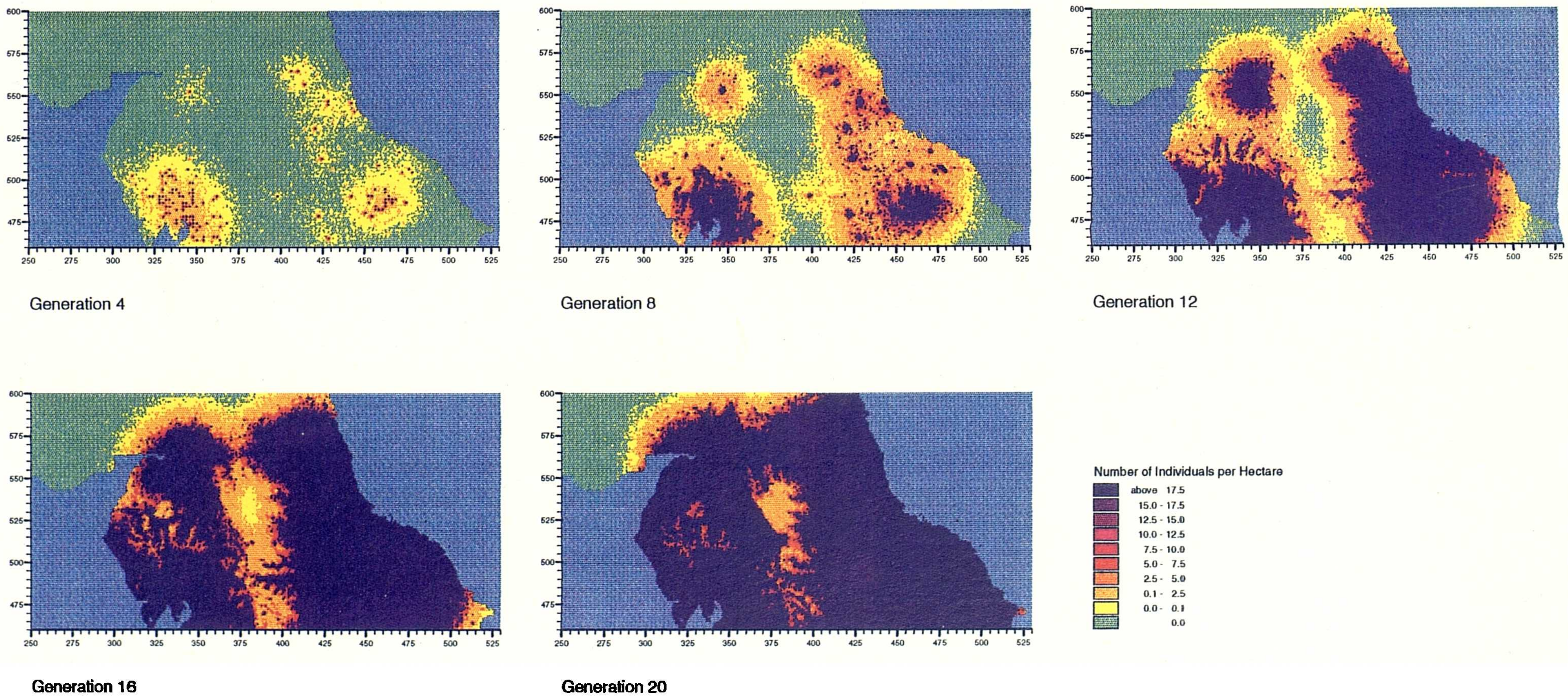
Generation 16

Generation 20

Fig. 4.22 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be heterogeneous with relative carrying capacity values as shown in Fig. 4.12. Climatic restrictions acted throughout the area covered by the simulation by reducing the relative carrying capacity values according to the modern day probability of occurrence of *T cordata* at the modal altitude of each 10 km square (see section 2.3.2). If the probability of occurrence was less than a threshold of 0.5 then the relative carrying capacities in that 10 km square were set to zero, otherwise they were modified by multiplying by the probability of occurrence.

Migration of Tilia through a homogeneous environment with 2 degree increase in August temperatures

L = 1.000 km; a = 50.00 m^2; T = 25 years; *P(survive)* = 2.500e-04, 1.000e+00, 9.130e-01; S = 83200.0, 160000.0;
Dispersal within parent cell; P(0) = 0.990000; Amalgamation = 1; Furthest cell = 1;
RMSD1 = 9.70 km; P(RMSD1) = 0.010000; Amalgamation = 3; Furthest cell = 16; Dispersal sums = 0.9696, 0.0100; Total = 0.9996;
Random number seed = 62; k_mod[0] = 0.200; Climatic restrictions acting; Random number seed = 56.



Generation 4

Generation 8

Generation 12

Generation 16

Generation 20

Fig. 4.23 The results of a simulation of the migration of *Tilia cordata* in northern Britain using case I parameter values (see Table 4.6). The environment was assumed to be homogeneous with a relative carrying capacity of 0.2. The reproduction of *T. cordata* was assumed to be limited by the mean daily August maximum temperature which was set at 2°C above its current value and fluctuated on an annual basis according to a normal distribution with a standard deviation of 1.6 (see Fig. 4.16).

CHAPTER 5

Concluding Remarks and Suggested Areas for Further Research

5.1. Conclusions

MIGRATE has shown itself to be a useful exploratory tool for investigating the effects of different parameter values on the rates and patterns of migration. Although it is a simple model it captures all the essential processes regarding reproduction and dispersal which have been used in similar models of migration. Simulations carried out in section 4.3 showed that the migration rates predicted by MIGRATE are in good agreement with both the observed rates and the rates predicted by the models of Van den Bosch *et al.* (1992) for the collared dove, house sparrow and muskrat. If attempts were to be made at incorporating more detail into MIGRATE it would become increasingly difficult to analyse its behaviour. In view of the success in predicting the observed rates of migration for the collared dove, house sparrow and muskrat it would seem that there is no extra value to be gained by trying to incorporate more detail into the model. It would be far better to concentrate efforts on gaining more accurate data for assigning values to the existing parameters which are known to be important in determining the migration rates and patterns.

The simple nature of MIGRATE enables sensitivity analyses to be carried out to determine where more accurate parameter values are needed. Such analyses carried out with the one-dimensional version of MIGRATE were described in Chapter 4. The results indicated that the following parameters play an important role in determining the migration rate:

- the number of propagules which survive to maturity;
- the age of first reproduction;
- the frequency and distance of long-distance dispersal events.

The number of propagules which survive to maturity is a product of two parameters in the MIGRATE model, the number of propagules produced per individual per generation (*S*) and the probability of a propagule reaching the age of first reproduction (P_1). *S* may be estimated fairly easily from data in the literature, however, data on the probability of survival to the age of first reproduction is very scarce. All that is known about P_1 is that it is very small. For long-lived species such as trees, long-term studies are needed in order to determine more accurate values for this parameter and how it is affected by variations in the environment.

The age of first reproduction is also affected by variations in the environment. It is known that trees in the open can start producing propagules up to ten or more years before trees growing in a forest environment. For example, Pigott (1991) notes that in the open, *Tilia cordata* begins to produce small quantities of seed when it is 12-20 years old, however, in a woodland seed production may not begin until it is 25-30 years old and may even be delayed until 30-40 years. If more accurate data could be obtained on the age to first reproduction with respect to environmental conditions then this a refinement which may be worth incorporating into the model. The results from the sensitivity analyses indicate that if the migration rate is primarily determined by those trees at the leading edge of the migration front then a decrease in the age of first reproduction from 25 to 10 years may lead to an almost doubling of the migration rate.

The review of the literature on seed dispersal given in Chapter 1 and the attempts at measuring it in the field as described in Chapter 3 suggest that it is not possible to quantify the frequency of dispersal distances much greater than a few hundred metres by carrying out field studies. The low value of the dispersal half distance as determined by field studies in conjunction with knowledge on the rates of migration and population increase suggests that dispersal operates at two scales with a few seeds going a long way and not therefore being detected. The palaeoecological record can be used to derive estimates for the long-distance dispersal parameters as described in section 2.2. However, this then means that the palaeoecological record can not be used in validating the results produced by MIGRATE. Ideally some independent means for measuring the long-distance dispersal of propagules is required. One possibility would be to use dispersal models capable of simulating the dispersal pattern of propagules under realistic meteorological conditions. Such models should include both the effects of turbulence and the aerodynamic properties of propagules. Currently such models are not detailed enough to do this sufficiently accurately for particles such as seeds. However, as already noted in Chapter 1, secondary dispersal may play a very important role in determining the final resting place of dispersed propagules. There is a very limited amount of quantitative data on secondary dispersal so this represents another area where further research is needed, although its very nature will make it a difficult subject to tackle.

Another area of interest which is closely related to the form of the long-distance dispersal function is how the probability of propagule survival changes with increasing distance from the parent tree. Results from sensitivity analyses have suggested that if the propagules that are dispersed over a long distance have a greater chance of survival because they escape density dependent mortality factors then the migration rate may be significantly increased. There is various evidence both for and against the escape hypothesis, some of which was discussed in Chapter 1. Again, this is another area where further research is needed.

Most of the models of migration that have been developed to date have assumed the environment to be homogeneous. This restriction is relaxed, however, in the two-dimensional versión of MIGRATE where a spatially explicit heterogeneous landscape can be used to represent reality. Some recent models have been developed which can make predictions about migration rates in a heterogeneous environment, but, as they are not spatially explicit they can not show the pattern of spread. The formulation of the two-dimensional version of MIGRATE allows features of the real environment to be captured. For example, some of the simulations carried out in Chapter 4 used land cover and climate data. MIGRATE could easily be refined to incorporate any spatially referenced data set as required.

There are two different schools of thought regarding the pattern of post-glacial tree migration. These were reviewed in Chapter 1 and can be briefly summarised as Davis' model in which spread is assumed to occur as a more or less continuous front and Bennett's model in which spread occurs by the establishment of small scattered populations with gradual infilling. The results obtained from MIGRATE can be used to support either of these models of spread.

In the case of Bennett's model, MIGRATE confirms that for low intrinsic rates of population increase (i.e. < 0.01) spread will occur as a shallow front with population densities taking approximately 200 km to rise from very low values at the range limit to the equilibrium density value (for example, see Fig. 4.6). In two-dimensions it is clear that under these conditions, spread occurs by the formation of many small populations which slowly increase in size and merge together. These results are not unexpected as in order for migration to occur fast enough the rare long-distance dispersal events must be very large in order to compensate for the very low value of the intrinsic rate of population increase. There is very little direct evidence for dispersal distances in excess of 100 km although the palaeoecological record suggests that dispersal did occur over such distances in the past (see section 1.4.5). With Bennett's model, MIGRATE predicts that in order for the necessary migration rates to have been achieved dispersal distances in excess of 100 km may have occurred .

With regard to Davis' model, it can be seen that when the intrinsic rate of population increase is greater than about 0.08 the population front will appear very steep when viewed at the scale of several hundreds of kilometres. Measurements of the extent of the population front suggest that it could actually take up to 20 km for the equilibrium density value to be reached. Intuitively this may sound more realistic than the value of several hundreds of kilometres simulated by MIGRATE under conditions of lower intrinsic rate of population increase. Although a value of the intrinsic rate of population increase of 0.08 falls outside the range 0.01-0.0039 predicted for *Tilia cordata* by Bennett (1983) it does not imply that this value is too high. Bennett (1986) quotes some values for the intrinsic rate of population increase of trees determined from modern day studies on increasing tree populations. These values range from 0.087 to 0.002. It is clear that a few cases have values which are in excess of 0.02 which is the approximate maximum determined by Bennett from the pollen record. This discrepancy could be due to one or more of the following factors.

- The rates of population increase determined from the pollen record do not reflect the true rates of population increase.

- Some modern tree populations are actually increasing faster than tree populations increased during their post-glacial migration history due to more favourable conditions today than in the past.

- The intrinsic rates of population increase for the tree species determined from modern day studies are different to the rates of those species investigated by Bennett due to differences in their natural history.

Crawley (1990, page 29) has deduced formulae for estimating the range within which the intrinsic rate of population increase lies. However, as these formulae require values for the number of propagules produced as a result of the first seed set and the probability of a propagule reaching the age of first reproduction they are not very helpful. The range within which the intrinsic rate of population increase (α) lies is given by:

$$\frac{1}{T}\ln\left(\frac{SP_1}{T}\right) < \alpha < \frac{SP_1}{T}$$

So, if $T=25$, $S/T = 6400$ and $P_1 = 5\times10^{-5}$ (default parameter values for *Tilia cordata* used in the sensitivity analysis) then $-0.045 < \alpha < 0.32$. Crawley suggests that the true value of α is normally much closer to the lower bound than the upper bound and the approximation works well when the first seed set at age T is relatively large. This result does not therefore give firm support for either of the two models of spread. To conclude, the value of 0.08 for the intrinsic rate of population increase resulting from a simulation which gave a pattern of spread fitting Davis' continuous front model may not have been too large.

In order to clarify which model of spread is the most likely, more information is needed on (1) the relationship between the pollen accumulation rate and tree density and (2) the frequency and distance of long-distance dispersal events. Davis and Sugita (submitted) have made an attempt at investigating the first by using a model that simulates the deposition of pollen from an advancing population that has a continuous front. From their results, they conclude that the shape of the population front depends on:

- the dispersal properties of pollen;
- the rate of migration;
- the size of the lake from which the pollen sample was taken.

Therefore, because of these factors they conclude that it is inappropriate to use the gradient of the natural logarithm of the pollen accumulation rate versus time to determine the intrinsic rate of population increase. However, despite this, it would be very interesting to determine the values of these gradients to see if they are in agreement with those determined by Bennett. If the gradients are in agreement then this would be strong evidence in support of Davis' continuous front model of tree migration. If, however, the gradients do not agree then it may be that the shape of population front used by Davis and Sugita needs to be modified. For example, it may be more appropriate to use a model of migration such as MIGRATE that can simulate population fronts with a variety of shapes, depending on the values given to the reproductive and dispersal parameters, in conjunction with the pollen dispersal model POLLSCAPE used by Davis and Sugita in their model of pollen deposition by migrating populations of trees.

Results from the two-dimensional simulations have illustrated how the pattern of spread can be affected by the values assigned to the reproductive and dispersal patterns.

However, as discussed above it is not possible without further data to say whether Davis' model or Bennett's model is the best model of how post-glacial migration occurred. The two-dimensional simulations have, however, enabled the effects of habitat and climate suitability to be investigated. Simulations have shown that habitat loss and fragmentation will significantly reduce the ability of trees to respond to the predicted future climate change. It can be shown through the use of probability of occurrence values generated from climate response surfaces (Huntley *et al.*, 1995) that the factors which currently limit the distribution of a species may no longer limit its distribution in the future. The use of probability of occurrence values in conjunction with other spatially explicit data relevant to the successful establishment of species therefore offers a good opportunity to investigate how species may respond to future changes in climate and land use.

The factors which control the rates and patterns of the migration of a particular species are very complex. Even MIGRATE which is a fairly simple model has been able to show that the simulated migration rates and patterns can depend upon the interactions of several parameter values. In particular the sensitivity of MIGRATE to a particular parameter value can be affected by the values assigned to the other parameters. For example, it was shown in section 4.6 that parameter values which simulated migration according to Davis' model of spread were less sensitive to changes in the probability of reaching the age of first reproduction than the set of parameter values which simulated migration according to Bennett's model. In contrast, the Davis parameter values were more sensitive to a decrease in the age of first reproduction than the Bennett parameter values.

5.2. Future work

As has already been discussed above, there are several areas where data are insufficiently accurate. This problem is particularly acute with respect to trees due to their longevity. It would therefore be worthwhile trying to validate the model with a shorter-lived plant species such as an annual or a biennial in order to confirm that MIGRATE is able to accurately simulate observed patterns of spread. In order to do this, independent measurements will be required for the dispersal and reproductive parameters. It is quite probable, however, that the problem of assigning values to the long-distance dispersal parameters will be encountered again. It would be possible to use MIGRATE to determine values for these parameters so that the observed migration rate is achieved. However, MIGRATE would then have to be validated at another site where it would have to be assumed that the dispersal parameters from the first site still apply.

The simulations done with future climate scenarios do not include the direct effects of an increase in carbon dioxide. An increase in the growth rate resulting from carbon dioxide fertilisation may be modelled simply by reducing the age of first reproduction. Plants will also be more water efficient due to a decrease in water loss through their stomata. This may enable them to survive in areas which are currently too dry. In order to make MIGRATE's predictions more accurate, these effects should be taken into account.

Research into the basic natural history of species including their reproductive and dispersal ecology and their current distribution needs to continue so that the quality of the data on which models such as MIGRATE depend can be improved. Further refinements to MIGRATE will be futile unless the quality of the data gathered for estimating the existing parameters can be improved.

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APPENDIX A

Dispersal Equations and Related Definitions

Abbreviations

RMSD	Square root of the mean square of displacement
D_H	Half distance of dispersal i.e. distance over which the seed density falls by a half
L	Cell length
x	Distance in the x direction
y	Distance in the y direction
r	$\sqrt{x^2 + y^2}$
k	Gradient of the straight line when an exponential curve is plotted on a logarithmic axis
$f(x)$	Dispersal density with respect to distance x from the seed source (one-dimensional formula)
$f(r)$	Dispersal density with respect to distance r from the seed source (two-dimensional formula)

The following equations have been normalised so that for the one-dimensional formulae the area under the curve from $x = -\infty$ to $x = +\infty$ sums to 1.0 and for the two-dimensional formulae the area under the curve from $r = 0$ to $r = +\infty$ sums to 1.0. It is assumed that dispersal occurs equally in all directions. The formulae were obtained from statistical text books unless otherwise stated.

A1 Normal distribution

$$f(x) = \frac{L}{\sqrt{\pi}.\mathrm{RMSD}}.\exp\left\{\frac{-(x)^2}{\mathrm{RMSD}^2}\right\}$$

In the above one-dimensional distribution the RMSD equals $\sigma\sqrt{2}$ where σ is the standard deviation.

A2 Bivariate normal distribution

$$f(r) = \frac{L^2}{\pi.\mathrm{RMSD}}.\exp\left\{\frac{-(r)^2}{\mathrm{RMSD}^2}\right\}$$

In the above two-dimensional distribution the RMSD equals the standard deviation.

A3 One-dimensional negative exponential distribution

$$f(x) = \tfrac{1}{2}L.k.\exp(-k|x|)$$

The RMSD of a one-dimensional negative exponential distribution is given by:
$\mathrm{RMSD} = \frac{\sqrt{6}}{k}$
This formula allows the value of *k* to be set so that the RMSD of the negative exponential distribution is the same as a given normal distribution (M. Hill, pers. comm.).

k is related to the half distance of dispersal by the equation:
$k = \frac{\ln(2)}{D_H}$

A4 Two-dimensional negative exponential distribution

This formula was derived from the one-dimensional negative exponential distribution by M. Hill (pers. comm.).

$$f(r) = \frac{L^2K^2}{2\pi}.\exp(-kr)$$

A5 One-dimensional Weibull distribution

$$f(x) = \frac{1}{2}L.\left(\frac{c}{b}\right)\left(\frac{x}{b}\right)^{(c-1)}\exp\left[-\left(\frac{x}{b}\right)^{c}\right]$$

where *b* is the scale parameter and *c* the shape parameter. When c = 1 this distribution is the same as the one-dimensional negative exponential distribution.

A6 Two-dimensional Weibull distribution

This formula is an extension of the one-dimensional Weibull distribution as derived by Bergelson *et al.* (1993).

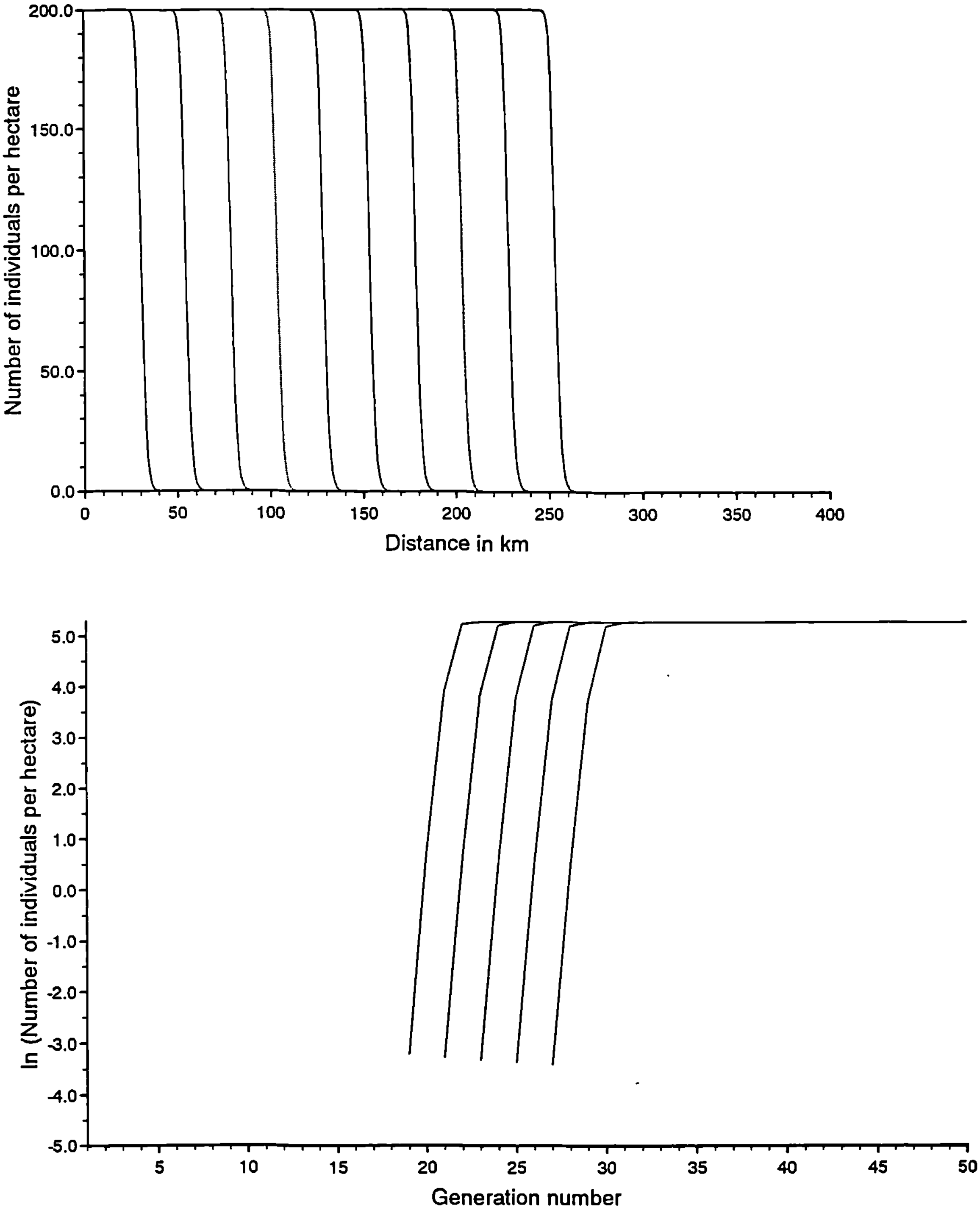
$$f(r) = L^2.\left(\frac{c}{2\pi b}\right)\left(\frac{r}{b}\right)^{(c-1)}\exp\left[-\left(\frac{r}{b}\right)^{c}\right]$$

APPENDIX B

Results from One-Dimensional Simulations

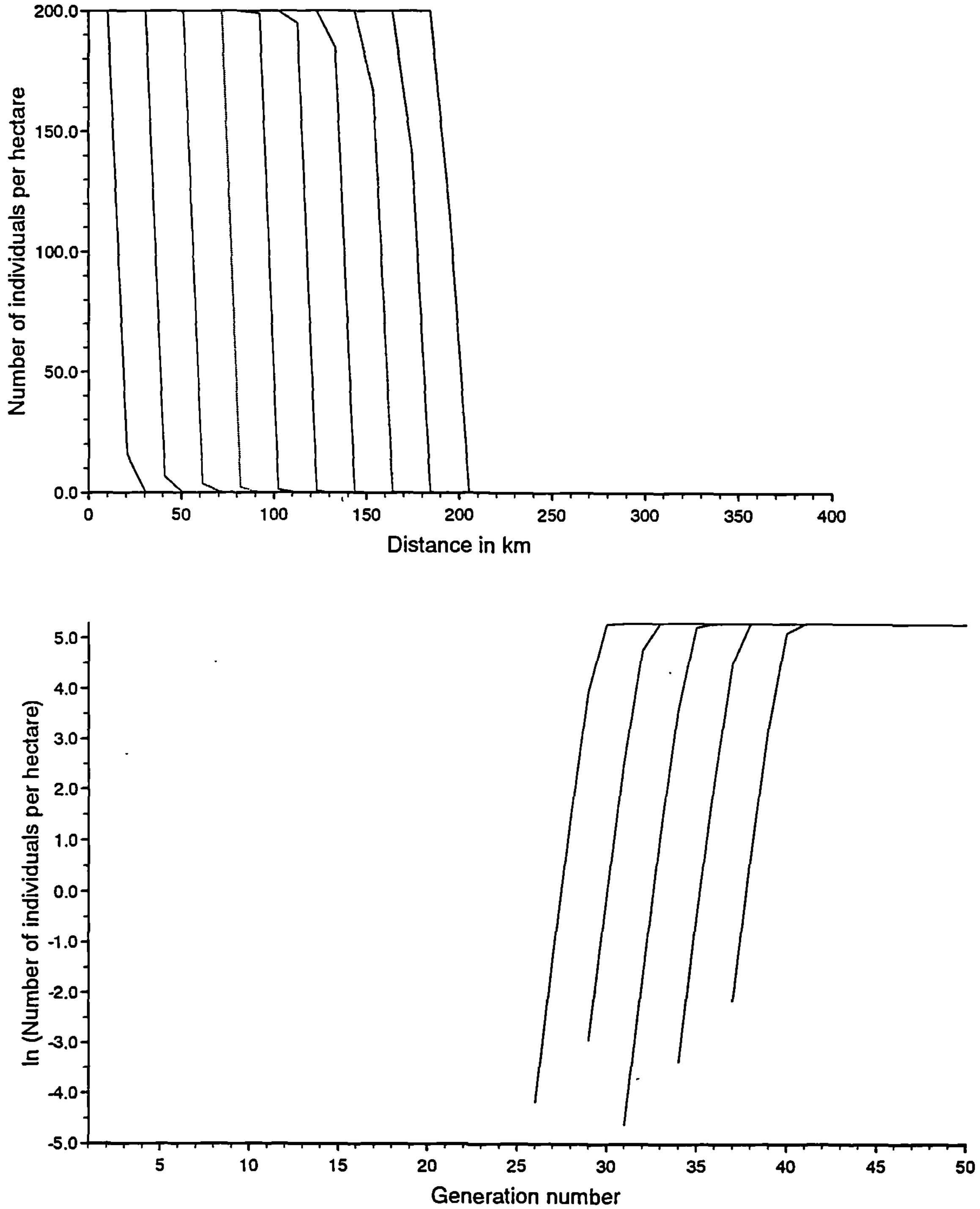
The simulations presented here were carried out in order to look at the sensitivity of MIGRATE to variations in its parameter values and to investigate some of the issues raised in Chapter 1 regarding the post-glacial migration of trees. An explanation of the graphical output and parameters used in the model is given in section 2.1. Unless otherwise stated, the lower graph displays the rate of population increase at distances 100 km, 110 km, 120 km, 130 km and 140 km from the origin. The initial distribution of trees was set as being full occupation of the first 10 km of cells. The simulation results are discussed in Chapter 4.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.9130;
S = 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



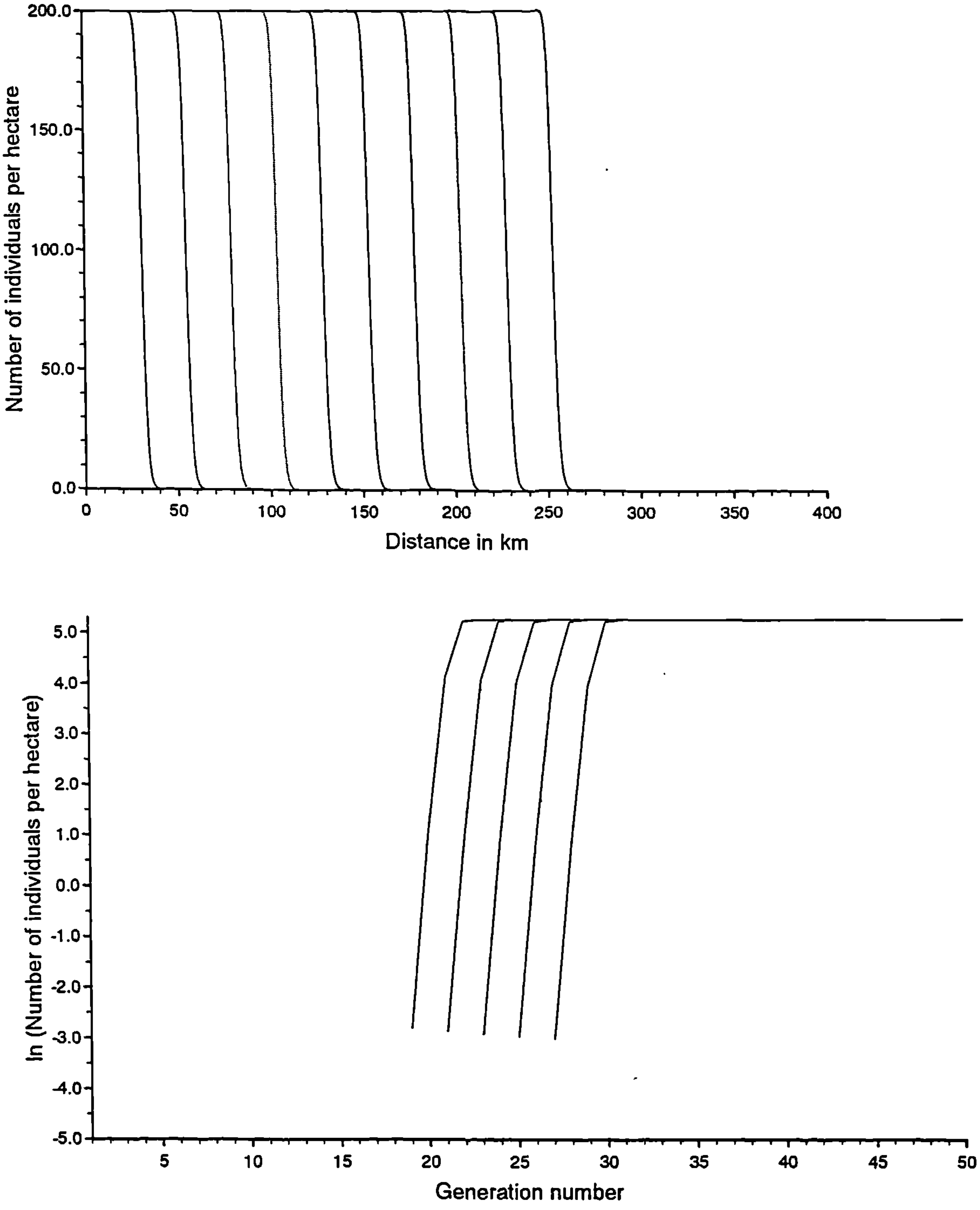
B1. Migration rate = 0.20 km yr^{-1}, α = 0.15.

L = 10.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.9130;
S = 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.6267; Total = 1.6267; Furthest Cell = 3 ;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



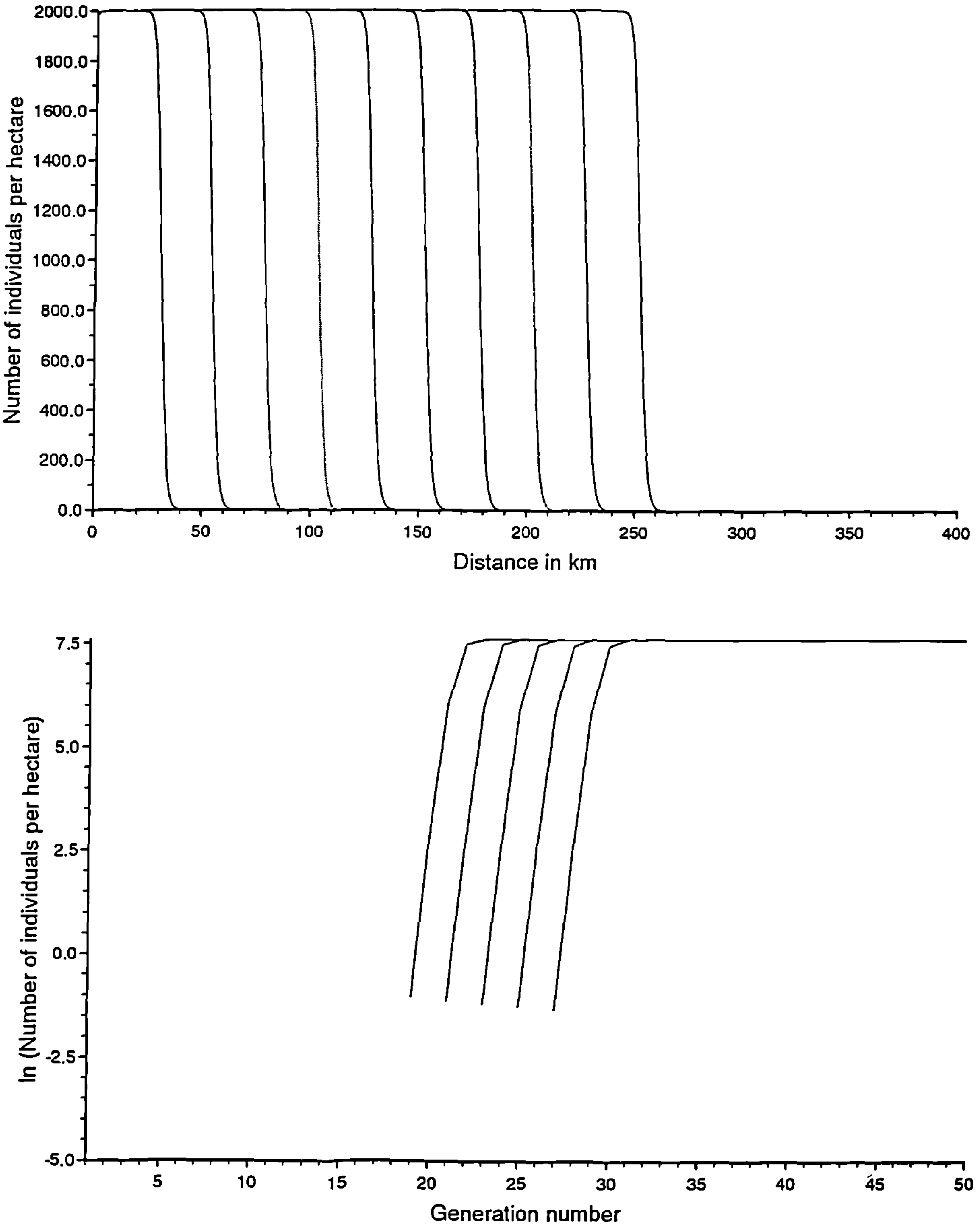
B2. Migration rate ≈ 0.16 km yr^{-1}, α ≈ 0.10.

L = 0.10 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.9130;
S = 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 180;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



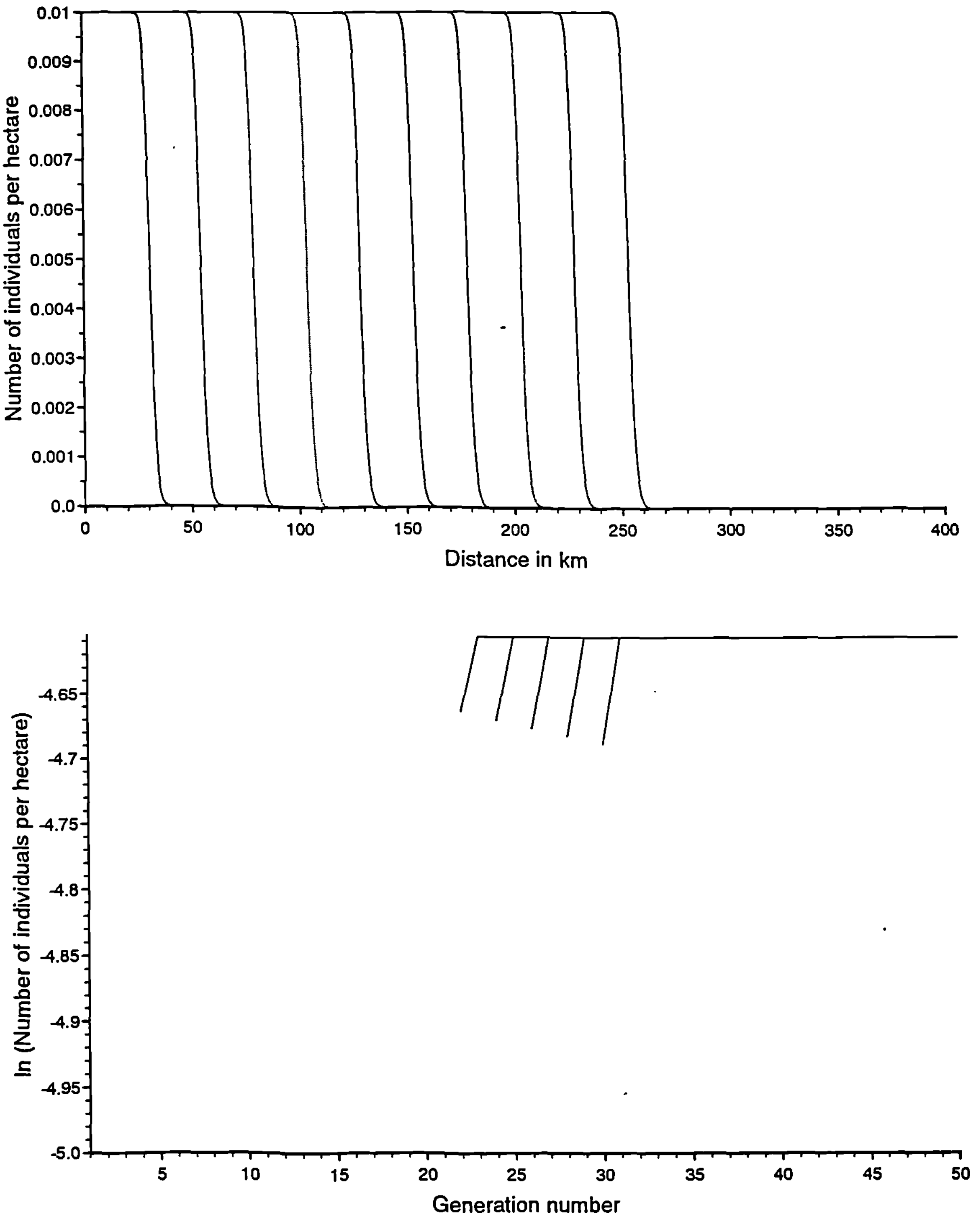
B3. Migration rate = 0.20 km yr^{-1}, α = 0.15.

L = 1.00 km; a = 5.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.0000;
S = 160000.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



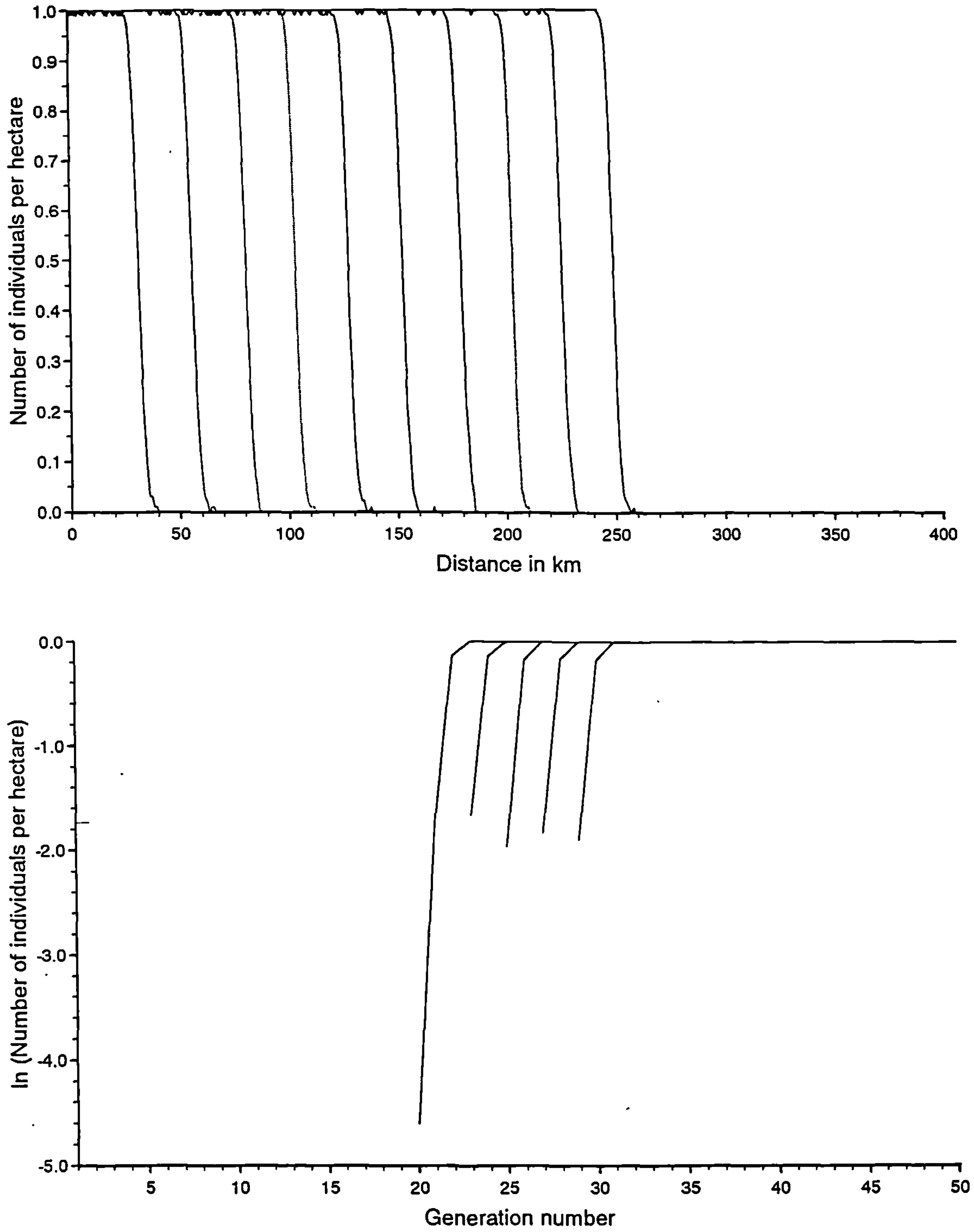
B4. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.15.

L = 1.00 km; a = 1000000.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.9130;
S = 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



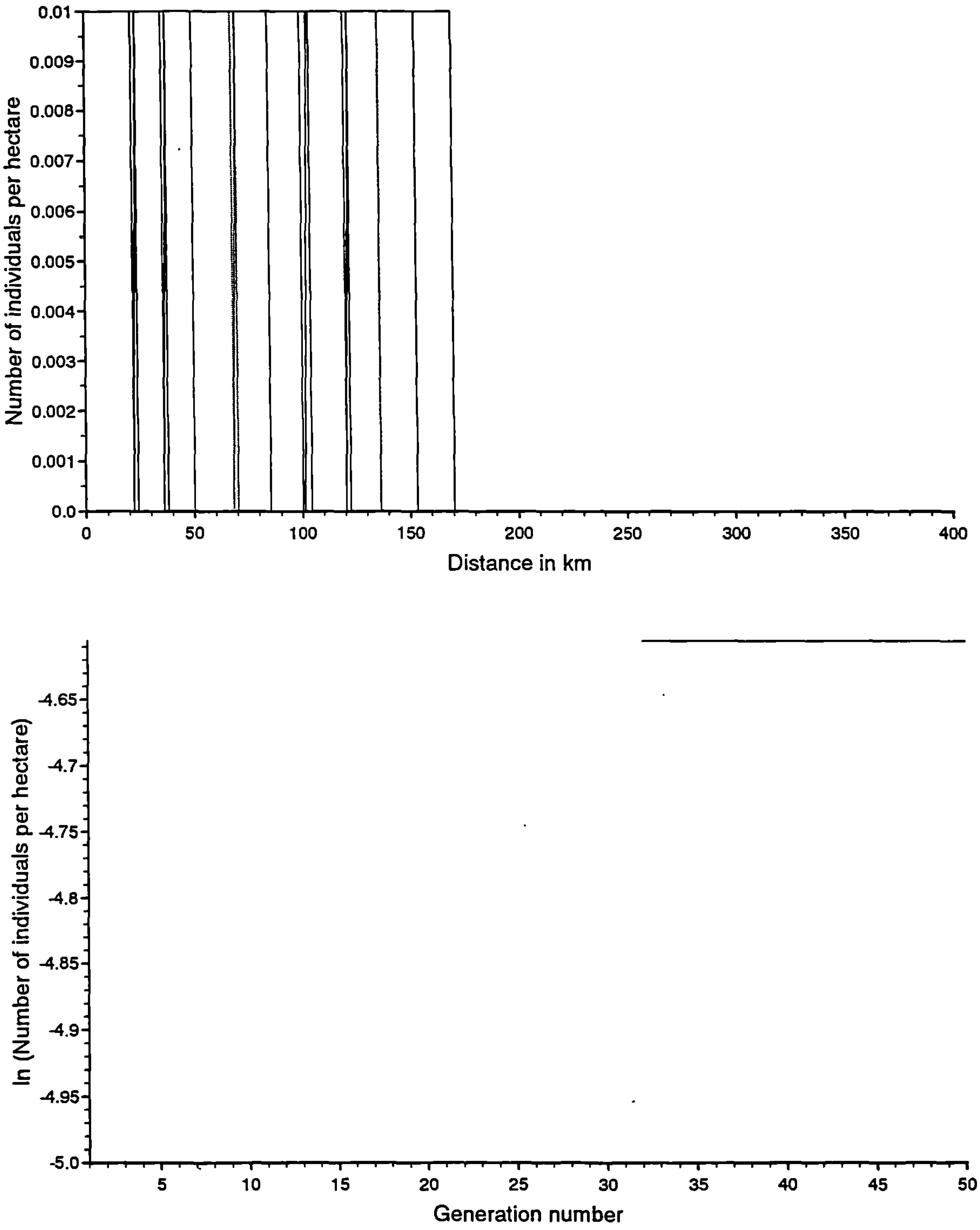
B5. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.10.

L = 1.00 km; a = 10000.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.0000;
S = 160000.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; Random number seed = 31; No climatic restraints;
Output interval = 5 generations; Last generation = 50



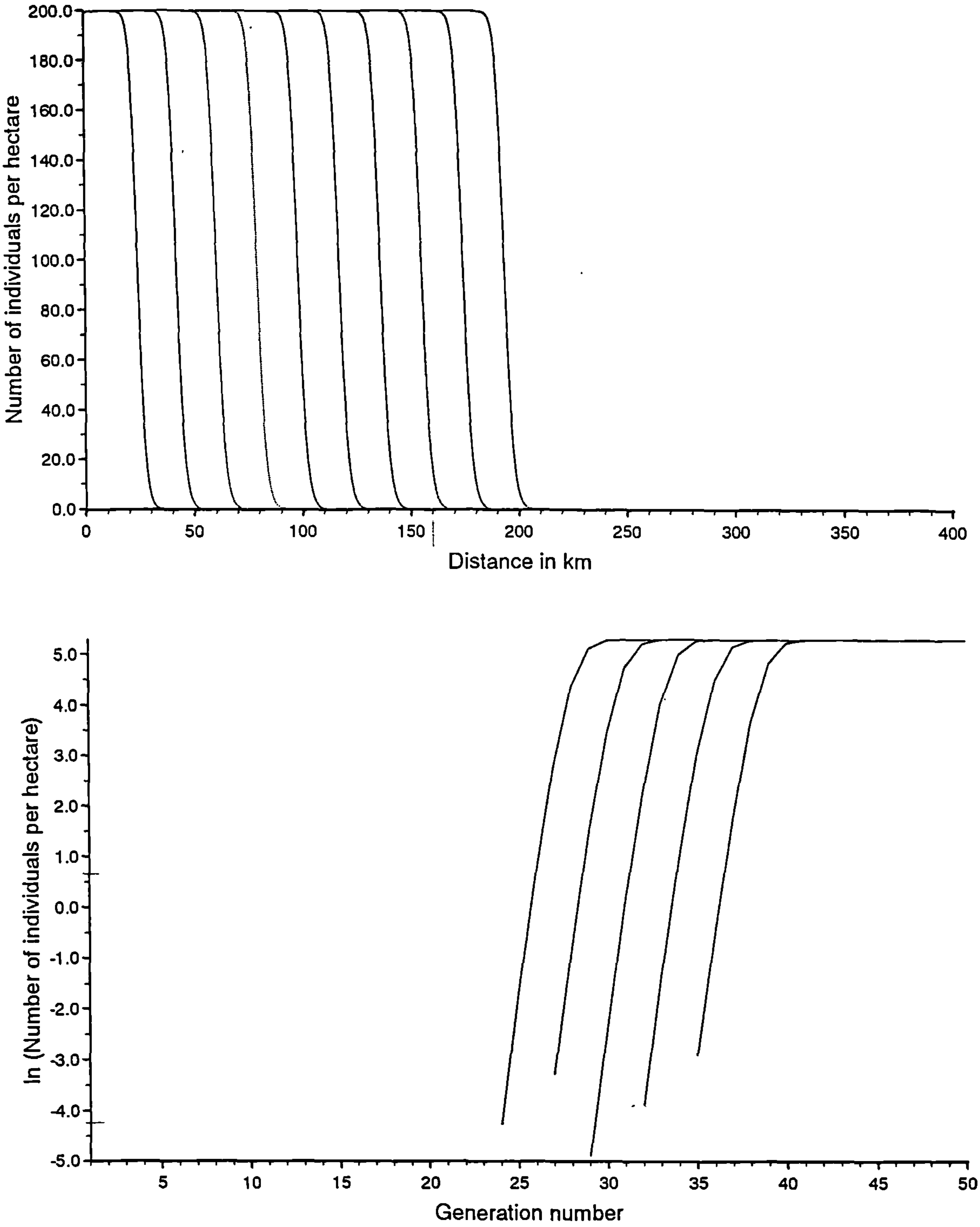
B6. Migration rate = 0.19 km yr^{-1}, α = 0.1.

L = 1.00 km; a = 1000000.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.9130;
S = 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; Random number seed = 31; No climatic restraints;
Output interval = 5 generations; Last generation = 50



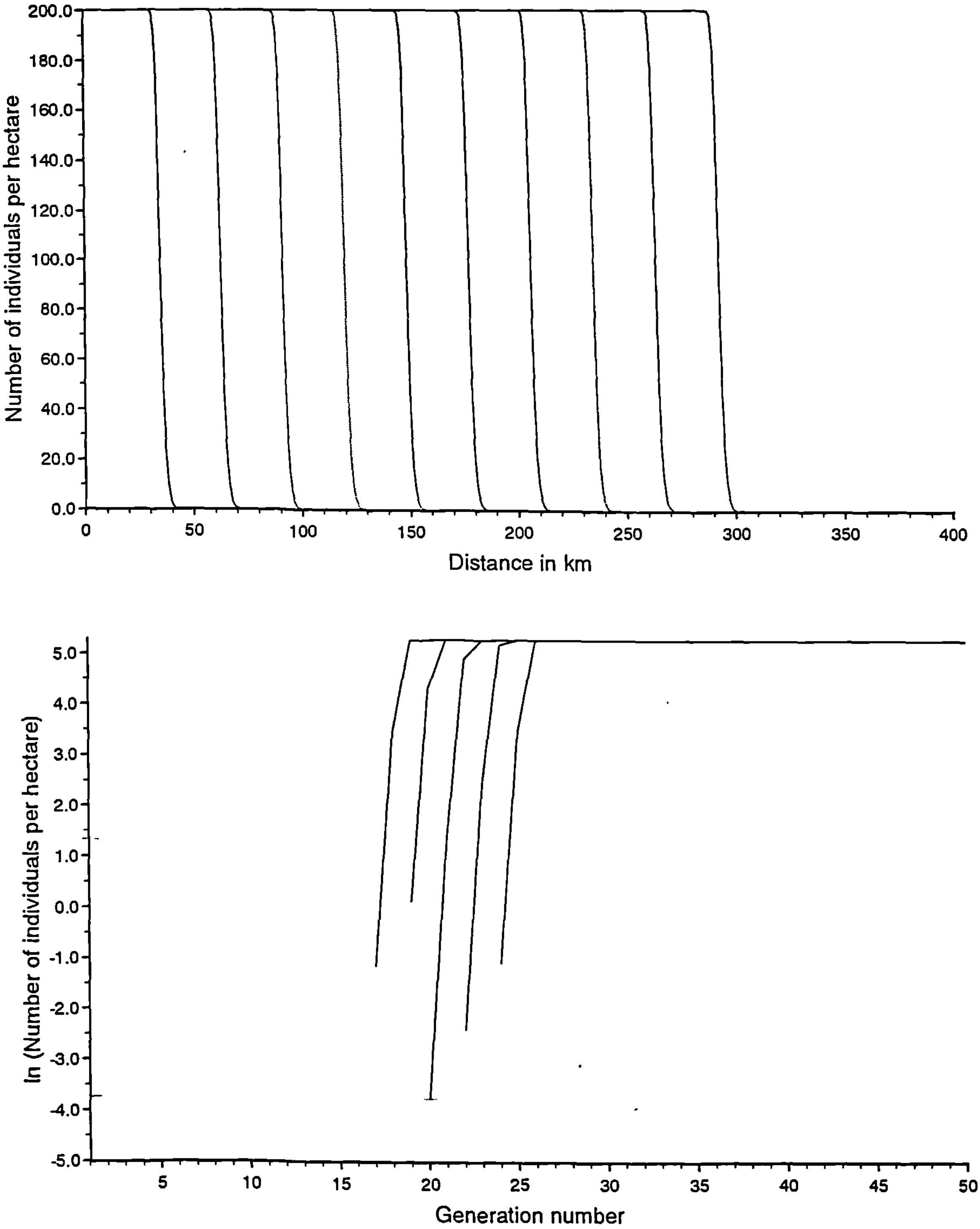
B7. Migration rate ≈ 0.20 km yr^{-1}.

L = 1.00 km; a = 50.00 m^2; T = 10.00 years;
Survival probabilities = 0.000050, 0.9660;
S = 64000.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



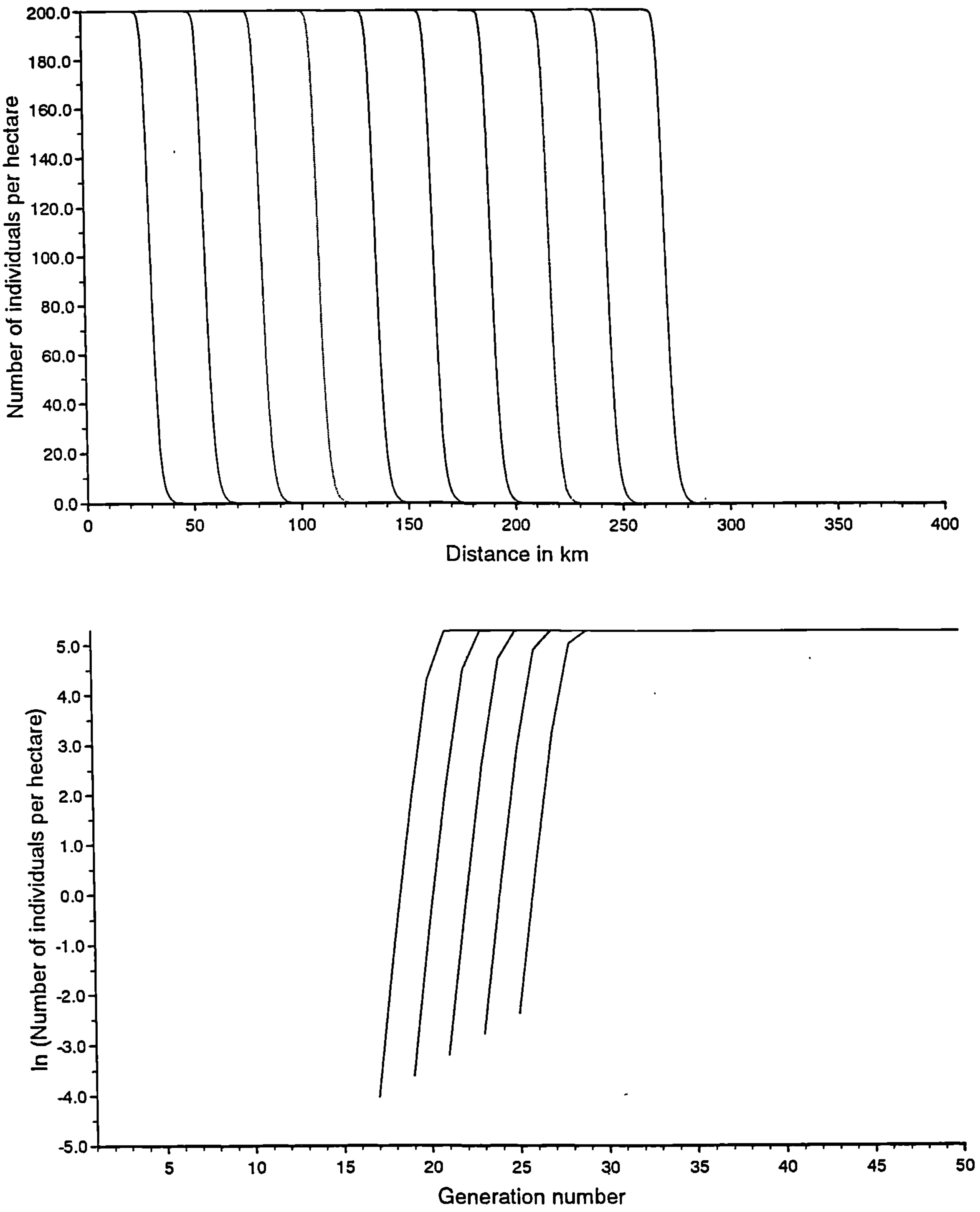
B8. Migration rate ≈ 0.38 km yr^{-1}, α ≈ 0.25.

L = 1.00 km; a = 50.00 m^2; T = 50.00 years;
Survival probabilities = 0.000050, 0.8190;
S = 320000.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



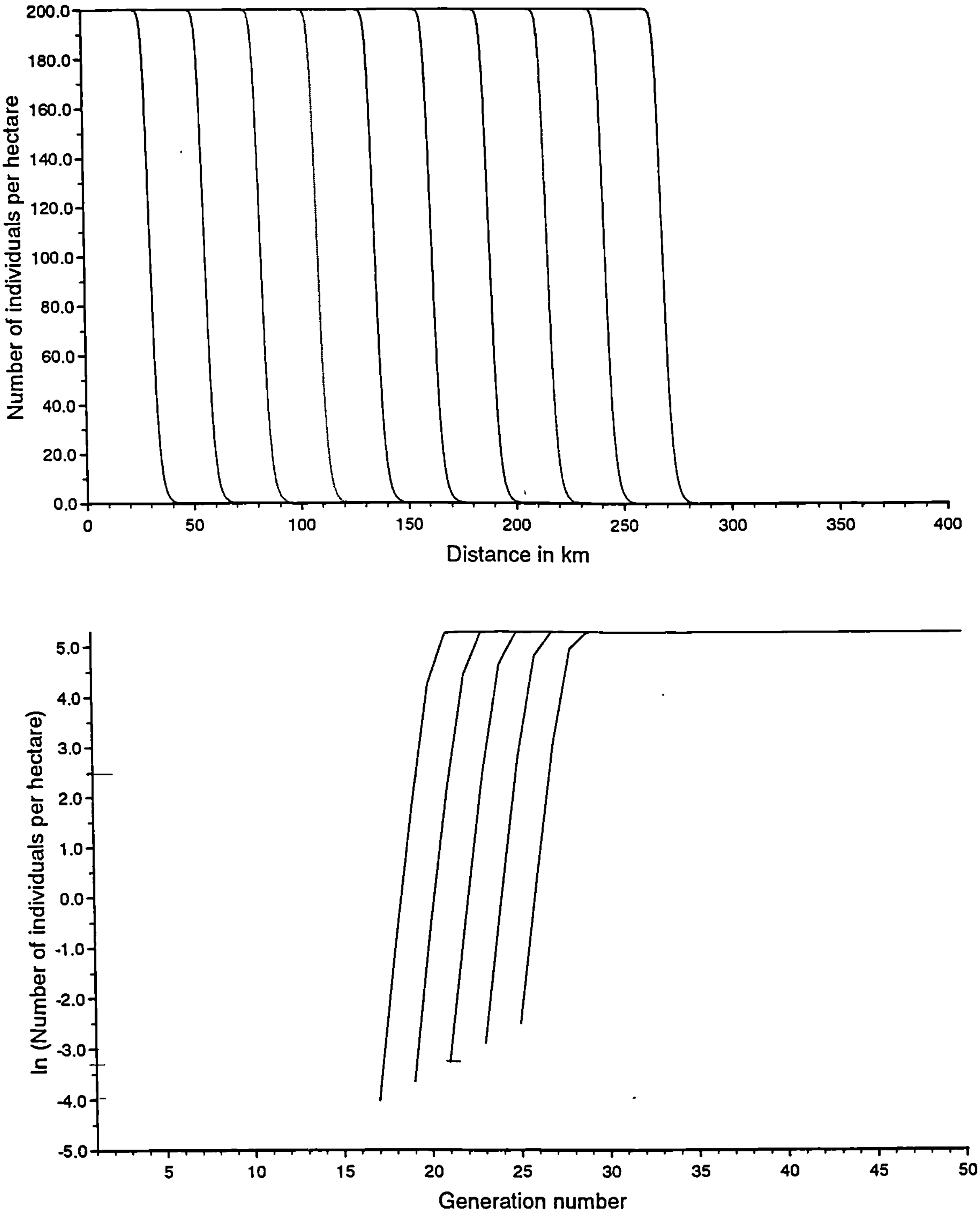
B9. Migration rate = 0.12 km yr^{-1}, α = 0.10.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.9130;
S = 160000.0;
H1 = 0.98 km; P(H1) = 1.000000;
Dispersal sums = 1.0412; Total = 1.0412; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



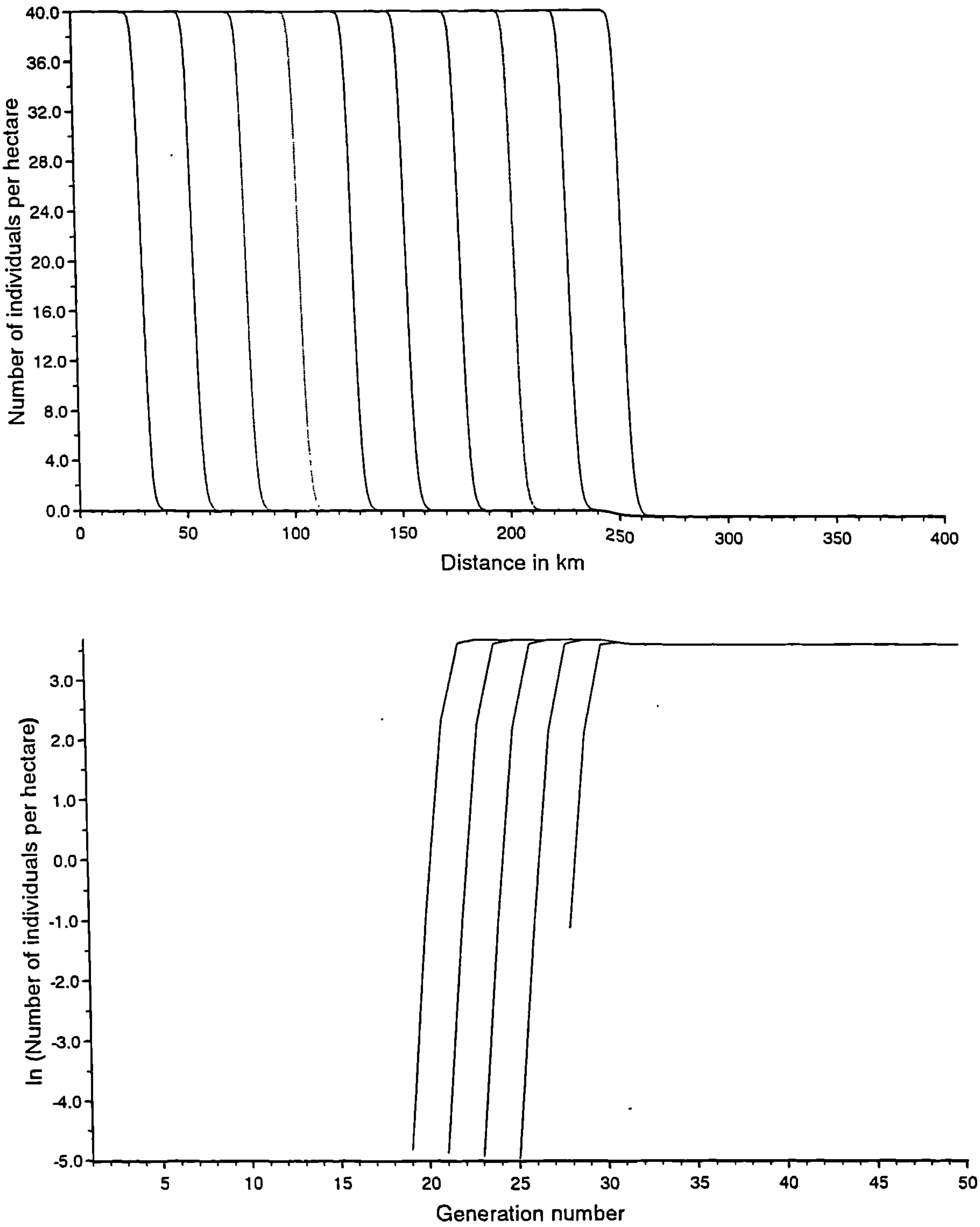
B10. Migration rate ≈ 0.21 km yr^{-1}, α ≈ 0.10.

L = 0.10 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.9130;
S = 160000.0;
H1 = 0.98 km; P(H1) = 1.000000;
Dispersal sums = 1.0004; Total = 1.0004; Furthest Cell = 180;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



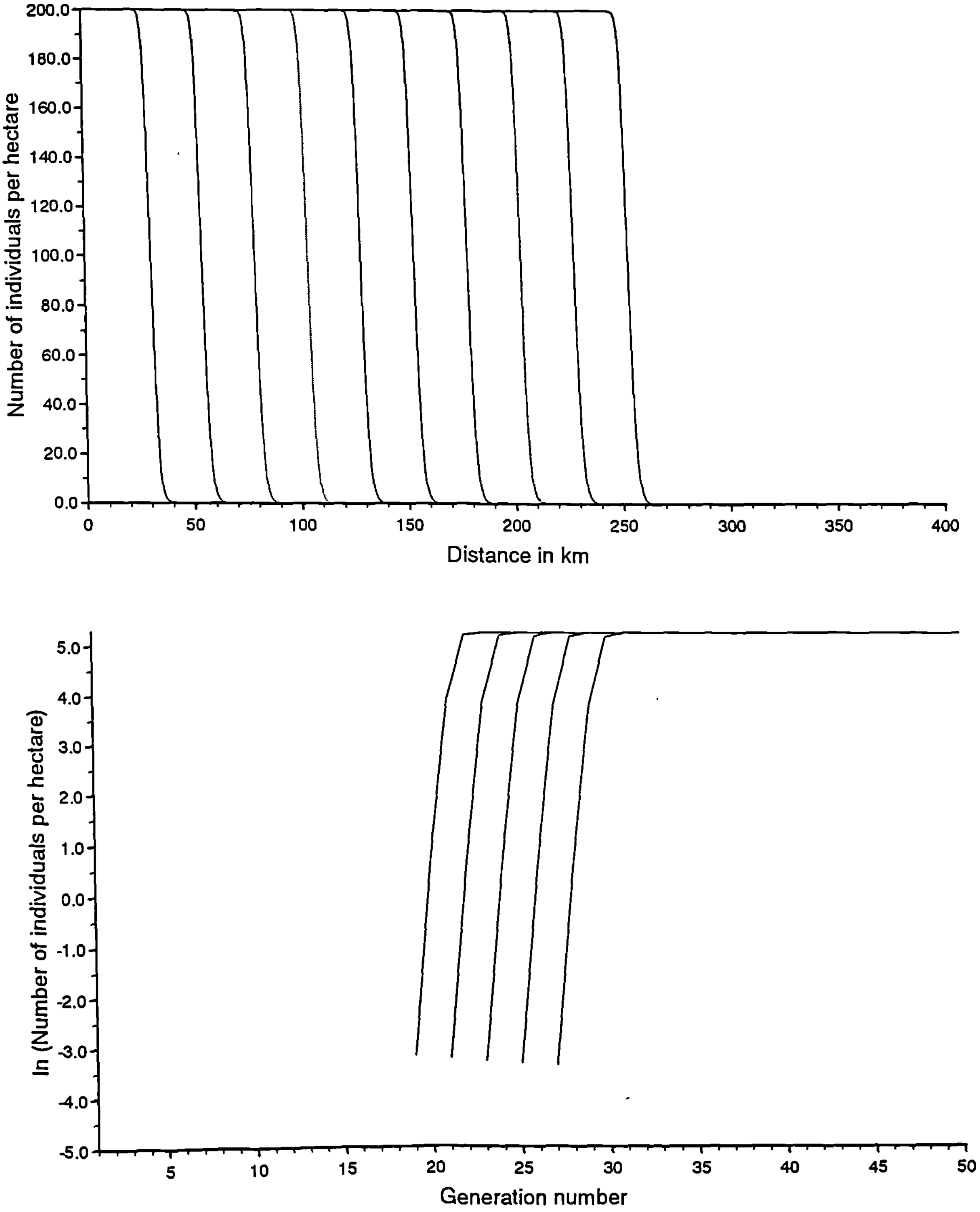
B11. Migration rate ≈ 0.22 km yr^{-1}, α ≈ 0.10.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0002500, 0.9130;
S = 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 0.20; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



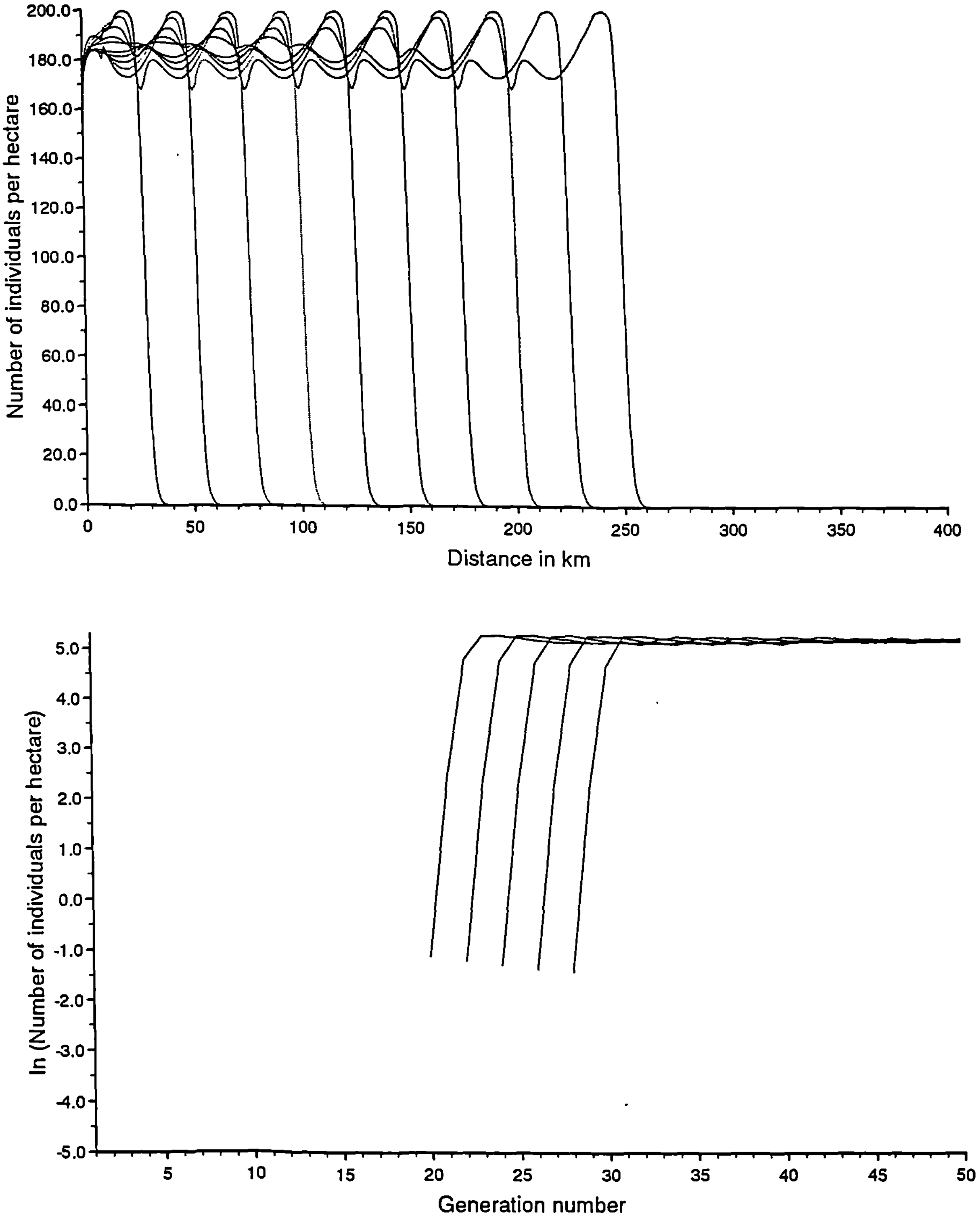
B12. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.15.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.00000;
S = 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



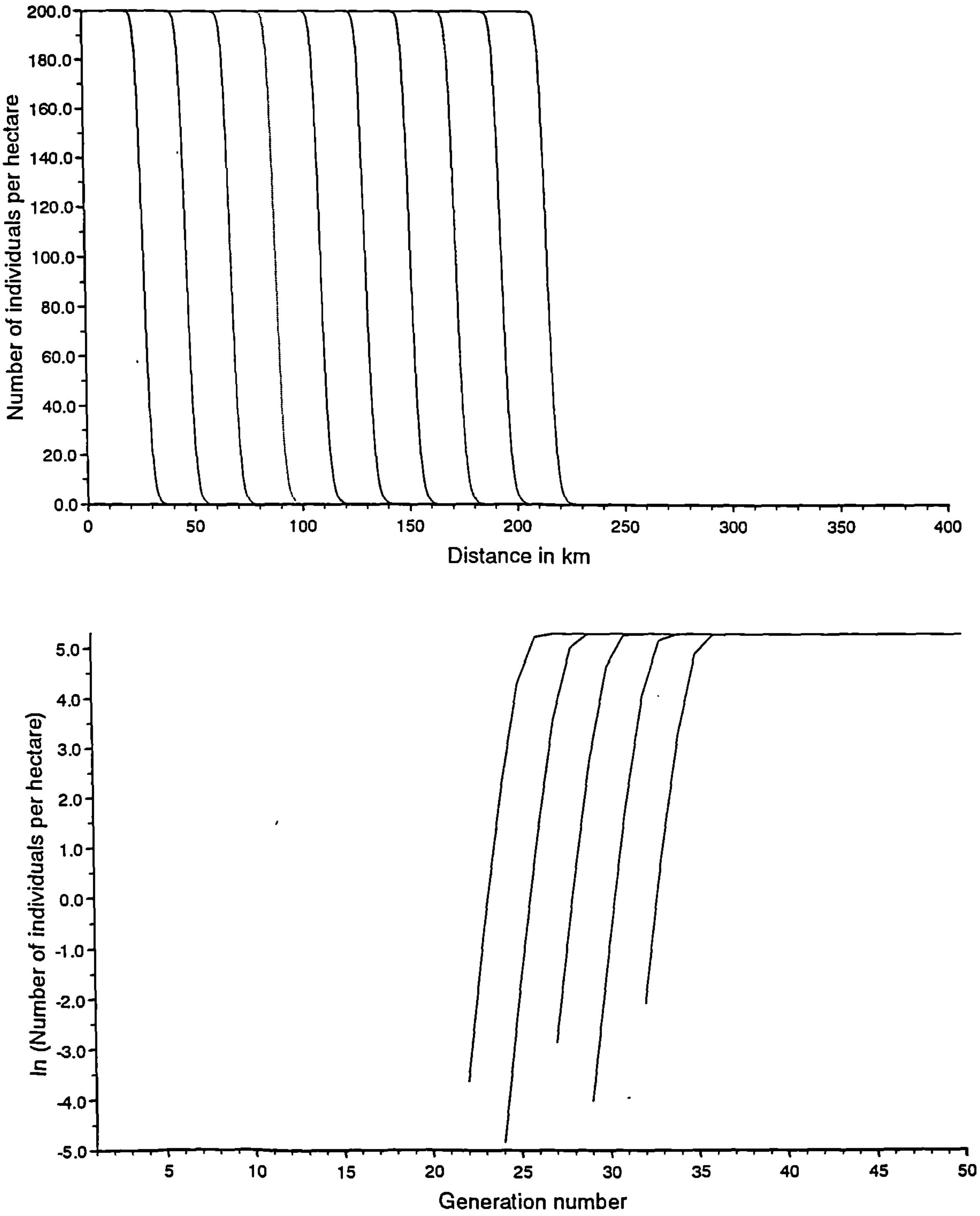
B13. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.15.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.00000;
S = 160000.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



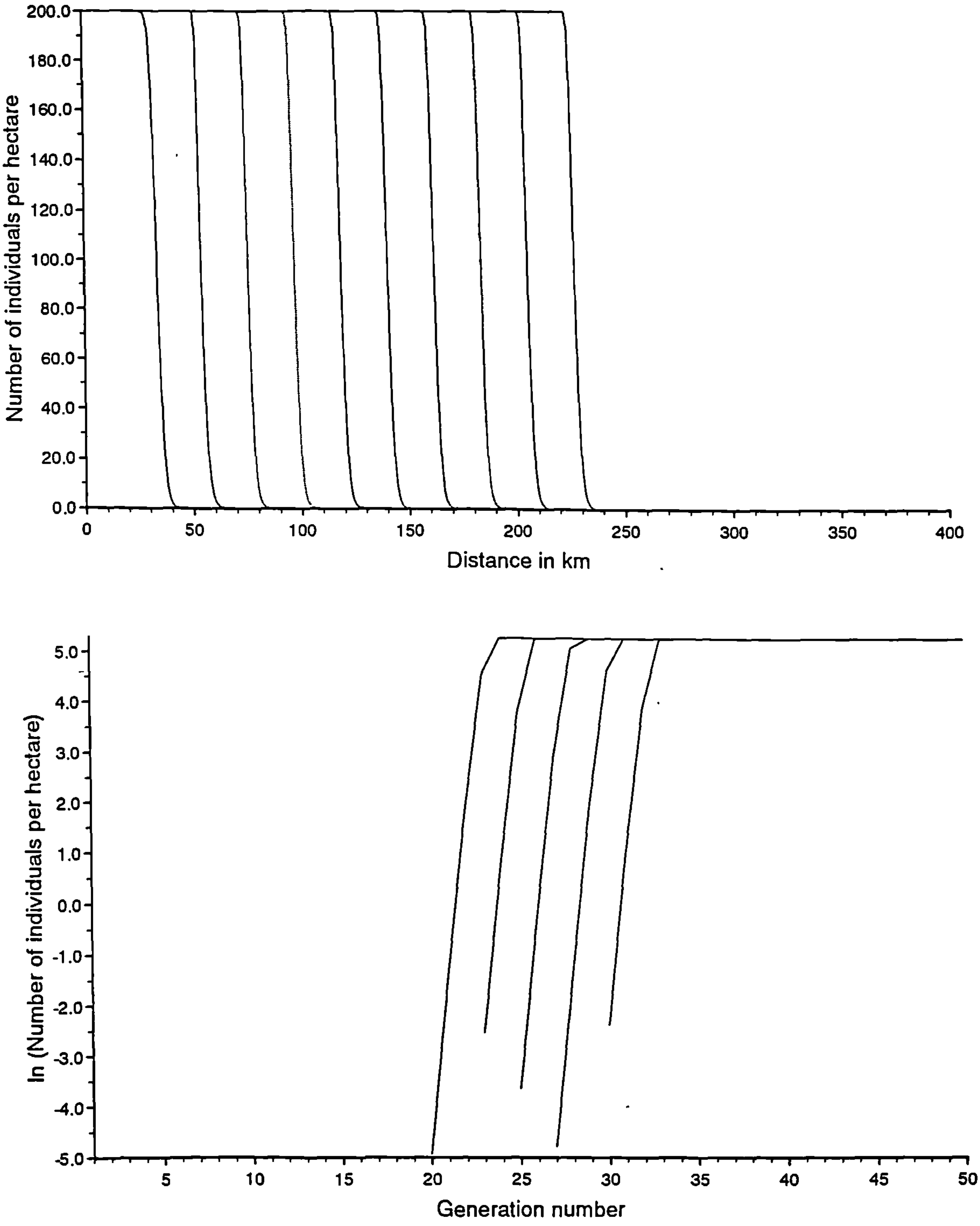
B14. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.15.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.00000;
ζ = 83200.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



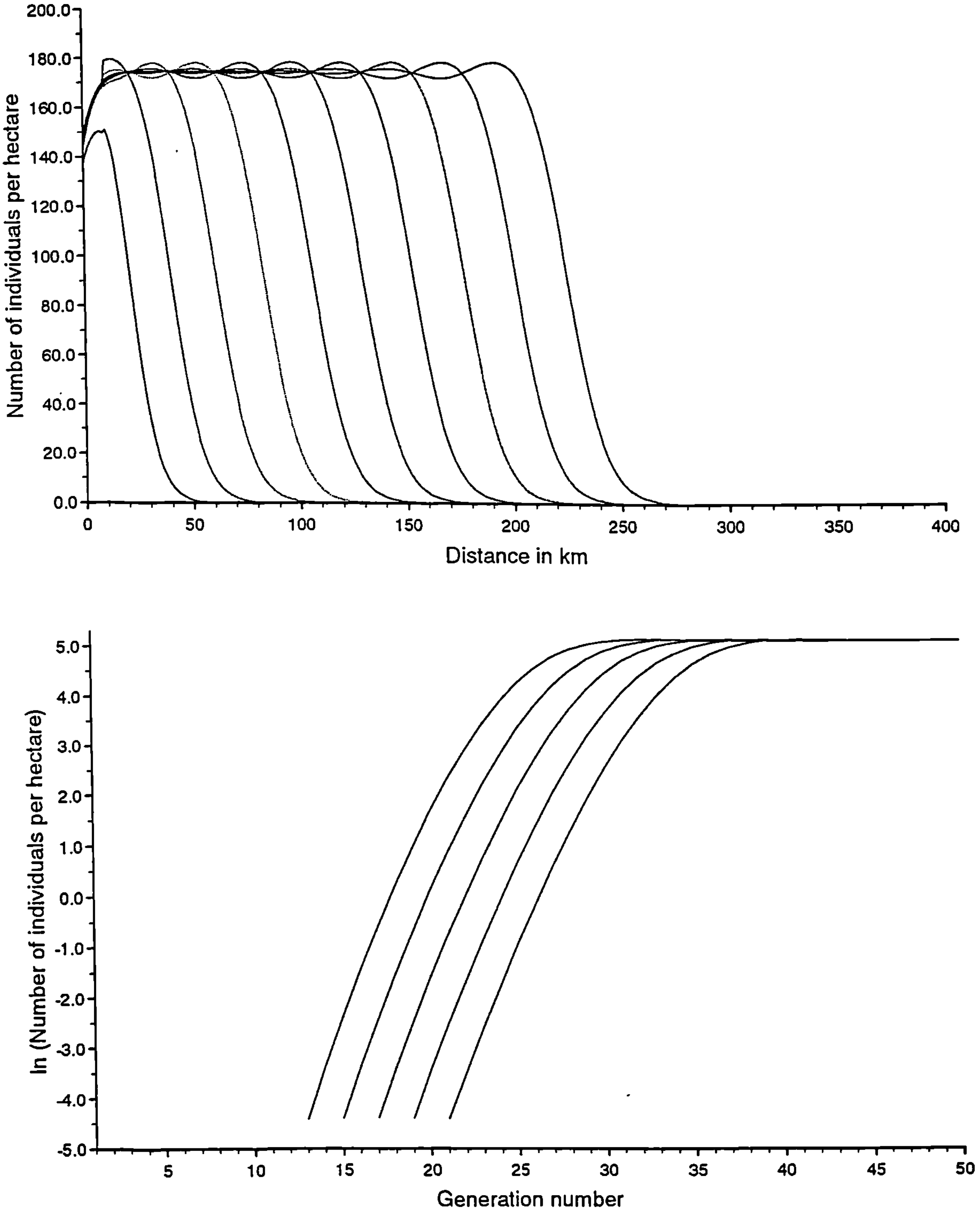
B15. Migration rate ≈ 0.17 km yr^{-1}, α ≈ 0.11.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300;
S = 8.320e+04, 1.600e+05, 1.600e+05, 1.600e+05, 2.560e+10, 1.600e+05, 1.600e+05, 1.600e+05, 1.600e+05, 1.600e+05;
RMSD1 = 3.47 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 18;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



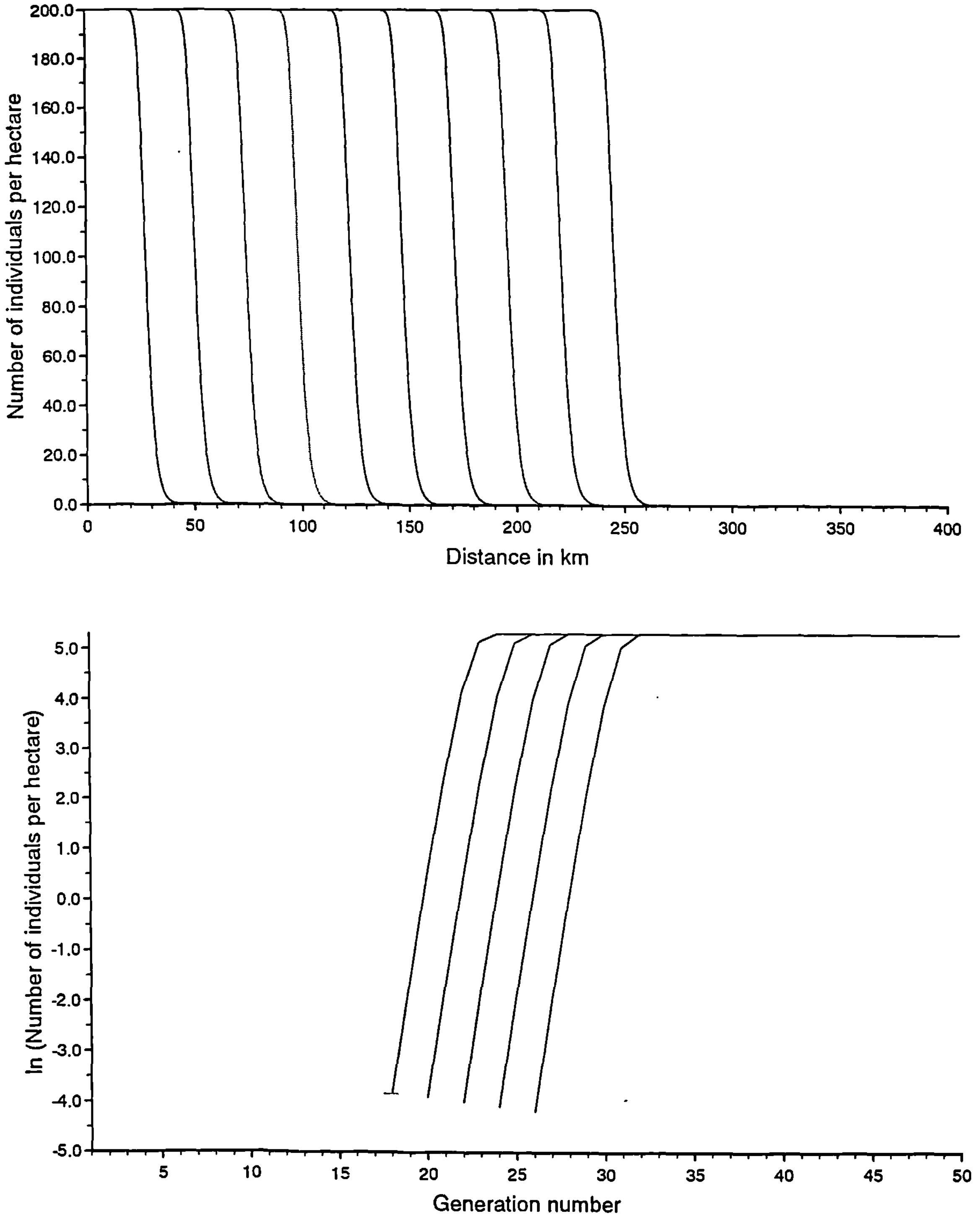
B16. Migration rate = 0.17 km yr^{-1}, α = 0.13.

L = 1.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000005, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.91300, 0.00000;
$\underline{S}$ = 83200.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0, 160000.0;
RMSD1 = 11.00 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 55;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



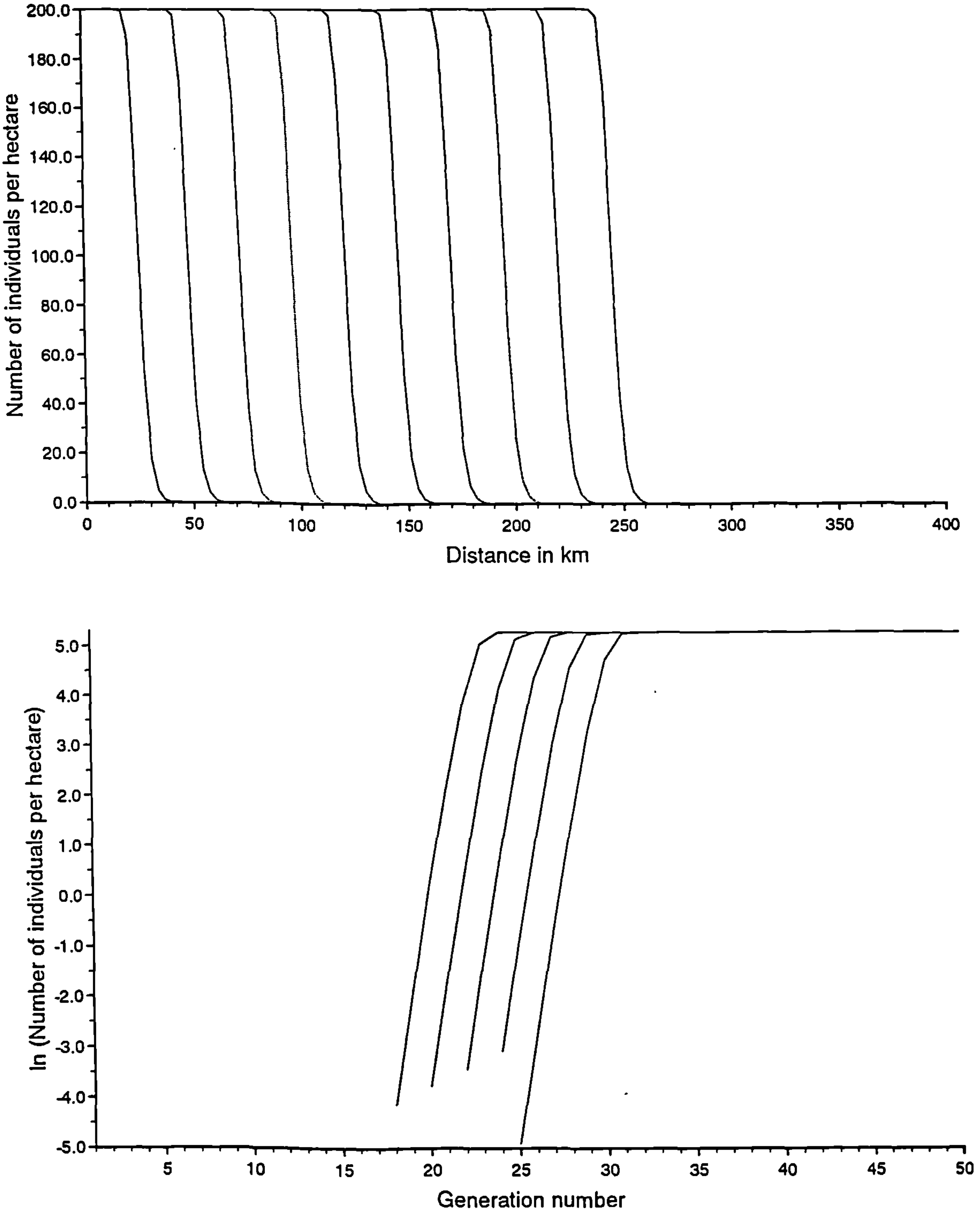
B17. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.03.

L = 0.10 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300;
S = 83200.0, 160000.0;
RMSD1 = 0.20 km; P(RMSD1) = 0.900000; RMSD2 = 6.70 km; P(RMSD2) = 0.100000;
Dispersal sums = 0.9000, 0.1000; Total = 1.0000; Furthest Cell = 350;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



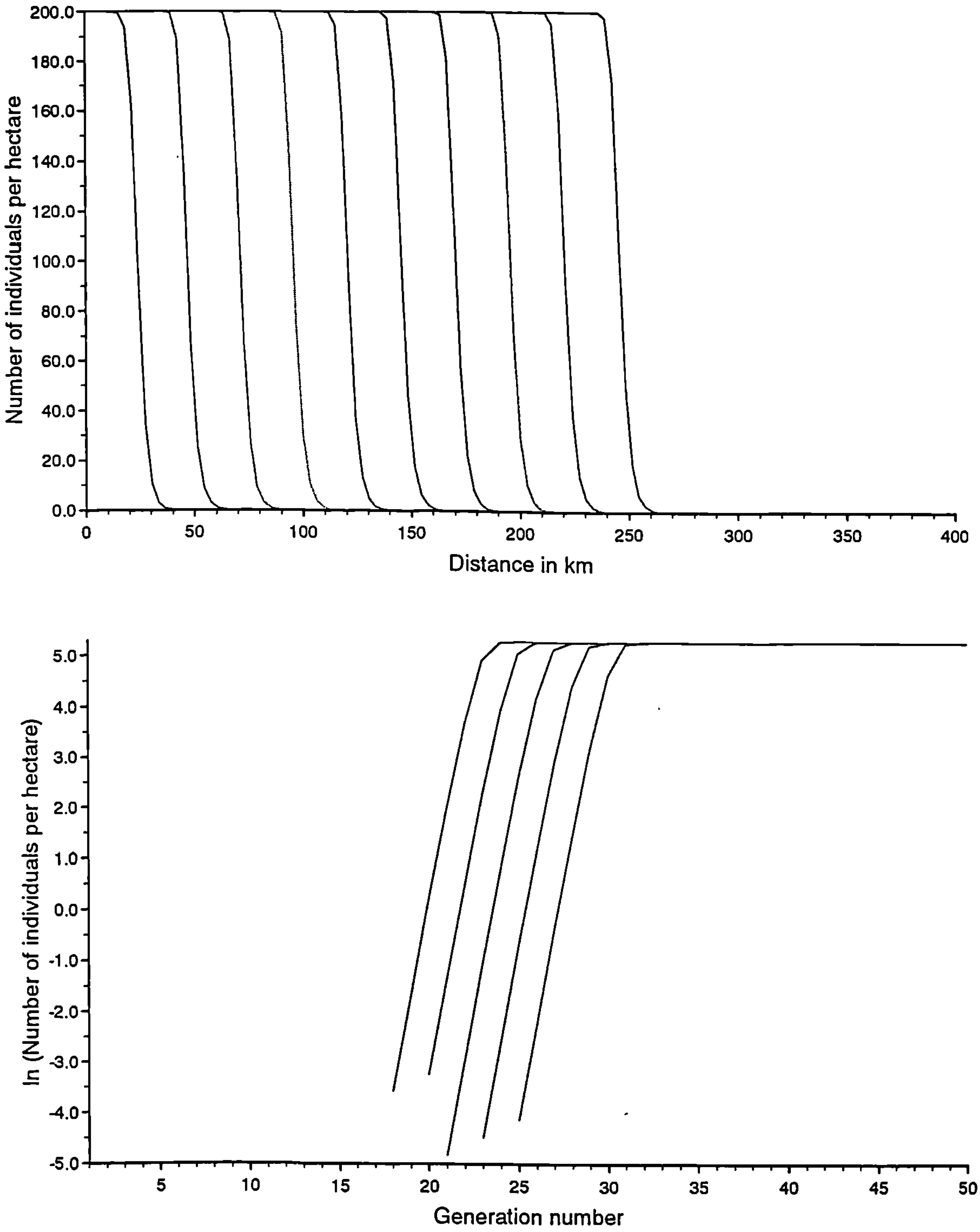
B18. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.09.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300;
S = 83200.0, 160000.0;
All offspring placed in parent cell; P(1) = 0.900000; RMSD2 = 6.70 km; P(RMSD2) = 0.100000;
Dispersal sums = 0.9000, 0.1000; Total = 1.0000; Furthest Cell = 12;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



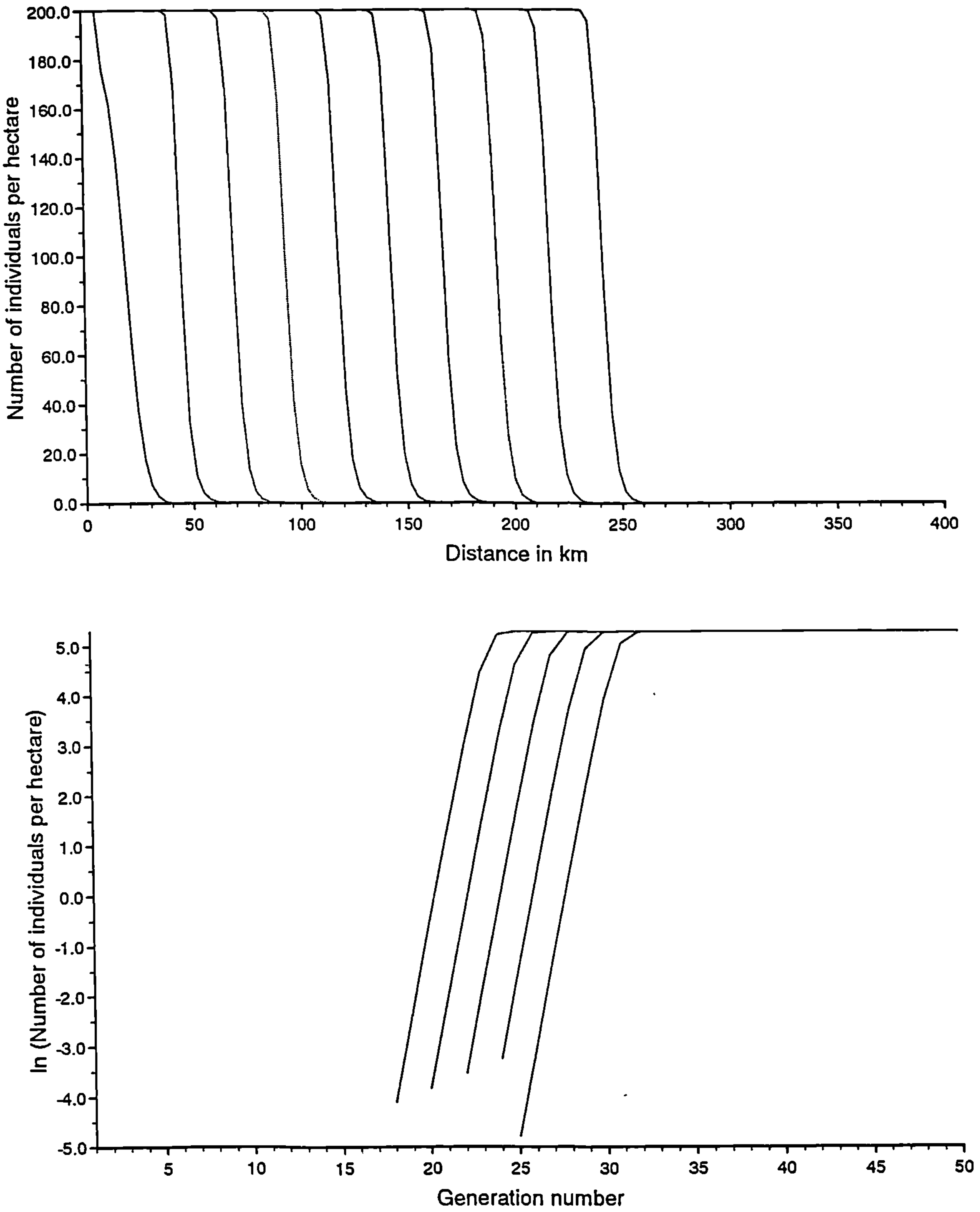
B19. Migration rate ≈ 0.20 km yr^{-1}, $\alpha \approx 0.09$.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300;
S = 83200.0, 160000.0;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 9.70 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 16;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



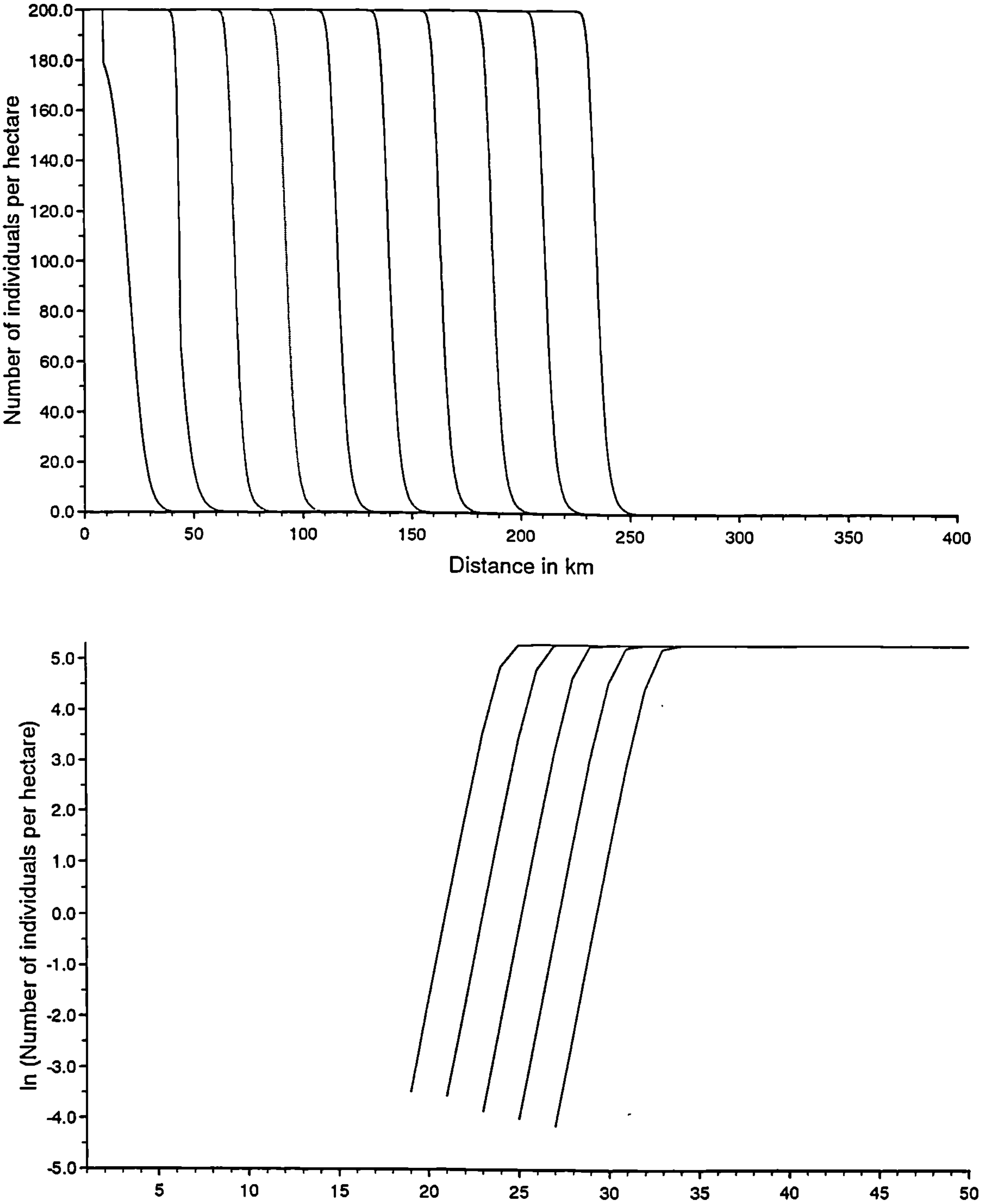
B20. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.08.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300;
S = 83200.0, 160000.0;
All offspring placed in parent cell; P(1) = 0.999000; RMSD2 = 12.30 km; P(RMSD2) = 0.001000;
Dispersal sums = 0.9990, 0.0010; Total = 1.0000; Furthest Cell = 22;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



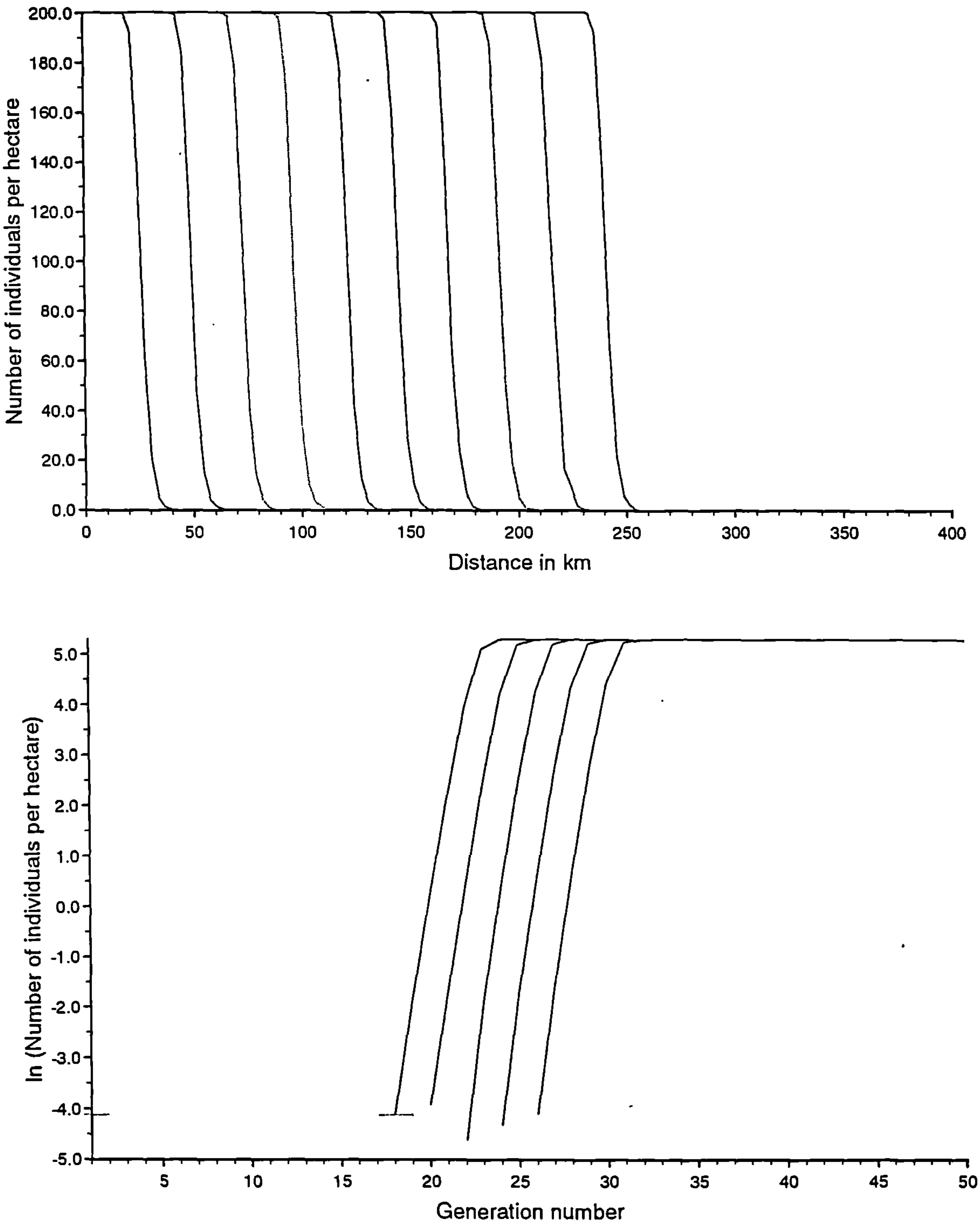
B21. Migration rate = 0.20 km yr^{-1}, α = 0.08.

L = 0.10 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300;
S = 83200.0, 160000.0;
All offspring placed in parent cell; P(1) = 0.999000; RMSD2 = 12.30 km; P(RMSD2) = 0.001000;
Dispersal sums = 0.9990, 0.0010; Total = 1.0000; Furthest Cell = 350;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



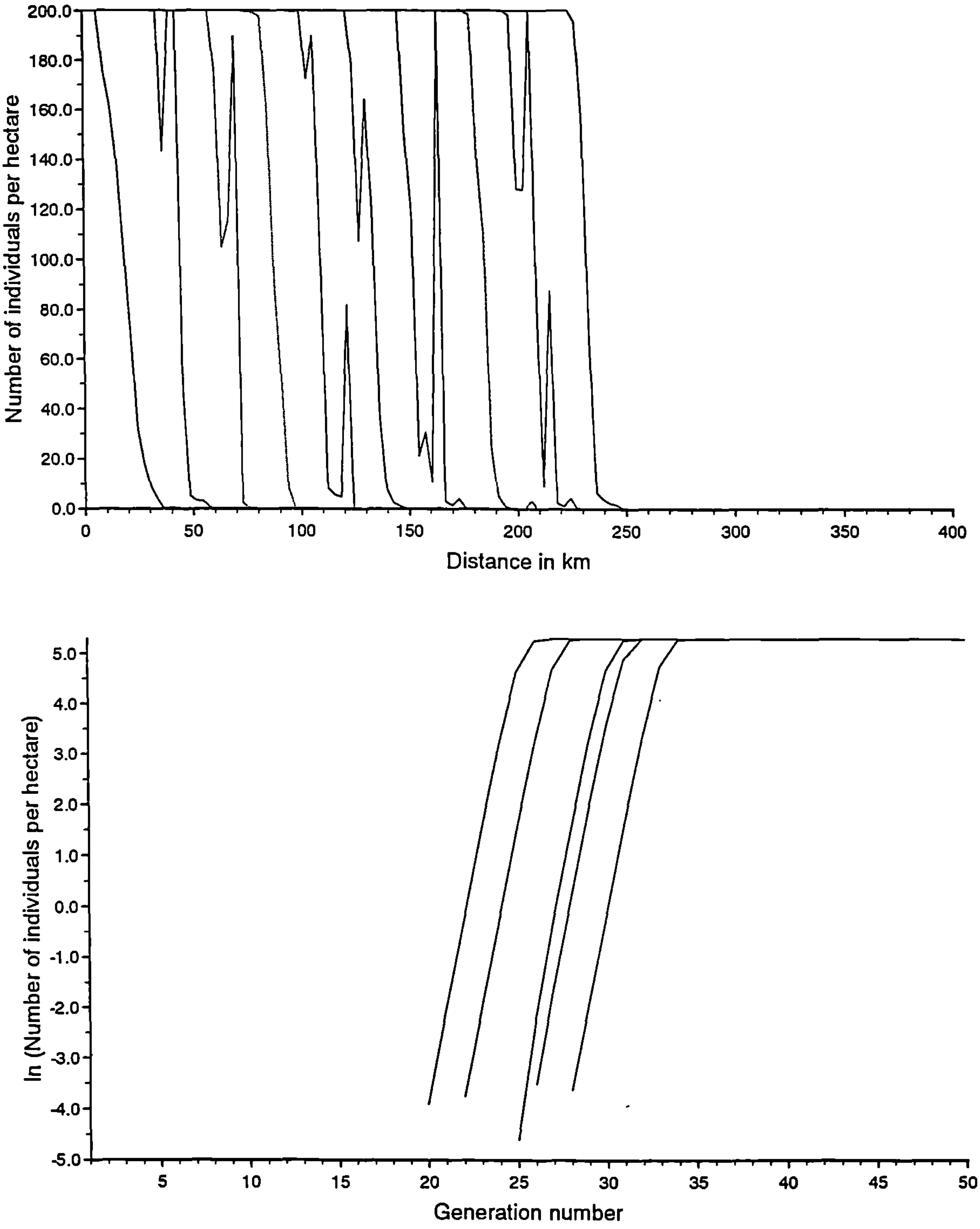
B22. Migration rate = 0.19 km yr^{-1}, α = 0.08.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000500, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.999000; RMSD2 = 6.70 km; P(RMSD2) = 0.100000;
Dispersal sums = 0.9990, 0.1000; Total = 1.0990; Furthest Cell = 12;
K = 1.00; Random number seed = 1037; No climatic restraints;
Output interval = 5 generations; Last generation = 50



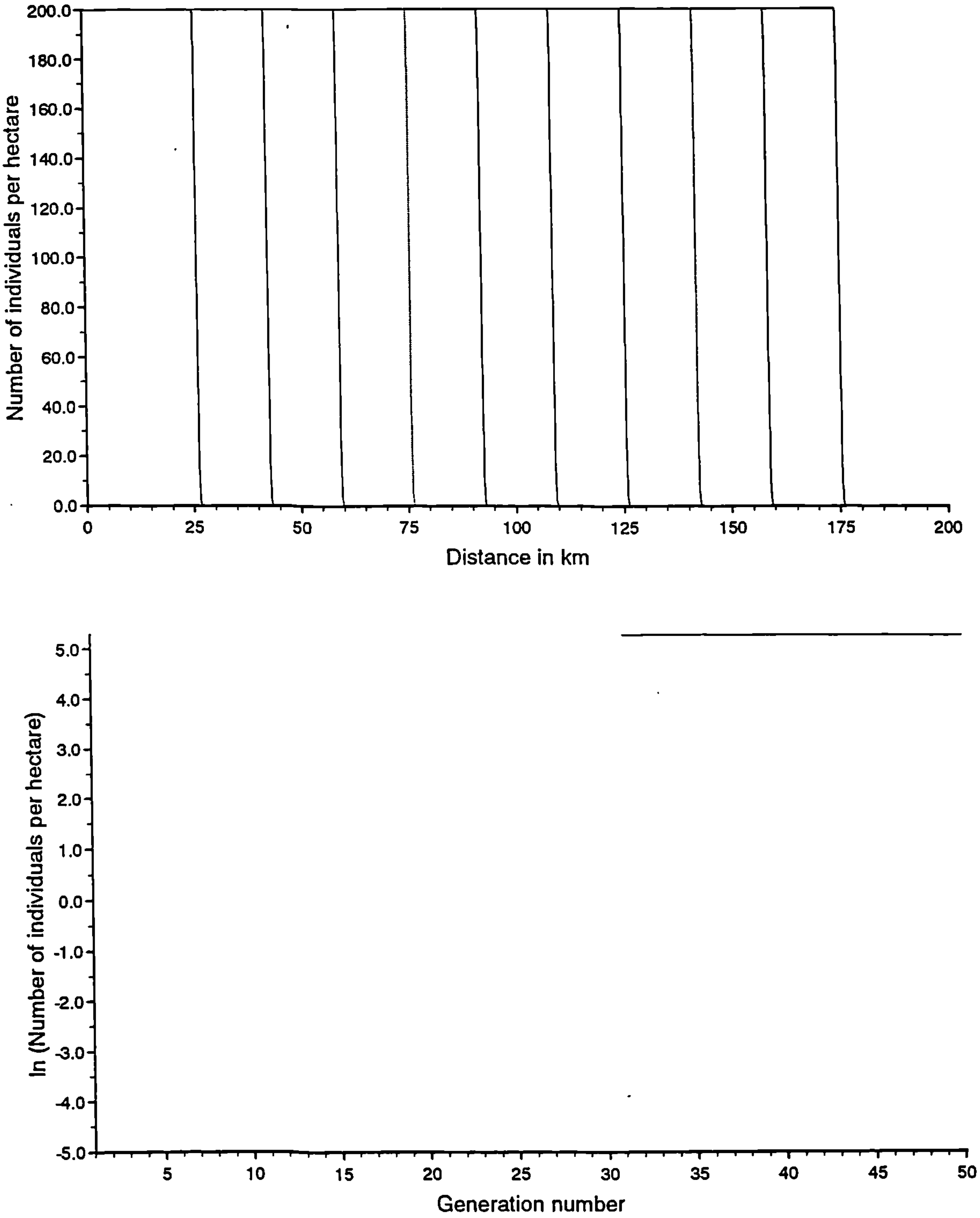
B23. Migration rate ≈ 0.19 km yr^{-1}, α ≈ 0.09.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.000050, 0.91300;
S = 83200.0, 160000.0;
All offspring placed in parent cell; P(1) = 0.999000; RMSD2 = 12.30 km; P(RMSD2) = 0.001000;
Dispersal sums = 0.9990, 0.0010; Total = 1.0000; Furthest Cell = 22;
K = 1.00; Random number seed = 1037; No climatic restraints;
Output interval = 5 generations; Last generation = 50



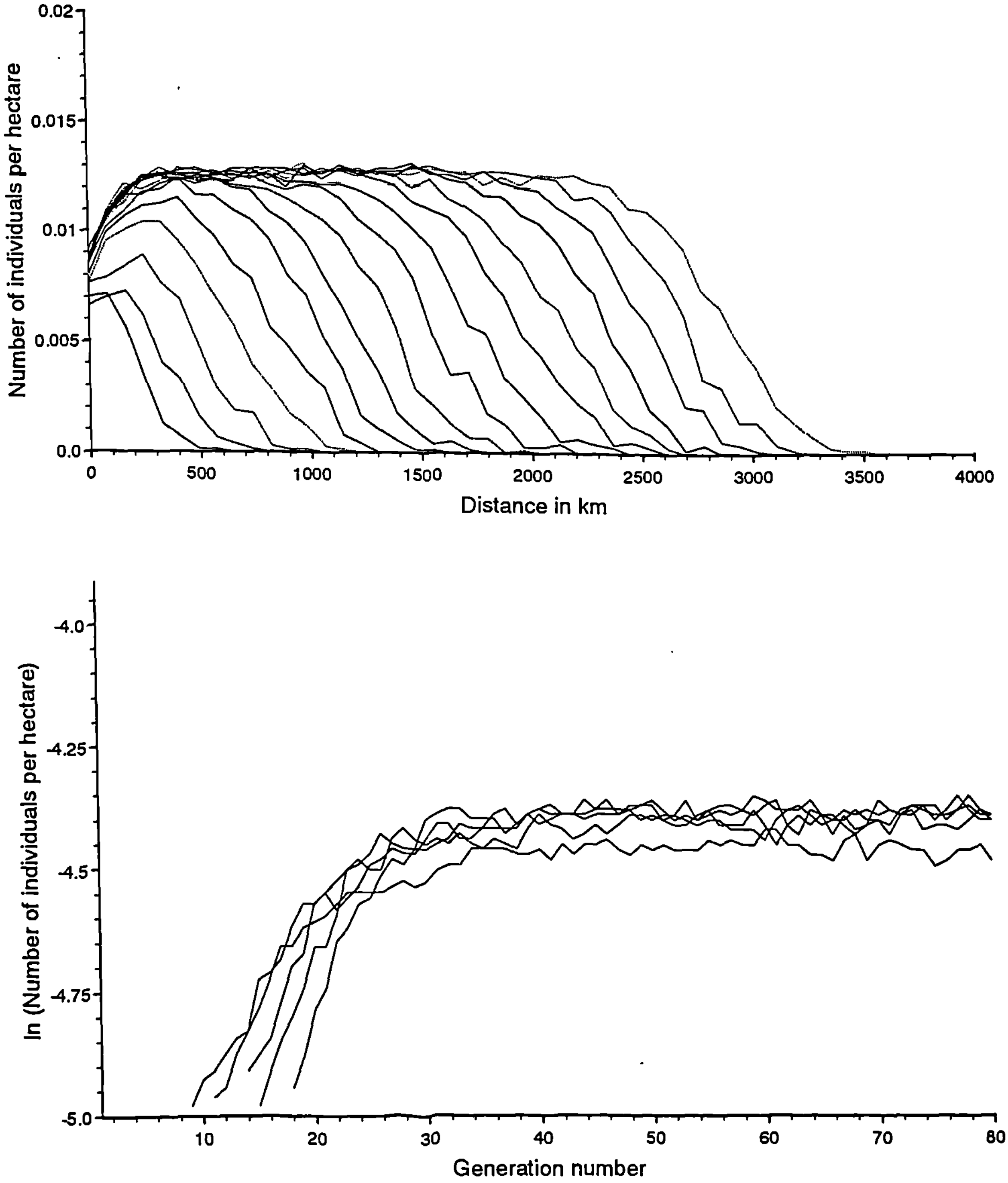
B24. Migration rate ≈ 0.19 km yr^{-1}, α ≈ 0.07.

L = 0.25 km; a = 50.00 m^2; T = 66.70 years;
Survival probabilities = 1.0000000, 0.7600;
S = 8.000e+06;
RMSD1 = 0.83 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 20;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



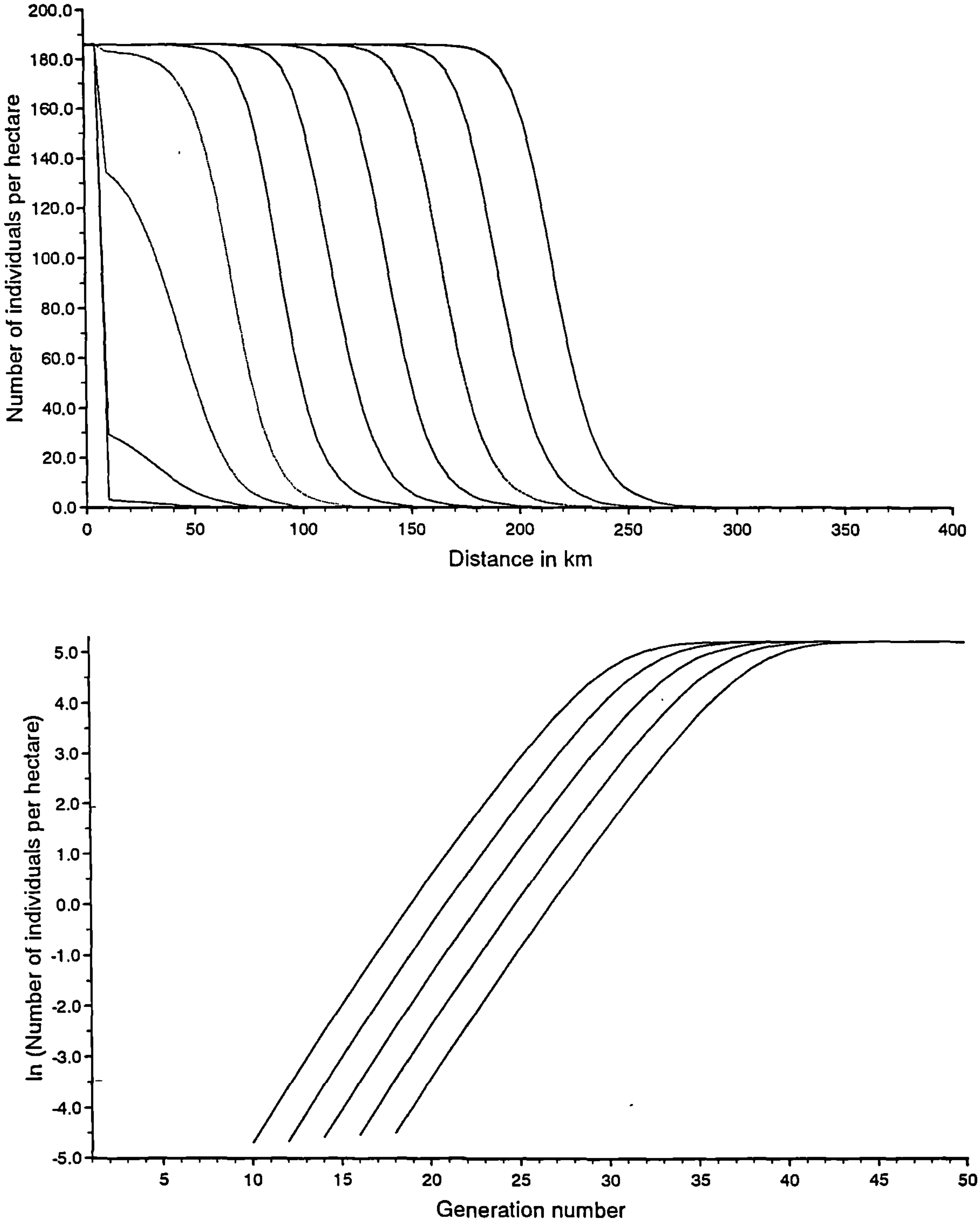
B25. Migration rate ≈ 0.20 km yr^{-1}.

L = 80.00 km; a = 500000.00 m^2; T = 0.50 years;
Survival probabilities = 0.8600000, 0.60500, 0.59800, 0.74200, 0.56500, 0.53800, 0.57100, 0.50000, 0.50000;
S = 0.000e+00, 1.600e-01, 1.560e+00, 1.560e+00, 1.560e+00, 1.560e+00, 1.560e+00, 1.560e+00, 1.560e+00;
RMSD1 = 190.00 km; P(RMSD1) = 1.000000;
Dispersal sums = 1.0000; Total = 1.0000; Furthest Cell = 13;
K = 1.00; Random number seed = 3; No climatic restraints;
Output interval = 5 generations; Last generation = 80



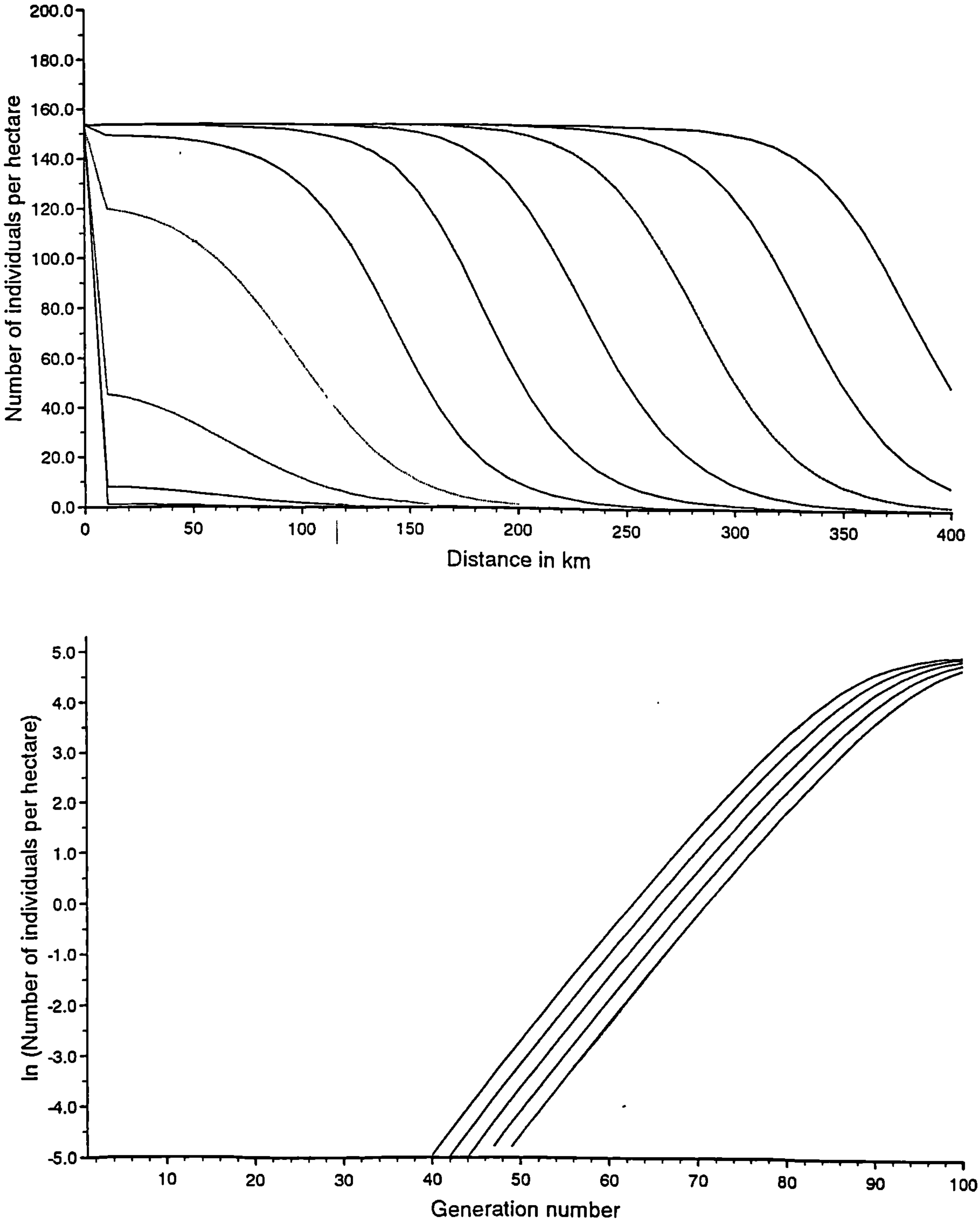
B26. Simulation of the migration of the collared dove using parameter values as given in Van den Bosch *et al.* (1992). Migration rate ≈ 81 km yr^{-1}.

L = 5.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000050, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 35.00 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 35;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 5 generations; Last generation = 50



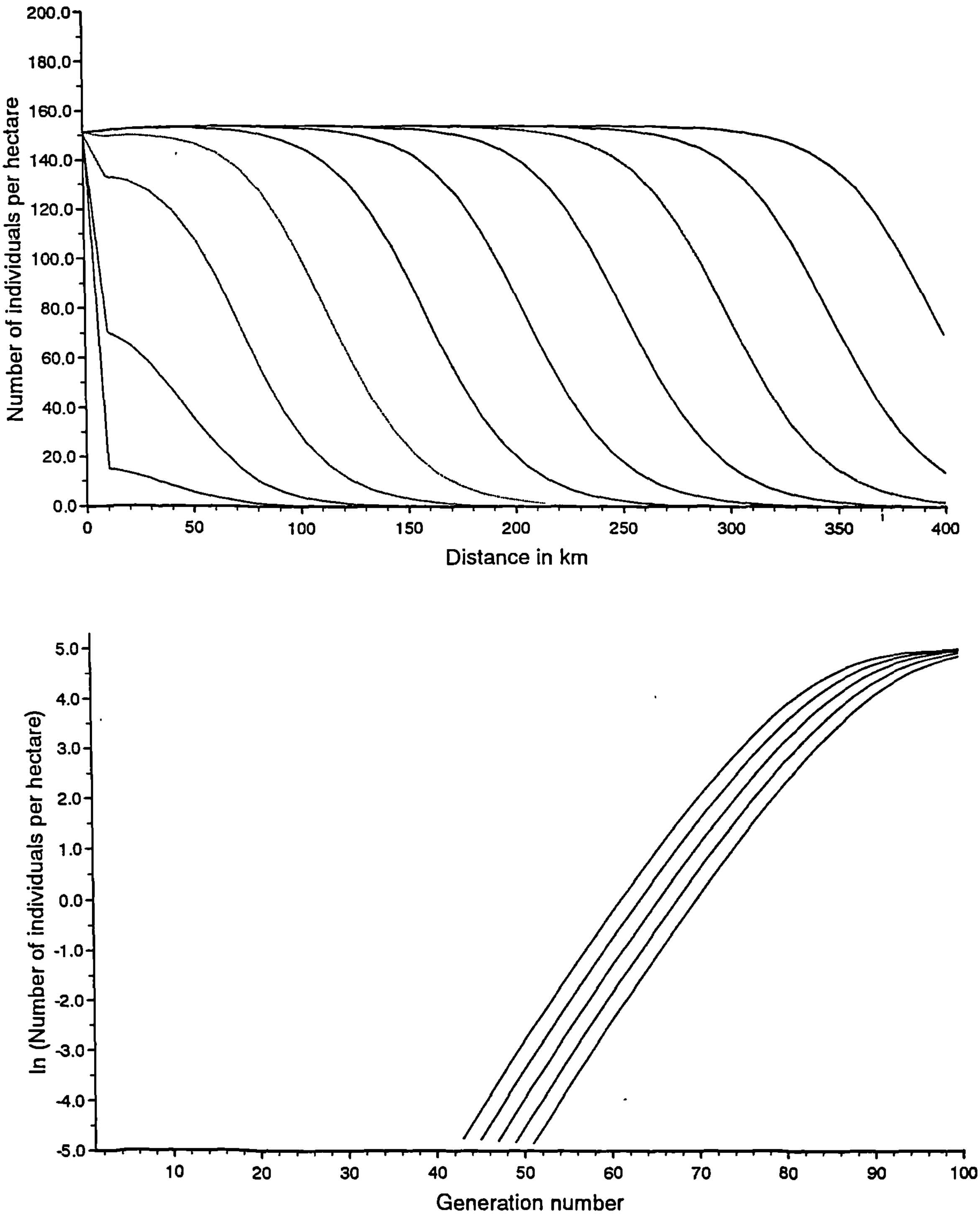
B27. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.02.

L = 10.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000020, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 75.00 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 40;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 100



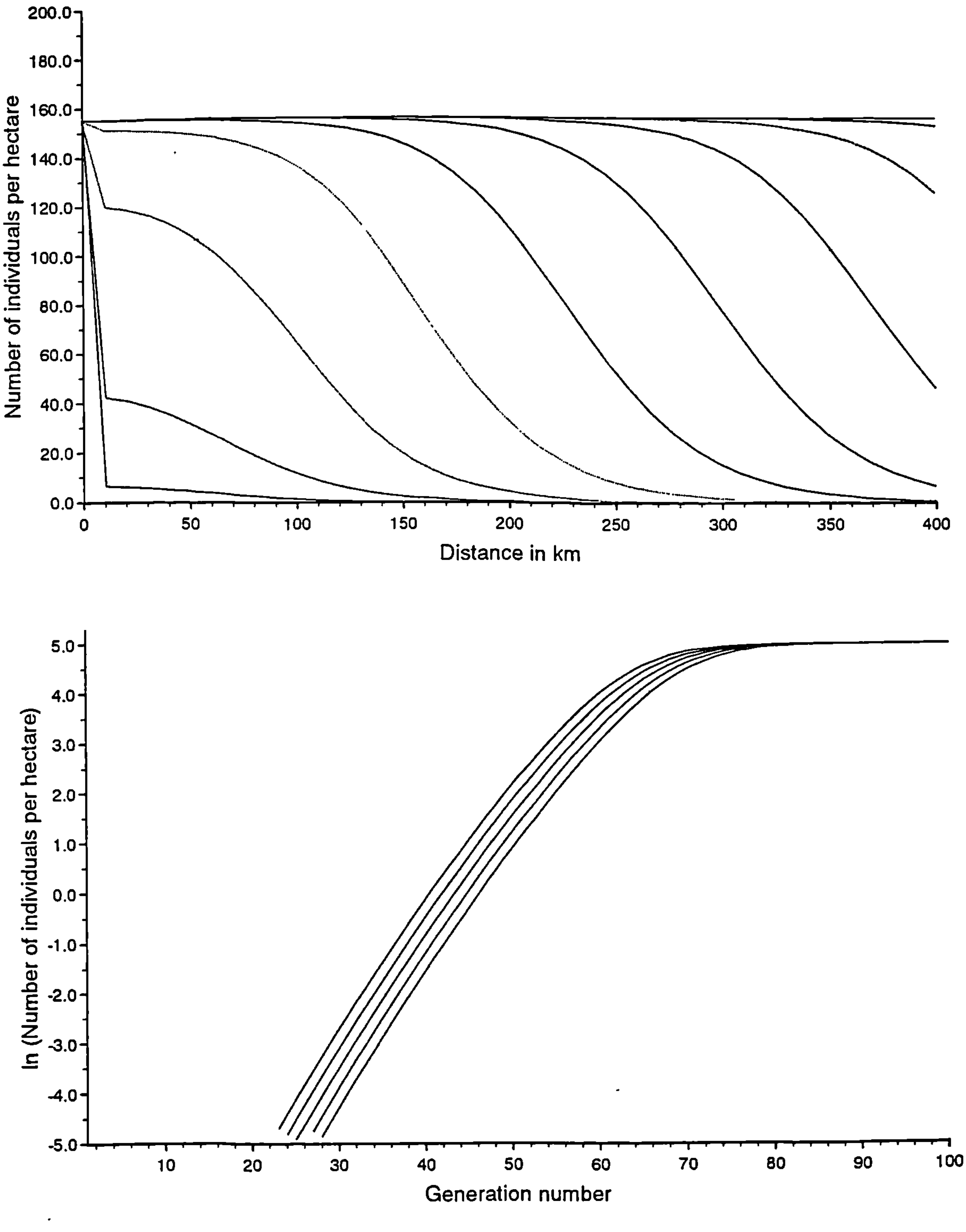
B28. Migration rate ≈ 0.20 km yr^{-1}, α ≈ 0.009. Population increase was observed at 300, 310, 320, 330 and 340 km.

L = 10.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000020, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.900000; RMSD2 = 45.00 km; P(RMSD2) = 0.100000;
Dispersal sums = 0.9000, 0.1000; Total = 1.0000; Furthest Cell = 40;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 100



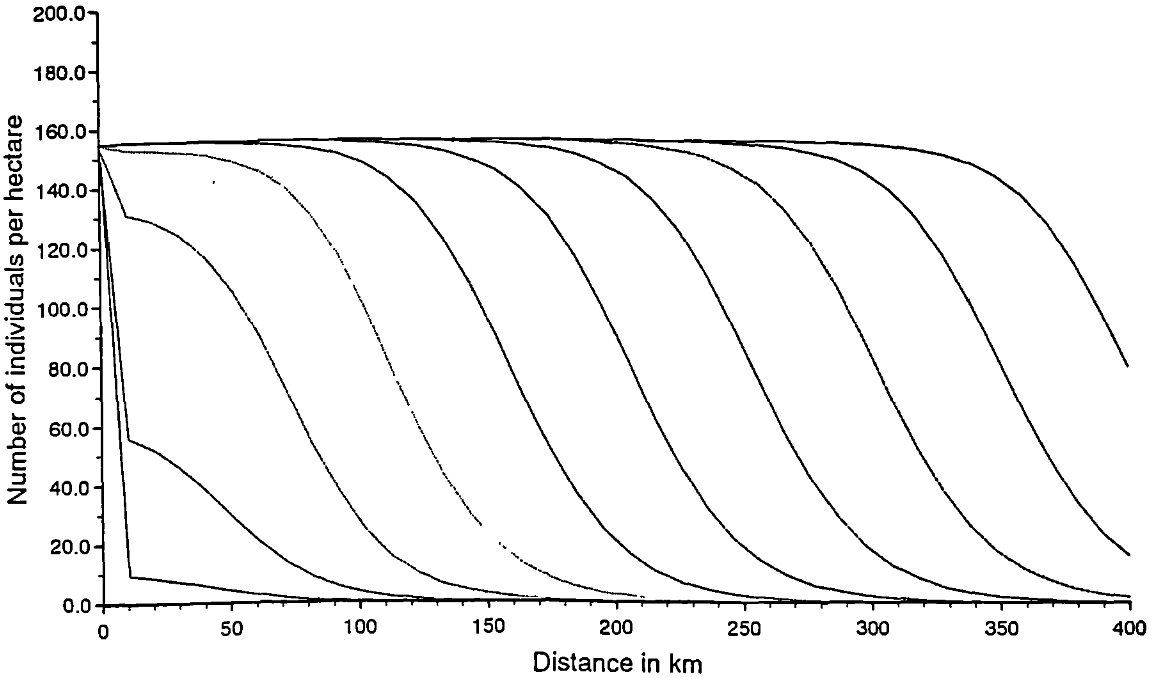
B29. Migration rate ≈ 0.19 km yr^{-1}, $\alpha \approx 0.01$. Population increase was observed at 300, 310, 320, 330 and 340 km.

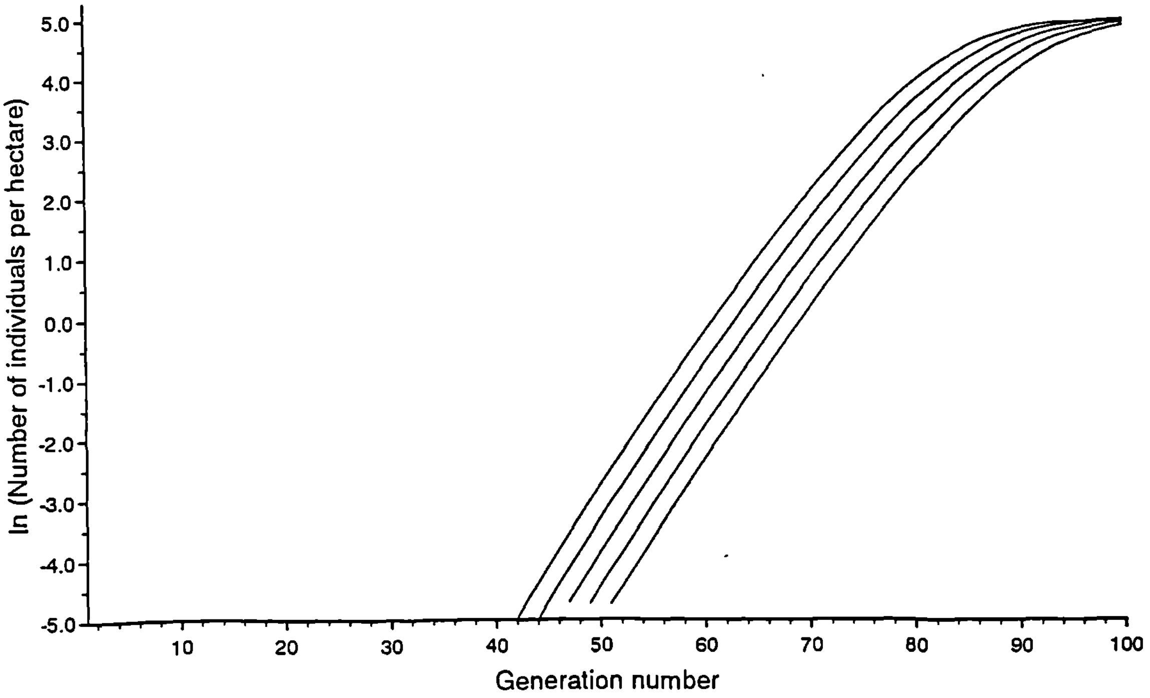
L = 10.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000020, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 75.00 km; P(RMSD2) = 0.060000;
Dispersal sums = 0.9900, 0.0600; Total = 1.0500; Furthest Cell = 40;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 100



B30. Migration rate ≈ 0.28 km yr^{-1}, α ≈ 0.01. Population increase was observed at 300, 310, 320, 330 and 340 km.

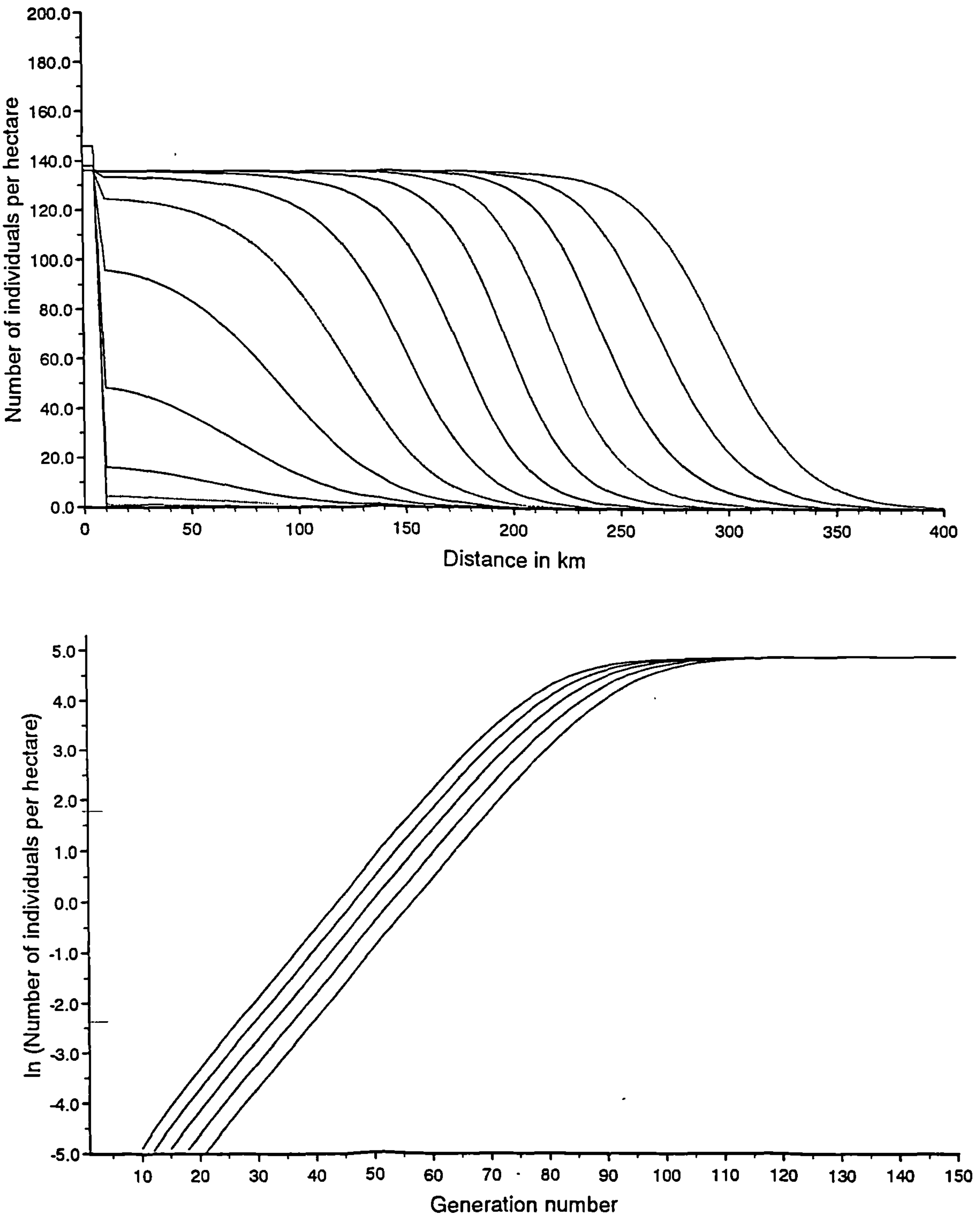
L = 10.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000020, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 50.00 km; P(RMSD2) = 0.060000;
Dispersal sums = 0.9900, 0.0600; Total = 1.0500; Furthest Cell = 25;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 100





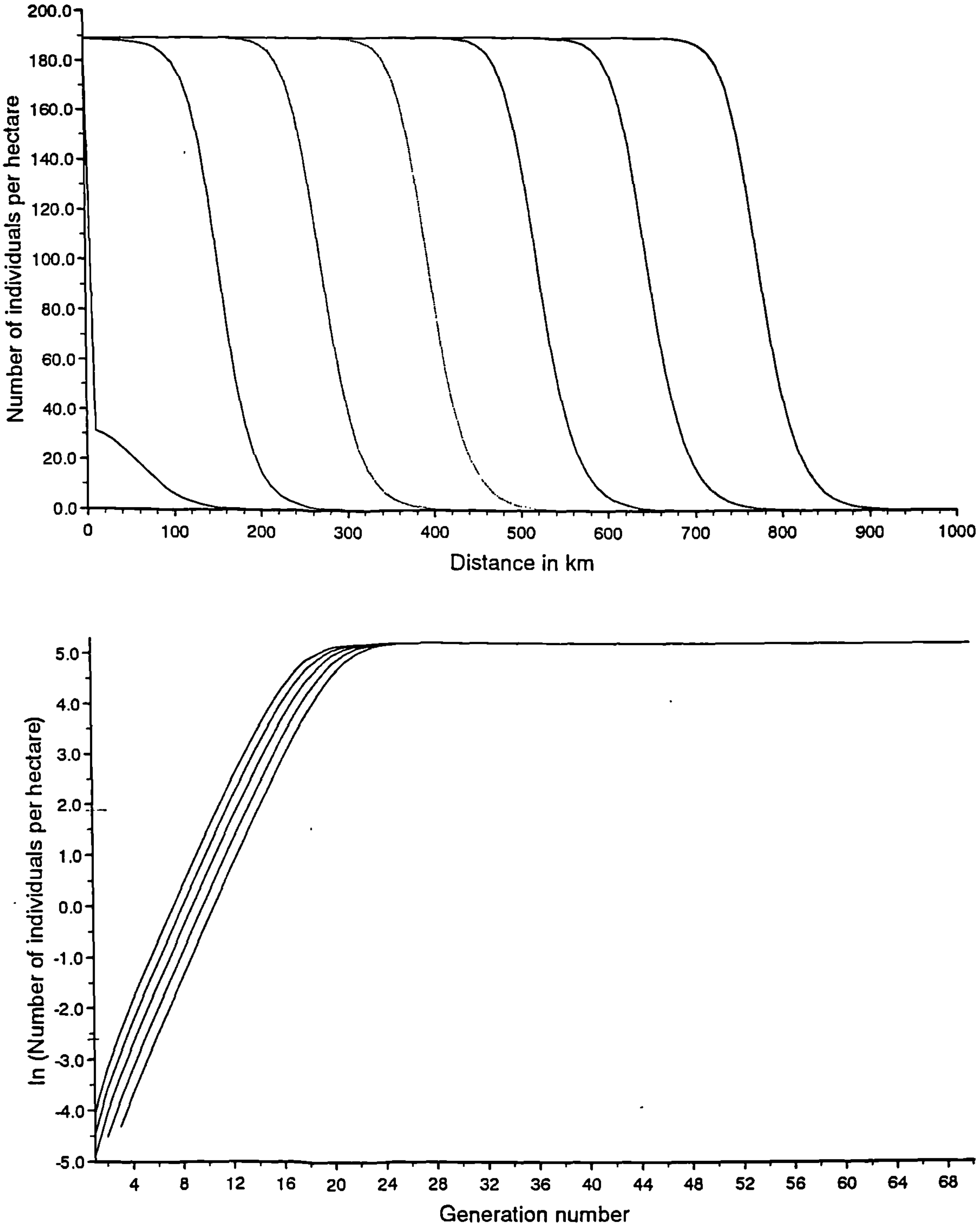
B31. Migration rate ≈ 0.19 km yr^{-1}, α ≈ 0.01. Population increase was observed at 300, 310, 320, 330 and 340 km.

L = 5.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000015, 0.91300;
S = 83200.0, 160000.0;
All offspring placed in parent cell; P(1) = 0.999000; RMSD2 = 75.00 km; P(RMSD2) = 0.001000;
Dispersal sums = 0.9990, 0.0010; Total = 1.0000; Furthest Cell = 75;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 150



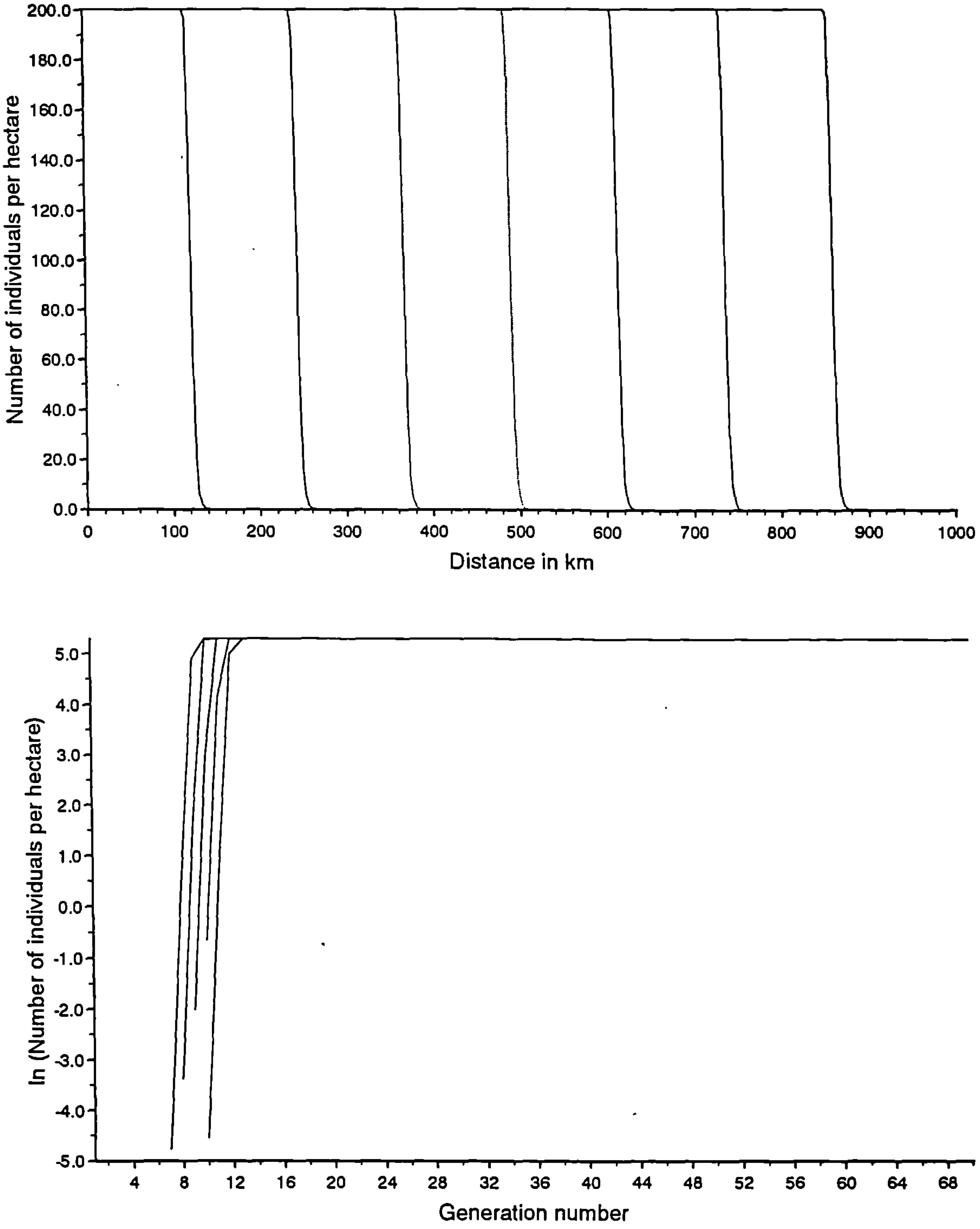
B32. Migration rate ≈ 0.10 km yr^{-1}, α ≈ 0.005. Population increase was observed at 300, 310, 320, 330 and 340 km.

L = 10.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0000060, 0.91300;
ς = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 75.00 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 30;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 70



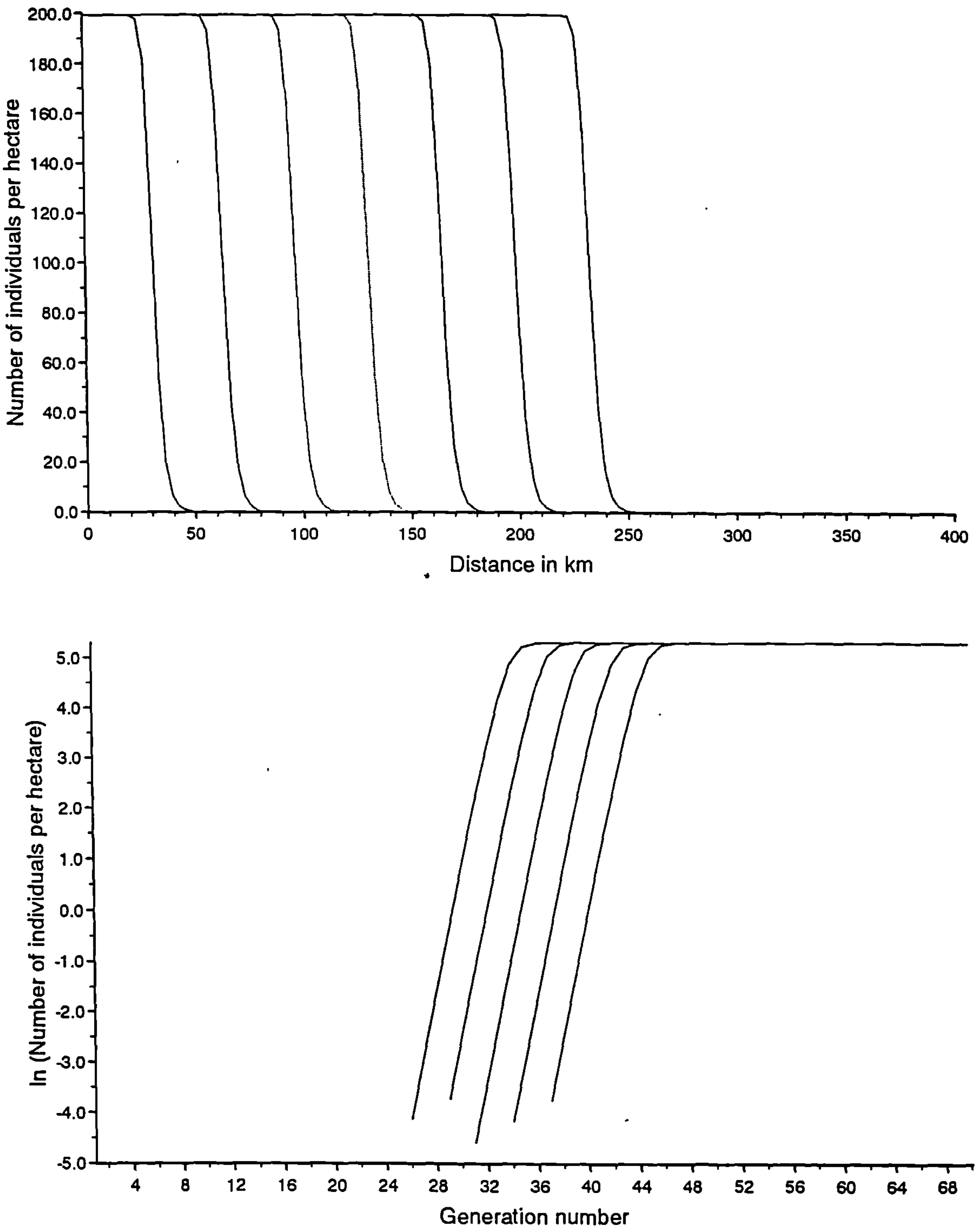
B33. Migration rate ≈ 0.50 km yr^{-1}, α = 0.02.

L = 3.00 km; a = 50.00 m^2; T = 25.00 years;
Survival probabilities = 0.0015000, 0.91300;
S = 8.320e+04, 1.600e+05;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 9.70 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 16;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 70



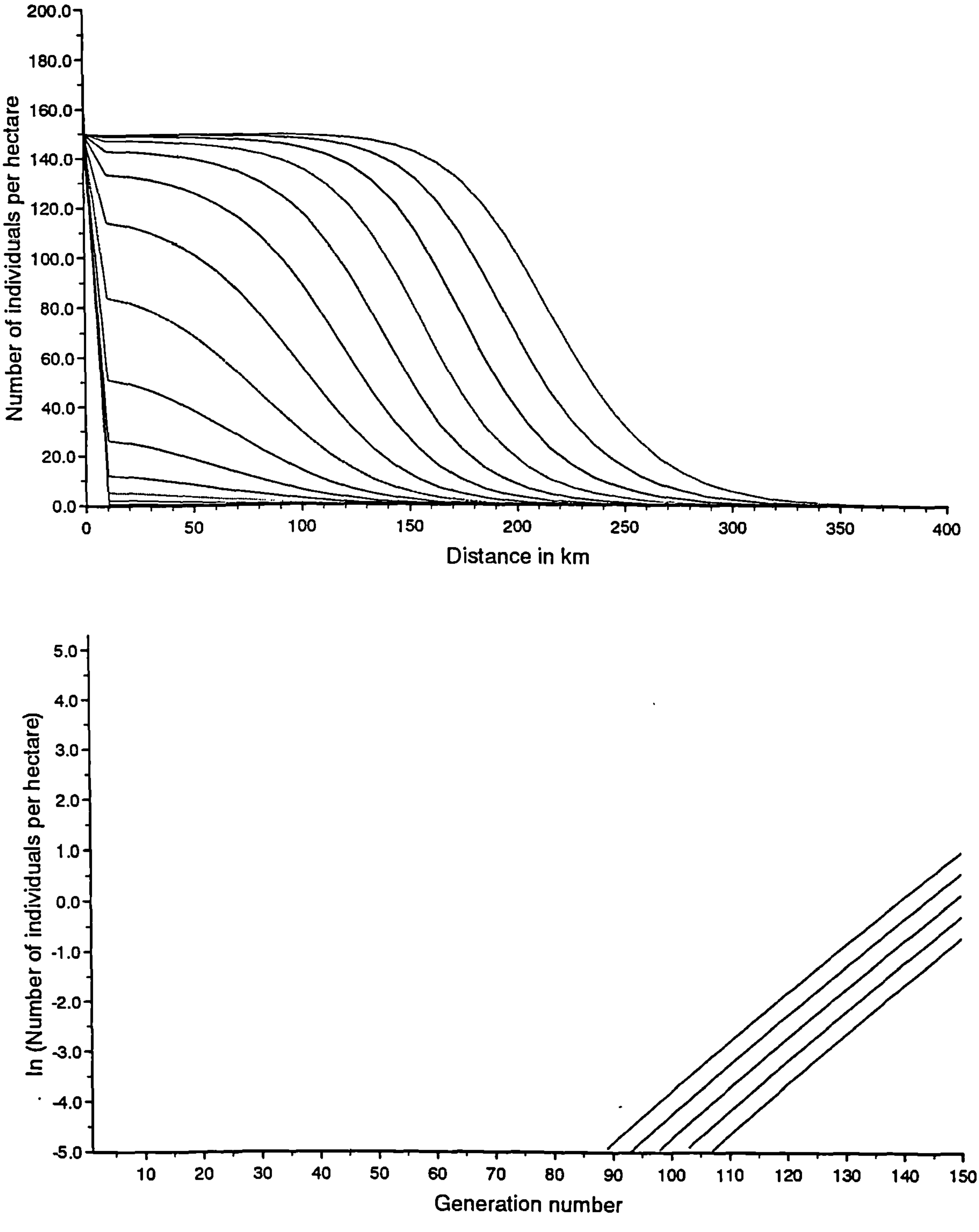
B34. Migration rate ≈ 0.49 km yr^{-1}, α ≈ 0.20.

L = 3.00 km; a = 50.00 m^2; T = 10.00 years;
Survival probabilities = 0.0000500, 0.91300;
ς = 3.520e+04, 6.400e+04;
All offspring placed in parent cell; P(1) = 0.990000; RMSD2 = 8.70 km; P(RMSD2) = 0.010000;
Dispersal sums = 0.9900, 0.0100; Total = 1.0000; Furthest Cell = 30;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 70



B35. Migration rate ≈ 0.34 km yr^{-1}, α ≈ 0.12.

L = 10.00 km; a = 50.00 m^2; T = 10.00 years;
Survival probabilities = 0.0000020, 0.96600;
S = 3.520e+04, 6.400e+04;
RMSD1 = 75.00 km; P(RMSD1) = 0.010000; All offspring placed in parent cell; P(2) = 0.990000;
Dispersal sums = 0.0100, 0.9900; Total = 1.0000; Furthest Cell = 30;
K = 1.00; No rounding in this simulation; No climatic restraints;
Output interval = 10 generations; Last generation = 150



B36. Migration rate ≈ 0.21 km yr^{-1}, α ≈ 0.01.Population increase was observed at 300, 310, 320, 330 and 340 km.