Modelling the spread of an invasive woody taxon: Rhododendron ponticum L.

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Modelling the spread of an invasive woody taxon: *Rhododendron ponticum* L.

by

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ABSTRACT.

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Simulation of the present-day distribution and abundance of rial*Rhododendron ponticum* L. at the Glen Etive study site in the Western Highlands of Scotland was achieved using a simple deterministic model (MIGRATE). The model utilises the demographic and dispersal parameters characteristic to a species and a knowledge of the environmental history of the area through which it spreads to simulate patterns of spread.

Biotic parameter values were derived from simple field measures and from data in the literature. "Habitat maps" were constructed on the basis of observations made in the field as to the likely relationships of *Rhododendron* to biotic and abiotic features of the habitat. Habitat features and their attributes were digitised and recorded in an ARC/INFO Geographical Information System (GIS). The simulation of changes in habitat through time was attempted using different habitat maps composed of cells containing unique values for relative carrying capacities, which were representative of the state of the habitat at a certain time. These habitat maps could only influence the dynamics of spread at the intervals between generations. Implementation of habitat changes was dependent on the cohort structure of the model which limited the resolution and exact order of changes that could be taken into account.

Model simulations were tested for accuracy against the present-day distribution and abundance of the invading population as mapped in the field, and as seen in aerial photographs from 1946.

"Null" simulations showed that environmental factors were important determinants of the migration rate.

Having achieved accurate simulation of a past and present distribution at a fine spatial scale from two initial foci of introduction in 1910, predictions were made as to the likely pattern of future spread. Predictions for the future were then made considering the effects of control regimes.

The importance of the implications of the pattern of spread to migration research and to conservationists, considering the ecological impacts of *Rhododendron* observed at the study site are discussed in relation to previous findings. More specifically the importance of the long-distance dispersal function to the invasion process is highlighted, and it is suggested that evolution should favour strategies resulting in long-distance dispersal. The reason for large seed crops is discussed in this light.

This project represents an integration of field techniques, biotic data available from the literature, a deterministic model, a GIS and aerial photography.

LIST OF ABBREVIATIONS.

mm	millimetre
cm	centimetre
m	metre
km	kilometre
ha	hectare
GIS	Geographical Information System
SSSI	Site of Special Scientific Interest
OS	Ordinance Survey
°C	degrees Celsius
NVC	National Vegetation Classification
yr	year

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In looking at nature, it is most necessary to keep the foregoing considerations in mind, never to forget that every single organic being may be said to be striving to the utmost to increase in number, that each lives by a struggle at some period of its life, that heavy destruction inevitably falls either on the young or the old, during each generation or at recurrent intervals. Lighten any check, mitigate the destruction ever so little and the number of the species will almost simultaneously increase to any amount.

Darwin, The Origin of Species.

Chapter 1: INTRODUCTION.

1.1 Introduction.

The introduction examines the various reasons for the rise in importance of the migration response of organisms in ecology, and the relationship of migration to dispersal and disturbance. The importance of dispersal to migration is emphasised later, with a summary of the findings reported in the literature on the characteristics of plant dispersal as measured in the field, and the findings of previous attempts that have been made to model this phenomenon. This leads on to the biological attributes of the species to be modelled that are reported in the literature, and the distinctive features of the habitats through which it is spreading.

Disturbance theory was a major direction in invasion research, which tended to examine the invasion process in relation to properties of ecosystems. The "new" approach (as developed by Hengeveld and others) emphasises modelling the invasion process "proper" without a necessary understanding for its causes, relying on measures of the organism's demographic and dispersal traits for prediction. These models are thus only predictive in a limited sense. Also the large spatial scales at which they work limits their applicability to real world management problems.

Ideas on the value of modelling are also introduced, before leading into a description of the model used in this project.

The principal aim of the current project is to assess the feasibility of modelling the migration rate of a sessile organism in relation to environmental change. The organism chosen in this case is the woody shrub *Rhododendron ponticum* L. The model used is a two-dimensional modification of the MIGRATE program developed by Collingham, Hill and Huntley (submitted). It is deterministic and works at the level of the individual to produce population scale effects. Using the organism's attributes and a knowledge of the environmental history of the area through which it spreads, simulation is attempted at a fine spatial scale. The model incorporates equations directly relating to the life-cycle characteristics of an individual and its characteristic dispersal patterns. These parameters are quantified, according to certain assumptions, from the analysis of measures taken in the field or from the literature. The processes involved in these preliminary stages of the project are given in the methods section.

The overall plan for the present study is composed of subsidiary aspects which represent original ideas in modelling research. Firstly, an attempt is made to incorporate interaction between the organism and its habitat. This is achieved through the structure of the model which utilises a grid whose cells contain unique limits to carrying capacity. The relative carrying capacities of the grid cells are assumed to depend on the quality of the habitat, assessed from the ecological relationships of the organism to this habitat type determined in the field, and according to the maximum dimensions of the organism possible. This represents an attempt to incorporate the spatial structure of the habitat into the model (Dwyer, 1992; Tilman, 1994; Holmes, Lewis, Banks and Veit, 1994; Goldwasser, Cook and Silverman, 1994) and, in a more applied way, the physical characteristics of the site in relation to the invader (Swincer, 1986).

Secondly, the project aims to incorporate habitat changes through time thus adding a temporal dimension to the model, through the use of "habitat maps". Knowledge of environmental history is essential for the production of habitat maps and can be obtained from current and historical maps and aerial photographs of the study site. This information is captured on a Geographical Information System (GIS) initially, and then using conversion programs, as outlined in the methods section, this spatial and attribute data is utilised by the model.

Environmental history is essential to the modelling process in providing not only the date of initial introduction but also, through the use of aerial photography, an idea of the past distributions of the organism concerned. Using past and present distributions, the accuracy of model prediction can be assessed and "tuned" before prediction of the future is attempted.

Thirdly, the project examines the possibility of prediction at small spatial scales, which is important to the fourth aspect of this project which aims to use this fine resolution modelling of species/habitat interactions, and apply it to management problems associated with invasive species and to suggest possible management scenarios to reduce rates of spread.

The applied nature of this project to a particular invasive species introduced into a particular geographical area is also examined in terms of the ecological relationships of *Rhododendron ponticum* to other members of the invaded communities (Orians, 1986), and to the physical attributes of particular habitat types (Luken and Mattimiro, 1991). The potential effects of *Rhododendron ponticum* on the flora and fauna of the area are of great interest to conservation bodies (Usher, 1986; Usher, 1988) and so this lesser aspect of the project is discussed.

The discussion also considers the findings of the model in relation to the original aims as set out above, and in relation to previous work. Especially with regard to invasion and climate change research and the links between the two, suggesting new avenues for research and possible extensions to the model.

Therefore, the generalities of this project represent an attempt to fulfil the ambitions set out by Levin (1985). The specifics represent an attempt to answer the challenges of Thomson, Radford, Norris and Good (1993), who, using aerial photography and ground surveys to gather information on the past and present distributions of *Rhododendron ponticum* in the Snowdonia National Park, assessed the extent of spread in relation to differing habitat types. Their study concluded that the spread was predictable and therefore potentially controllable and by using modelling and GIS techniques strategies could be planned. The current project investigates this avenue of applied research, as well as tackling the more central problem of the possibility of modelling a species response to environmental changes from a knowledge of biological attributes and environmental history.

1.2 Review of studies on migration, from Quaternary time scales to present day succession and invasion research with its use of models.

1.2.1 Background to the rise of the migration theory of species response in ecology.

The study of dispersal in biological systems has a varied background, from the preliminary analytical studies of Skellam (1951), based on diffusion equations, to the models of island biodiversity developed by MacArthur and Wilson (1967). Models of dispersal have graced many different sub-disciplines in biology including palaeoecology, biogeography, conservation biology, epidemiology and ecology. There is much overlap in these fields in the natural and theoretical sense, although the uses to which different or even the same theoretical models have been put definitely has a disciplinarian character.

Conservation biology is an emerging discipline which has utilised the ideas from genetics, ecology and epidemiology which have practical value. Concerns over species conservation in relation to habitat fragmentation have led to an upsurge in the number of models of metapopulation ("a population of populations", Hanski and Gilpin, 1991) dynamics. For example, the metapopulation structure of endangered butterfly species has been modelled (Hanski and Thomas, 1994) in terms of the dynamics of patch occupancy in heterogeneous habitats through space and time. In the interests of conservation the invasion of deleterious alien species has also been modelled, although these studies do not consider the specifics of patch occupancy and availability (Hengeveld 1989; Hengeveld, 1994). May (1994) suggested an analogy between the findings of epidemiology on host utilisation by diseases, and the dynamics of patch occupancy by an endangered species. The stability of these relationships, put simply, depends on the frequency of creation, the duration and magnitude of "suitable" patches and the life history traits of the species in question, as well as the incidence of stochastic events. He proffered that advances made in the mathematics of this discipline could perhaps be transferred to the field of conservation. The focus of these studies may seem qualitatively different but in reality it is simply a question of the spatial scale of study, and the differences are quantitative.

Palaeoecology has studied the past migrations of animal and plant species and applied them to the compositional patterns of present day communities (Davis, 1967; Davis, 1994). These ideas have largely been subsumed within the field of dynamic biogeography, which also uses a knowledge of the shifting patterns of geography, both human and geological, and a knowledge of the autecological characteristics of the species in question to explain patterns of diversity.

Many ecologists are now becoming involved in the field of dynamic biogeography which includes zoogeographic and phytogeographic elements (Hengeveld, 1989). The reason for the rise of the dynamic perspective in ecology is because the static structured concept of communities could not explain patterns of change observed in the past, and was thus not seen as a valid and central way to represent species responses to an environment where change was the rule (Huntley and Webb 1989; Pease, Lande and Bull, 1989).

Migration represents a subset of the dynamic responses available to organisms to respond to the norm of environmental change. The nature of the realised response and its rapidity will depend not only upon the type of environmental change, i.e. its intensity, rapidity, spatial and temporal extent, but also upon the possible effects of anthropogenic factors, topographic diversity, edaphic conditions, life-cycle characteristics (i.e. the autecology of the organism concerned) and hysteresis (which is the influence the past history of a community has on its subsequent response to a given changed condition) (Ritchie, 1986). The scale of the study obviously determines the extent to which these other factors have to be taken into account (e.g., Prentice, Sykes and Cramer, 1991), a principle first pointed out by Good (1931).

Change occurs on all scales, and thus organisms have had to evolve life strategies to cope with these different scales of change as optimally as possible considering the unpredictability inherent in many disturbance regimes and considering other constraints imposed by the life history requirements of the organism. Prentice *et al.* (1992) point out that ecological processes are more likely to be major determinants of vegetation composition on the shorter temporal scale of centuries. Prevailing climatic conditions still hold primacy though and variations in the climate of the biosphere, in both time and space, are the principal source of variability in the environment of plants (Bartlein, 1988). The Quaternary record demonstrates unequivocally that plants respond to climatic change as individual taxa through migration, with entire biome types forming, dissolving, and re-forming within a single Milankovitch cycle, with some having no analogs at the present day (Huntley and Webb, 1989). As spatial and temporal frames of observation are diminished and resolution increased, biotic processes must eventually come to dominate (Prentice *et al.*, 1992). At sufficiently fine scales the main observable phenomena are successional responses to natural disturbance events (Davis, 1984; Prentice, 1986; Rull, 1992).

The migration response to environmental changes, and especially climate change, has come to the forefront of ecology in recent times mainly due to the recognition of past and future possibilities of change in the global environment. These two subjects have been linked mainly through palaeoecological research which has recognised the movements of species boundaries and thus changes in the distributions of the Earth's biota through time in relation to environmental dynamics. To a lesser extent the importance of migration, as realised in invasion rates, has been recognised by conservation bodies and ecologists working in all regions of the world, although especially on islands such as

Hawaii. The relations of invasions to past and present human activities are well recognised (Elton, 1958; Hengeveld, 1989), and so the prediction of migration being the response to larger scale, anthropogenically forced, climatic changes is not new.

The daunting prospect of climatic warming has led to research into the possible species responses in an increasingly human dominated and urbanised landscape. The findings of palaeoecology with its longer time scales and examples of past environmental changes of differing magnitudes have thus taken on greater significance. With a recognition that a certain level of understanding of the present requires a certain relevant span of historical knowledge, the evidence points to migration as opposed to evolution as being the principal form of dynamism open to species (Pease, Lande and Bull, 1989; Cronin and Schneider, 1990; Bradshaw and McNeilly, 1991; Huntley, 1991). This being the observed response of species on the time scales of glacial and interglacial cycles (Huntley and Birks 1983; Birks 1989), with migration rates for tree species in the order of 100-1000 m yr^{-1} probably representing the maximum obtainable (Huntley and Birks, 1983; Birks, 1989; Huntley and Webb 1989; Huntley, 1989; Huntley, 1991).

Migration is the response of taxa to climate change seen at the large temporal scales of the Quaternary, but migration is also an observable phenomenon at ecological time-scales. Here migration is represented by seasonal movements of mobile organisms, by successional advances into newly altered habitats or by other movements at different spatial scales into previously unoccupied habitats, either due to deliberate or unconscious introductions of anthropogenic origin, or due to natural colonisation events. These movements of organisms do not need to invoke climatic changes as necessary explanations for the migrations observed.

Therefore this project need not be concerned with modelling migration rates in relation to climatic changes. Rather, it assumes a constant climatic regime and attempts to simulate the spread of an exotic taxon introduced to a new geographical area by considering its biotic interactions with other types of disturbance event. Thus this project is more concerned with the dynamics of biological invasions, and the possibility for modelling such processes - with a hope to elucidating the possible reasons for this ecological phenomenon - than with the prediction of a species' response to probable climate change scenarios. Following the ideas of Prentice *et al* (1992), the time scale and probable direction of predicted climatic changes are outside the temporal resolution of this project and so are not considered, although this is not to say that the findings of this project will not have applicability to this field of research.

Basically, migration does not have to be the result of a climatic change, climate change only becomes an important factor to consider over longer time scales, although this may not be so in the future.

Considering the number of areas of research in which migration theory is applicable, and the applied nature and importance of these areas, the need to develop quantitative methods for the description ~~andtion~~ and prediction of population movements is of surpassing importance (Levin, 1985).

1.2.2 The relationship of migration to dispersal.

Migration is due in part to dispersal, but not all dispersal results in migration. They are different processes. Some dispersed "propagules" may fail or the environment may be completely inhospitable to the establishment of the species resulting in a static population range, i.e. with no migration. If this situation remains and if there is also no establishment within the colonised patch then the population may decline to extinction. This will also be the case if the colonised patch is too small to sustain a viable population in terms of the actual population size in relation to random extinction events and demographic stochasticity, as well as to the degenerate genetic effects of small population size (the 'extinction vortex' of Caughley, 1994). The patch size of suitable habitat remaining for a population can also determine the persistence of the population because of its effect on the balance between dispersal and population growth. The perimeter of small patches is relatively longer than that of larger patches, causing dispersal out of such patches into unsuitable habitat to overwhelm population growth (Pease, Lande and Bull, 1989).

Migration is not only important in propagating individuals through suitable unused habitats or for infilling the gaps within present habitats, but is also important in allowing for the *escape* of an individual or its genes in space and time (Southwood, 1978). The migratory movements of birds or large ungulates across the African plains represents not only a desire for better resources but also an escape response to the decay in resource quality and/or quantity in a previously utilised environment. It can be seen that dispersal in this sense could change the range distribution of an animal and that dispersal need not necessarily be linked to abundance. By contrast, the dispersal of propagules or young away from highly competitive environments allows for the establishment of populations elsewhere and thus for changes in abundance. The term migration is used in this project to denote any adjustments in the range limits of a taxon over a geographical area, these migrations having different spatial and temporal components. For example, the movements of many bird populations, covering thousands of miles, have an annual cycle whereas the migratory movements of trees are of a much smaller spatial extent, in a year, but have cycles with a periodicity of thousands of years (Sauer, 1988; Huntley and Webb, 1989).

Dispersal and establishment, or persistence in the case of individual animals, results in migration through space and time and thus is of fundamental importance to the dynamics of species ranges. Dispersal aids species survival in a dynamic environment if the bounded environmental tolerances of individuals is accepted. Therefore there will be strong selection pressures for effective patterns of dispersal (Augspurger and Kitajima, 1992), and, as Levin and Real (1991) note, "...the selection regime for dispersal is shaped by, and in turn shapes, the scale of environmental variation facing the species."

1.2.3 The association of migration with disturbance.

The idea of a patchy mosaic of habitats in a landscape with bounded continuums of quality for the organism concerned can be traced back to the ideas of Watts (1947). Use of the term "patch" is somewhat synonymous with use of the term "gap", although there seems to be a preference for using the term gap in plant literature only. This is probably because animal interactions with the habitat mainly deal with larger scale features of the landscape, due to behavioural attributes of animals such as locomotion and territories, whereas plant dynamics generally deal with near continuous cover and the utilisation of smaller scale features (an idea focused by the influential findings of Grubb, 1977). Basically, the term patch is used to denote a larger scale gap or a state of habitat, both being terms of suitability, although "gap" usually represents a portion of bare ground (Bergelson, Newman and Floresroux, 1993). Both concepts are somewhat circular in their reasoning in that a suitable patch or gap is only recognised as such, when it becomes occupied, and we cannot know if an apparently suitable patch *is* suitable until after the event. This problem is more associated with the term "niche", which is obviously closely related to these two terms. This problem should not detract from the theoretical value of these concepts, though, which form a useful framework for modelling the natural landscape if not for visualising its complexities.

Patches (on all scales) are the result of disturbance. We can say this because the term "disturbance" covers a wide range of 'environmental changes' such that it has become virtually synonymous with this term. Environmental changes occur at all scales depending on the "perception" of the organism, and so, therefore, do disturbances. Thus disturbance can range from wildfire to leaf abscission or from global warming to the pollution of a stream. Disturbance occurs continuously in a community, it is just that those of a larger spatial scale occur at a lesser frequency. This relationship is not necessarily proportional and can sometimes be reversed as Hengeveld (1990) points out in criticism of the nested hierarchy theory of Delcourt, Delcourt and Webb (1983). Disturbance regimes allow for and cause migrations, whether this be a local fire resulting in a succession being set in motion, or climatic forcing causing changes in the pattern of the Earth's biomes.

Disturbance is claimed as a key element in the invasion process (Kornberg and Williamson, 1986). It is thought to allow for recruitment (Grubb, 1977; Grime, 1979) and to mediate competitive interactions by producing spatial heterogeneity (Skellam, 1951; Crawley and May, 1987).

1.2.4 Invasion research.

Bazzaz (1986), defines an invader as a species that enters relatively intact and undisturbed vegetation and is able to strongly dominate or even displace it altogether. This definition distinguishes invaders from colonisers, which enter unoccupied or sparsely occupied sites and may initiate successions, and immigrants, which become integrated into communities without displacing or markedly depressing the resident populations (Bazzaz, 1986). These definitions, like many others, suggest that a species can act in only one way depending on its biological attributes, whereas, it is more likely that a species could take on all of these roles.

The initial work on biological invasions addressed three main questions, namely:

1. What are the factors determining whether a species will become an invader or not ?;
2. What are the site properties which determine whether an ecological system will be relatively prone or resistant to invasion ?; and
3. How should management systems be developed to best advantage, given the knowledge gained by attempting to answer the first two questions ?

These questions have been taken up by the Scientific Committee on Problems of the Environment (SCOPE) program (Williamson, Kornberg, Holdgate, Gray and Conway, 1986).

Predicting the possibility of an organism becoming an invader will often involve physiological or genetic work when either habitat conditions are altered, or when the species itself is changing (Hengeveld, 1994). Also it involves characterising the dispersal ability of the organism in question and relating this to the geographical location of the nearest suitable habitat. This aspect of invasion was central to the ideas of island biodiversity pioneered by MacArthur and Wilson (1967) and has been much studied since. The dispersal distances of species are important characteristics to define, although the stochastic influences on the dispersal process make it very difficult if not impossible to quantify. This is especially so for the long-distance events which may only occur very rarely, and yet are often of greatest interest as they can determine the actual rate of invasion (Hengeveld, 1989). Thus dispersal is usually thought of as being composed of two co-occurring processes, including deterministic, neighbourhood diffusion events and stochastic, long-distance dispersal events (Hengeveld, 1989). The importance of these two types of dispersal event to the past patterns of interglacial plant migrations have been debated. One school of thought suggests that the rates of spread derived from the palynological record are due to the expansion of low-density populations and individuals scattered across the landscape. Bennett (1986) claims that these low densities of trees beyond the margins of the main populations would not show up in the pollen record and under climatic amelioration tree populations increased, with doubling times of 100 years. This suggests that the high values given for the annual migration of tree species, considering their maturation times, may be unnecessary. Woods and Davis (1989) suggest two models for patterns of tree migration seen in the palynological record, which represent a sub-division of Hengeveld's (1989) dispersal process. Firstly, the outlier model which suggests that populations spread by the formation of small outlying populations with gradual infilling, and, secondly, the continuous front model which predicts that migration occurs as a more or less continuous front.

The questions posed by the SCOPE program are relatively narrow compared to the number of angles from which the problem of biological invasions can be approached. The program was more concerned with the biological interactions (Mollison's 'epidemic' and 'endemic' aspects of invasion, 1986) taking place between the invader and other members of the biotic community than with the actual pattern of the invasion process. As Mooney and Drake (1986) noted, the information required for predicting invasion success will include species properties, interspecific interactions, and properties of the system being invaded. These priorities in the study of biological invasions are of a more applied nature than the list of topics which Hengeveld (1994) addresses as being of interest in the study of biological invasions.

In a sense the SCOPE program was more concerned with dynamic interactions between the species and its new biotic and abiotic environment. It approached invasion at the level of the ecosystem (Vitousek, 1986; Vitousek, 1990) and there was little work carried out on modelling and prediction from individual species characteristics. It was Mollison (1986) who pushed the ideas of modelling forward in invasion research, and these ideas were developed by the likes of Hengeveld.

The work of Hengeveld, (1994) and that of others (Van den Bosch, Metz and Diekmann, 1990; Van den Bosch, Hengeveld and Metz, 1992) has moved away from the research areas outlined in the SCOPE program to concentrate specifically on species properties and the mathematical integration of these properties into models simulating the rate of spread of biological invasions.

Outside of predicting which species will become invaders and which will not, Hengeveld (1994) investigates the way the invasion progresses through space and time (the rate of invasion), and the local build-up of the newly settled population. He considers these three aspects to be part of the invasion process proper and the mathematical approach to these areas assumes a species has already become an invader and that it is adapted to its new abiotic and biotic conditions. This approach provides a null model for evaluating the impact of changes in abiotic conditions, or the impact of biotic conditions (Hengeveld, 1994), just as this project could for predictions concerning global warming.

Of more relevance to categories one and two of the SCOPE program are studies on either the adaptation or pre-adaptation of the invader itself to its new living conditions, or that of the native species to the potential or new invader, involving genetic, physiological and morphological investigations, and work at the level of the community. These are mentioned by Hengeveld (1994), but are not part of his model formulation. Identifying areas of potential invasion or species likely to invade is difficult to assess. For example, studies on invasion of marine habitats by *Elminius modestus* (a barnacle species) and *Biddulphia sinensis* (a diatom species) show that, even in relatively species poor habitats in which the species have been extensively studied, it is very difficult to recognise empty niches before the invasion event. Likewise, after the event a quantitative explanation of the important characteristics that allowed the invasion to occur cannot be given (Williamson and Brown, 1986).

Although the basic models of the new approach (e.g. Van den Bosch, Metz and Diekmann, 1990; Van den Bosch, Hengeveld and Metz, 1992) and the assumptions made, are the simplest possible, both the model and its translation into parameters are complex (Hengeveld, 1994).

The models described in these papers, as with the MIGRATE model (Collingham *et al.*, 1994), use two groups of parameters: those that describe the aspects of the life history relevant to population growth and those that concern dispersal (Hengeveld, 1994). Although the model of Hengeveld's can produce predicted rates of invasion for mobile organisms such as *Sturnus vulgaris* (starling), *Streptopelia decaocto* (collared dove), *Passer domesticus* (house sparrow), *Bu~~m~~buculus ibis* (cattle egret) and *Ondatara zibethicus* (muskrat) that are close approximations to those observed, the model has not been tested on sessile organisms, or in an applied way, such as in the uses outlined in proposal 3 of the SCOPE program.

In summary, the approach of Hengeveld and others has been to coalesce the secondary and tertiary stages of the invasion process - quoted by Mollison (1986) to include arrival, establishment, spread and persistence - into equations representing the invasion process "proper". The models are tested at the population scale of invasion at national spatial scales. This is the scale to which the stages given by Mollison (1986) refer. These successive stages, though, can also be recognised as being applicable to every individual of an invading population, and thus modelling could be achieved by a recognition of the interaction of every individual with the dynamic environment. The idea of the current project is to use the reproductive, growth and dispersal attributes of a species, as determined from the field, and a knowledge of the heterogeneity of the environment through which it spreads to predict the stages of invasion as outlined by Mollison (1986). These stages being applicable to every propagule dispersed from the initial parent or parents.

The invasion models of Van den Bosch *et al.* (1990) and Van den Bosch *et al.* (1992) are summarised in Hengeveld (1994). These models are known as one-dimensional and are appropriate when considering the migration of a population front via small steps, through a homogeneous environment (Collingham *et al.*, submitted). The one-dimensional version of MIGRATE gives almost identical results to the two-dimensional version, and is therefore to be preferred if the main object of interest is the rate of spread. In more applied situations, though, it is more appropriate not only to assess rate of spread but also the directions of spread through a habitat whose patterns of heterogeneity are changing through time. To simulate this interaction of the biotic attributes of an organism with a specific environmental set-up a two-dimensional model is needed.

As the resolution of a spatial scale is increased and the pattern of spread of an invasion front is examined in more detail, it will be found that the shape is very irregular. At such a scale it is no longer acceptable to average out differences in invasion rate in different parts of the habitat to give a measure of the circular expansion of the invasion front through space. These scales of resolution require recognition of the habitat types and a two-dimensional model, if prediction is to be of use.

1.2.5 Models as theoretical and simulation tools.

The theoretical constructs used to deal with data capture, retention, interplay and manipulation in ecology, as in many other disciplines have been models. The route taken to simulation of the present and prediction of the past and future depends on the developmental time-scale of the pattern to be studied, as this dictates the scope of the collection of information needed about the species and its environment. The degree of precision required for the environmental data will depend on the spatial scale of the pattern, the resolution of the temporal scale used to recreate the pattern and the structure of the model itself.

The comparison of theoretical frameworks in ecology, even at the verbal level, shows large differences in the scales at which they are working. All theory is modelling, and just as theory can be at the level of a single hypothesis, so can modelling. Theories are an aggregate picture formed and tuned from the accumulation of lines of evidence. Once a theory is formed a larger-scale test may be applied, but the theory will only be accepted if it simulates the real world occurrences. If it does not, then a new theory is formulated on the basis of the old evidence or research is conducted into newly suggested areas. Sometimes, and perhaps less scientifically the evidence may be reinterpreted in the light of the existing theory and the real world situation may be made to fit the theory. Experimental tests with controls are supposed to reduce the occurrence of the latter, although they are not the only way for progress in science, many experiments being suggested through theoretical reflection on a problem. Models, like theory thus have a role to play, and just as experiments lead to conclusions describing the pattern of a certain level of complexity in terms of patterns expressed at lower levels, so models simulate patterns, and "explain" them in terms of their component processes. One explanation is verbal, the other mathematical, the two often combining. The component parts of a whole do not necessarily have to be *explained* to predict behaviour over a larger scale, smaller patterns can simply be simulated and used to formulate the whole. Models typically describe processes at one level of organisation in terms of phenomenological models at a lower level (Prentice and Leemans, 1990).

Although ecological models have been the subject of much criticism (my own reservations included) on the subject of their realism, Levin (1981) points out that theory must be recognised as an activity closely tied to, but separate and independent in objectives from field observation and experimentation. Too literal interpretation of models, and rigid insistence on immediate congruence between theory and observation, have led to abuses and distortion of the role of theory.

There are two main aspects to modelling:

1. the classical view of modelling as an iterative process where model predictions are repeatedly tested against real world observations, with the model either being rejected or modified sufficiently that prediction converges upon observation; and

2. the inductive process of extrapolation from a limited study to derive generalisations about the world beyond.

Levin (1981) considers that it is in the second phase that the most serious abuses occur, and it is here that the most careful scrutiny is justified.

Models may in some instances be taken literally and used for prediction, but their more usual and more powerful role is metaphorical: as organisers of thought, as aids to explanation, and as guides to experimental design (Levin, 1981). This may all seem rather philosophical, but difficulties in the justification of scientific methods is not new. Models are particularly useful in circumstances where the effects of changes in the environment cannot be studied experimentally (Collingham *et al.*, submitted). For instance, in the prediction of consequences of an action that would otherwise be expensive, difficult or destructive and unethical to do with the real system. Also computer simulations of the dynamics of spread have benefits in focusing the observer onto the dynamics of the system simulated, such that areas of inaccuracy become apparent as the pattern unfolds. It gives an appreciation for the history of a pattern as well as its present-day state. For a more negative justification of the benefits of models, I suspect, that verbalised theories, if placed on a similar standing with models with all their assumptions and circularities laid out, would also be judged as unrealistic. I believe realism in modelling is a lesser philosophical problem than the circularity of the derivation of that realism, and just as this problem plagues many theories, so the line between refinement and circularity in modelling is not often clear.

1.2.6 Modelling the properties of seed dispersal.

Previous studies on the distribution of wind dispersed seeds about a parental plant or population have led to it being generally accepted that the deposition of seeds follows the form of a negative exponential. This relationship has been derived not only from field studies using seed traps (Boyer, 1958; Roe, 1967), but also from the analysis of established seedlings in transects leading from the hypothesised parent or parents (Johnson, 1988) and from the findings of experimental seed release (Augspurger and Franson, 1987). Although the dispersal curve is of a negative exponential form it is also right-skewed (Johnson, 1988; Augspurger and Franson; 1987).

Johnson (1988) found limitations to his method of estimating the shape of the dispersal curve in that the pattern of established individuals changed through time, as one might expect, due to density and distant dependent mortality. Thus this method may not produce a true reflection of the actual shape of the dispersal function, and, at best, it is only a qualitative representation of the actual seed dispersal function due to the effect of other factors on the viability, germination and establishment of the seeds (Cremer, 1977). Johnson (1988) acknowledges that the slope of the seed and seedling density curves will be similar only if the micro-environmental conditions for germination and survival and the spatial distribution of seed predators and secondary dispersal agents are reasonably uniform along the distance axis. Spatial variation in patterns of recruitment will also be affected by the distribution and abundance of parents and their differential fecundities (Ribbens, Silander and Pacala., in press).

The trajectory of dispersal of a single propagule can be expected to vary between sites according to the initial height of release, local meteorological conditions, the aerodynamic "topography" (both naturally and physically created) of the surface over which dispersal is occurring and the morphological and thus aerodynamic characteristics of the seed species involved (Greene and Johnson, 1989; Augspurger and Franson, 1987). For a whole crop of seeds from a single individual or population of an area, the dispersal function can be modelled by taking *additional* variables into account (Sharpe and Fields, 1982). These include variable terminal velocities between seeds, the timing of seed release (i.e. is it a discrete event in time or does it occur over an extended period depending on the maturation rate and also upon prevailing environmental conditions of humidity, temperature and wind speed), and the average wind speeds between the height of release and the ground. This final factor is not only important from the point of view of a seed falling through the air, but also from the point of view of the portion of the plant releasing the seed, there being vertical variation in initial height of release according to plant height and its cropping pattern.

1.3 Description of the study species, study site and model used.

The choice of the study species and study site for this project are inextricably linked to a large extent, in that both fulfilled certain requirements of the project. The main factor leading to the choice of this particular area, though, was the small spatial-scale of the spread observed at the present day. The spread was localised, being restricted to the valley floor of the glen, and so was amenable to survey by an individual during the fieldwork period. The small-scale also suggested that the environmental history of the area could be traced and might be accessible to investigation, one of the requirements of the modelling process being the ability to predict not only the final present day pattern but also the pattern as it unfolds. In this respect the Glen Etive site was again ideal in that the surrounding vegetation was mainly composed of grasslands and heaths with some scattered patches of deciduous woodland (the conifer plantations being of recent origin), and thus an evergreen shrub should be discernible from black and white aerial photographs. The initial survey of the site gave an idea of the probable points of introduction and the probable pattern of spread. In other areas containing *Rhododendron ponticum,* or other introduced species such as *Acer pseudoplatanus*, where establishment has been for a longer period or where growth is under a woodland canopy, it would be more difficult to assess past and present patterns of spread or to reconstruct past maps for habitat carrying capacities. Thus it was decided that there was the potential to model this species at this site.

1.3.1 The study species.

1.3.1.1 Taxonomy.

Rhododendron is a very large genus of shrubs, dwarf-shrubs and epiphytes within the family Ericaceae. There are over 600 species, concentrated mainly in south-east Asia, but with a few species in America, Asia Minor and Iberia.

The introduced British population contains a number of hybrids, and this might have some bearing on its invasive vigour. Characteristics of *Rhododendron maximum* and *Rhododendron catawbiense* have been noted in some areas whilst in others the typical ssp. *ponticum* or ssp. *baeticum* or hybrids between them are to be found. However, the British population is usually loosely referred to as *Rhododendron ponticum* (Tabbush and Williamson, 1987), which will mainly be referred to as "*Rhododendron*" from now on.

1.3.1.2 Introduction, establishment and current status of Rhododendron ponticum *in Britain.*

Rhododendron ponticum L. is an evergreen shrub with large pinkish purple blooms. The species is very variable in size and habit, being tall and spreading under a canopy and lower and more compact in more open situations (Cross, 1975). The first recorded introduction to Britain was in 1763 (Elton, 1958). Most plantings though have their origins in the 19th century, when they were used for visual effect on Victorian estates and for the grafting rootstock of less vigorous, more attractive species. With neglect of the plants and the estates, rootstocks developed shoots and flowers of their own, leading to population build-up and escape from these initial areas of introduction (Tabbush and Williamson, 1987). Such areas were manifold and well spread across the country thus leading to many different invasion foci, and perhaps to a broad genetic base in the population. It is still planted, without restriction, as an ornamental shrub and is widely used to provide low cover in shelter belts and game coverts. The present distribution of *Rhododendron ponticum* is shown in figure 1.3.

Rhododendron ponticum comes 15th in Crawley's (1987) list of the 20 most successful British aliens, and as one of only 19 alien species out of a total of 400 recorded invasions that has become widely established as a pest in this country (Williamson and Brown, 1986).

1.3.1.3 Natural distribution.

R. ponticum has a disjunct geographical distribution. One sub-species (*baeticum*) occurs in a small area of south-west Spain and central and south-west Portugal. The other (ssp. *ponticum*) occurs around the south and east coasts of the Black Sea in Bulgaria, Turkey, Caucasus and Lebanon. It rises to 1800-2000m on the eastern Black Sea coast, but is confined to lower altitudes farther west (Cross, 1975). The present day distribution suggests an affinity for coastal regions, perhaps for climatic reasons, but the palaeoecological remains found scattered through Europe and into Ireland suggest that it was formerly more widespread.

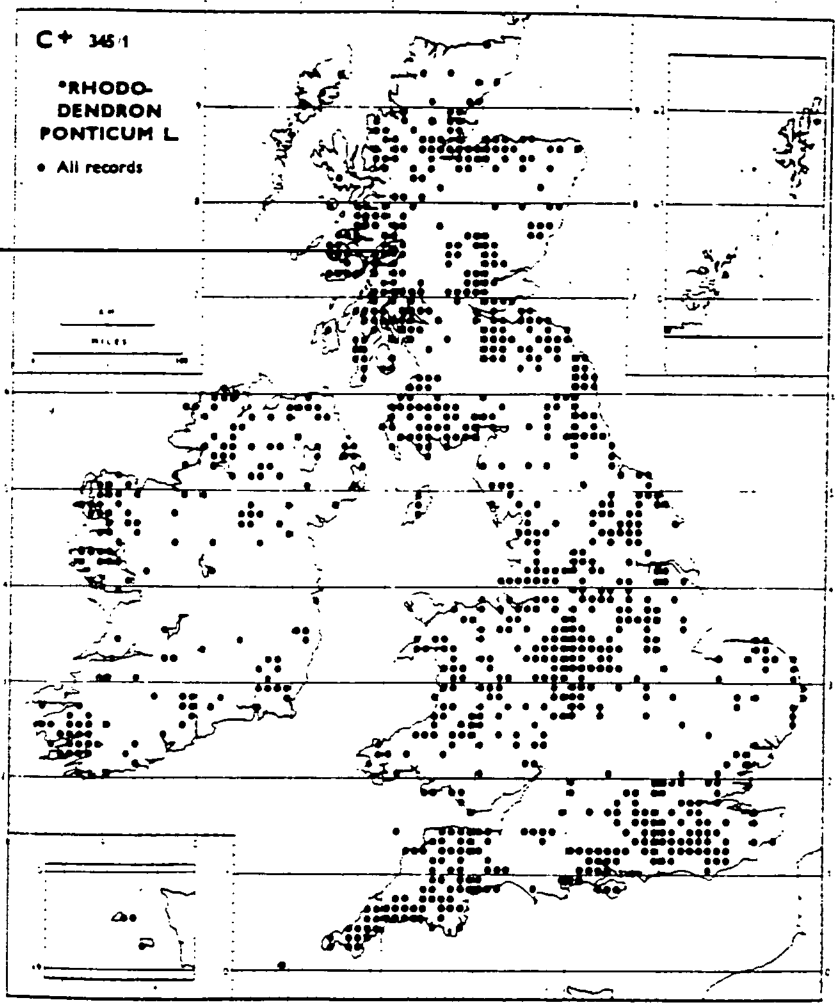
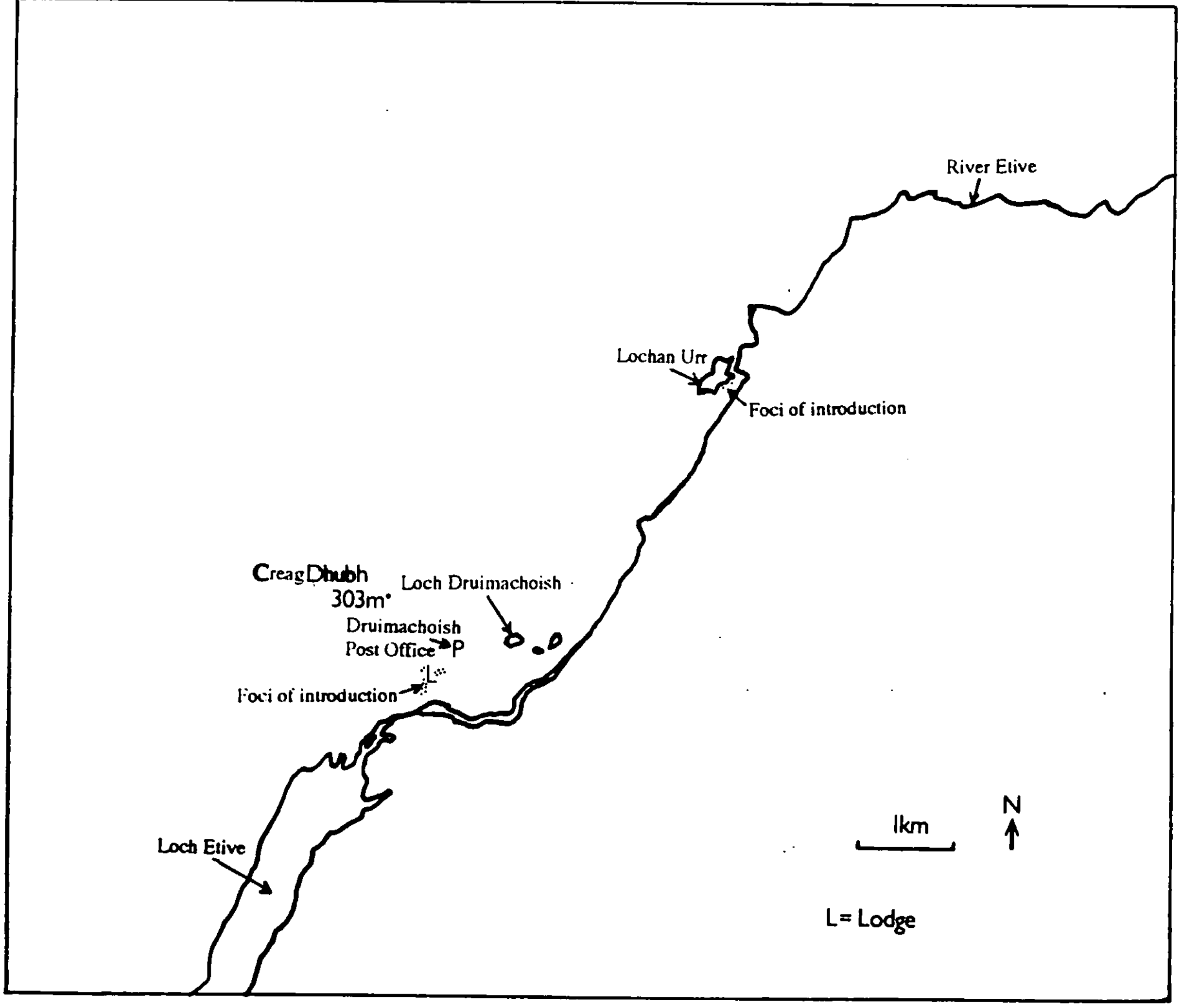


Figure 1.3 Map of Britain showing the distribution of *Rhododendron ponticum* L. in 1976 (Perring and Walters, 1990), and the geographical location of the study site in the Western Highlands region of Scotland. The exploded plan view shows the locations of the places mentioned in the text later.



Introduced into north-west Europe it is now also naturalised in Belgium and France. The British Isles represents one of its most northern locations and here it occurs from sea level to 370m in Derbyshire and to 530m on Torc Mountain, south-west Ireland (Cross, 1975).

1.3.1.4 Seed production and dispersal.

Flowering begins around the twelfth year and occurs annually (Cross, 1975). Each inflorescence produces about 5000 seeds which take the form of flattened discs and are similar in size to those of other ericaceous species at about 60µg each (Cross, 1975). The seeds are ripe by December and dispersed in February or March when the capsules open (Cross, 1975). The frill of short hairs at each end is thought to assist in animal dispersal and to have only a minor aerodynamic function (Brown, 1953). The sinking velocity of the seed in still air is about 1m sec^{-1} (Brown, 1953) which, in theory, allows for dispersal up to about 100m in strong winds. However, it is clear from observations in Snowdonia that seeds can occasionally be carried over much greater distances, i.e. a kilometre or more, particularly in the turbulent air conditions found in mountainous regions (Shaw, 1984). Thus seed dispersal is described as "effective" by Shaw (1984) and by Tabbush and Williamson (1987), and yet Thomson *et al* (1993) describe *Rhododendron* as having "limited powers of dispersal".

1.3.1.5 Germination and seedling establishment.

Seeds germinate in 5 or 6 days under favourable conditions. Light is essential (2-5% full daylight) and so they will not germinate under soil or leaf litter. Imbibed seeds are non-viable after 160 days (Cross, 1981). The characteristics of a safe site for germination are demanding, seeds generally becoming established on a carpet of moss less than 1cm in depth (Cross, 1981). Deeper mosses cause shading or desiccation of the newly emerged seedling because the roots cannot reach the soil. Bare soil is a hostile environment for seedling establishment because the unprotected surface can dry out very rapidly (Cross, 1981). Seedlings contain andromedo toxin which is highly toxic and so they are generally avoided by grazing animals (Cross, 1975). Thus it is said by Shaw (1984) and Cross (1981) that intensive grazing favours the spread of *Rhododendron* because it creates gaps for mosses and removes potential competitors, whereas Thomson *et al* (1993) claim that sheep grazing in general, especially in improved and wet rough grazing pastures, is an inhibiting factor to its rate of spread. Fuller and Boorman (1977) suggest that activities of rabbits, until the advent of myxomatosis in 1954, were important both in controlling and facilitating *Rhododendron* invasion in a dune slack habitat. The mature plant supports very few associated organisms such as insects and fungi (even on leaf litter) and the plant is not adversely affected by them or by diseases (Cross, 1975).

1.3.1.6 Vegetative propagation.

Shaw (1984) claims, in dispute of the findings of Cross (1975), that *Rhododendron* does not produce suckers. These instead being confused with adventitious shoots from the lower parts of the buried stem. Cross (1975) and Fuller and Boorman (1977) claim that reproduction is predominantly by seed and that vegetative spread is very limited, being most common on the edge of thickets where unsupported branches become prostrate, whereas Tabbush and Williamson (1987) claim that individual bushes spread readily by layering.

1.3.1.7 Summary.

Looking at the rather limited evidence provided by the literature there seems to be dispute in many areas of the biology of *Rhododendron*, but in particular with regard to the characterisation of its taxonomy, the effects of grazing regimes on its rate of spread, and its effectiveness at layering.

There have been few detailed studies on the causes of the effects observed in these areas and many assertions have been made on the strength of correlation or assumption. The disagreements are probably questions of degree, for example, Rotherham (1990) quotes four cases where intensive grazing by sheep, deer or rabbits has prevented the spread of *Rhododendron*, with low levels facilitating invasion.

Areas of agreement in the literature are more encouraging. There is general acceptance of the importance of the microclimatic and topographic character of the regeneration niche and the importance of disturbance associated with the creation of these niches for effective spread. Also it is often said that *Rhododendron* is tolerant of a wide range of environmental conditions, but avoids extremes (Thomson *et al*, 1993; Cross, 1975), growing best on freely drained acidic soils (Cross, 1975).

Tansley (1939; quoted in Cross, 1981) claims the replacement of *Ilex aquifolium* in the Killarney oakwoods in SW Ireland by *Rhododendron* as a rare phenomenon, in that it represents the successful invasion of an *undisturbed* community by an exotic species. Cross (1981) though, claims that it is the artificially high grazing regime in the woods, predominantly by the introduced Japanese sika deer (*Cervus nipon* Temminck), that causes the depauperate ground flora and predominance of bryophytes which allows for the colonisation by *Rhododendron*, and thus *Rhododendron* behaves as a characteristic alien species utilising a highly disturbed habitat (Cross, 1981).

1.3.2 The study site.

1.3.2.1 Time of study.

An initial survey of the site was carried out on the 26th of April to assess how appropriate and amenable to modelling the area was likely to be. The magnitude of spread was assessed and photographs were taken to relate characteristics of the site to the model's designer. This allowed for forethought on the likely methodologies needed to collect the relevant field data, and for changes to be made to the model to accept these data, the model having being designed initially to simulate migration at a much larger scale.

Some preliminary data were collected, and some initial impressions of the patterns of spread were gained. This preliminary visit also gave pointers as to the likely GIS coverages that would be needed.

Fieldwork commenced on the 14th of May and ended on the 7th of June.

1.3.2.2 Geographical location and description.

Glen Etive lies in the Argyll and Bute district of the Western Highlands of Scotland. The portion of the glen surveyed is covered by sheets NN 04/14 and NN 05/15 of the OS. 1:25000 Pathfinder Series (for the specific names of places referred to in this project, see figure 1.3). The glen aligns on a NE-SW axis, with Rannoch Moor to the north and Loch Etive (a sea loch) to the south. The glen is approximately 25km long, the southern half, containing the study site, falling mainly within the Glen Etive and Dalness estates and also the Ard Trilleachan SSSI (Jenny Rees, personal communication). The valleys of the glen are a typical U-shape in form, a relict of the Highland's glacial past, and the mountains (forming part of the Grampian Range) span altitudes from sea level to more than 1000m.

1.3.2.3 Physical characteristics of the site.

Western Scotland experiences a maritime climate because of its geographical location at the eastern edge of the Atlantic Ocean in a predominantly south-westerly airstream. The main features of a maritime climate are a small annual variation in mean air temperature, high wind speeds at sea level, and high rainfall fairly evenly spread throughout the year. The climate is described as warm and moist with an Accumulated Temperature Divisions range (day °C) of 1100-1375 and a Potential Water Deficit Divisions range (mm) of 25-50 (Bibby, Hudson and Henderson, 1982).

The high precipitation combines with the northern latitude temperature range, topography and the underlying rock type to give the soil types of the area and the boggy conditions characteristic of the region.

The rock types in the study area are predominantly intrusive granites (Glen Etive and Rannoch Moor being the site of a huge batholith feature), with metamorphic, Dalradian age, slates, phyllites, mica-schists, graphite-schists and quartzites. Despite the presence of these rock types at no great depth over most of the area, superficial mineral drifts derived from these rocks are widespread over the area. These deposits, mainly of glacial and peri-glacial origin, form the parental material on which the soils of the region have developed and include shallow drift material (colluvium and solifluction deposits), sands and gravels (of raised beach and fluvioglacial origin) and morainic drift (Bibby, Hudson and Henderson, 1982).

The soil types are mainly peats, peaty podzols, peaty gleys, and peaty rankers. Podzolisation and gleying with the presence of iron pans are characteristic of colder climates with high precipitation and poor drainage, which creates water-logged and anaerobic soil conditions. There are also some more skeletal alluvial soils, especially around the mouth of Loch Etive, and subalpine soils on the mountain tops consisting of thin peat and stony frost-shattered debris (Bibby, Hudson and Henderson, 1982).

In the glen there are scattered patches of bog which are very localised, the most extensive patches forming in hilltop hollows. This lack of extensive bog compared to nearby low-lying areas such as Rannoch Moor is probably due to the artificial drainage pattern imposed on the area, as witnessed by the straight line drainage channels and furrows on aerial photographs. Lochan Urr is the result of damming and this is the largest body of fresh water (surface area c.4ha) in the glen. Loch Druimachoish and the other minor lochans cover about 1.5ha in total.

At the SW end of the glen is the head of Loch Etive, and an area of salt marsh. The main river in the glen is the Etive, and this becomes very broad and braided as it approaches the sea.

1.3.2.4 Plant community types.

The combination of the physical environmental factors outlined above with the autecological characteristics of the plant species present, and with the historical patterns of plant migration after the last glacial, have given rise to the vegetation communities of this area. These have been further modified, though, and sometimes created, by the direct and indirect impact of human management (Rodwell, 1992).

Glen Etive has a large altitudinal variation and can thus accommodate different combinations of the physical phenomena characteristic of this region and create, for example, different drainage patterns, soil depths, temperature extremes, nutrient availabilities and a host of other altitude gradients in physical parameters, thus allowing for a greater variety of plant community types.

The rock ledges of the river gorges support a *Sphagnum capillifolium/quinquefarium-Erica tetralix* sub-community of the *Pinus sylvestris-Hylocomium splendens* woodland type (NVC type W18; Rodwell, 1991). The steeply sided river gorges represent a refuge for these relics of the once vast Caledonian forest.

The river corridors also had patches of broad-leaved vegetation with diversity characteristics of the *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* woodland type (NVC type W9; Rodwell, 1991).

The more open habitats have representative community types which suggest succession from mires to woodland, perhaps due to fire and grazing regimes imposed by man (Rodwell, 1992). The grasslands of the grazed areas and the rides are predominantly of the *Erica-tetralix* sub-community of the *Molinia caerulea-Potentilla erecta* mire type with patches of *Myrica gale* (bog myrtle) (NVC type M25; Rodwell, 1992). These communities are intergraded with *Sphagnum* spp. sub-communities of the *Betula pubescens-Molinia caerulea* woodland type, (NVC type W4; Rodwell, 1991). This *Sphagnum* sub-community is most typical of wetter and deeper peats where the water-table is sufficiently low for birch to become well established, but where there is enough surface moisture to sustain *Sphagnum*. This represents a shift away from the active bog and mire types (Rodwell, 1991).

On the flat and also in river gorge aspects were vegetation communities of the *Quercus petraea-Betula pubescens* type (typical sub-community), which depending on the proximity to water, had affinities towards the *Isothecium myosuroides-Diplophyllum albicans* sub-community type (NVC type W17; Rodwell, 1991). The high diversity of bryophytes and pteridophytes at the study site, particularly in damper and more shaded river and stream habitats was a notable feature.

All of the above vegetation classifications were based on personal observation of the larger vegetation patches and the full species list of the plants present is given in appendix 1. There was often much intergrading between the types cited and small patches more representative of other community types.

The glen is used for rough grazing, predominantly at the northern end, with some small enclosures of improved pasture with more intensive grazing within the study site. There is a patch of forestry at the loch end which has been planted with exotic conifer species, referred to in appendix 1. The glen supports populations of red deer (*Cervus elaphus*) and spans across two estates, Dalness and Blackmount, who provide for hunting on their lands. The glen is also used for other recreational pursuits such as canoeing, climbing and walking. Thus, overall, the glen is quite highly disturbed by human activities whether this causes erosion, trampling, fires or an increased grazing pressure.

1.3.3 The MIGRATE *model.*

1.3.3.1 Model description.

MIGRATE is described as a simple deterministic model for the migration of sessile organisms (Collingham *et al.*, submitted). The model can work in one or two dimensions, this project concentrates on the two dimensional version.

In contrast to models using one or more diffusion equations to simulate dispersal, MIGRATE explicitly incorporates both the biological processes and the attributes of the organisms that together are likely to affect migration

(Collingham *et al.*, submitted). Thus it is similar to the model user by Dwyer (1992) to examine the spatial spread of insect pathogens.

The model uses biological parameters that can be readily estimated from quantitative data in the literature or from the field situation (Hengeveld, 1994; Dwyer, 1992).

MIGRATE can be used to simulate the dispersal of any sessile organism. It simulates spread in a hypothetical environment consisting of a two-dimensional grid of cells. The plants spread across this simulated landscape, the grid resolution of which depends on the scale of spread to be modelled and the biological attributes characterising the species dispersal. Each cell in the array is assigned a measure of its carrying capacity.

It can be seen that three, broad, interrelated categories of biotic data are needed to describe the *potential* for spread in an organism, including fecundity, dispersal and survivorship data. It must be remembered though that this represents the potential, because it does not consider the effects of the environmental heterogeneity on these parameters.

The model includes equations for dispersal and population build-up.

1.3.3.2 Parameters required by the model.

Notation	Description
L	Length of cell (km)
a	Area occupied by a mature individual (m^2)
K	Proportion of each cell available for colonisation (i.e. relative carrying capacity)
T	Time in years to reach reproductive maturity
S	Number of seeds produced by an individual in one generation length
H or R	Half-distance or root-mean-square displacement of seeds (km)
P	Probability of seed survival between generations

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 length, i.e. $S \times P$

α	Intrinsic rate of increase, i.e. $\ln(F)/T$

Within each cell the population processes are represented by:

1. Random, density-independent death of seeds before they grow into mature individuals according to the probability of establishment determined and the probabilities of survival from one generation to the next (P);
2. Self-thinning, represented by a restriction of first-generation individuals to a proportion of the area that would be required if all seeds grew to maturity, the area available being unique to all cells depending on their area (A) and their relative carrying capacities (K) in relation to the area occupied by a mature individual (a);
3. Random death of adult individuals according to the probabilities determined (P);
4. Production of the next crop of seeds according to the number of individuals within a cell, the time to maturation (T) and the number of seeds produced by an individual in one generation length (S).

Between cells the only process represented is random dispersal of the seed crop according to the dispersal function used (i.e. H or R) (adapted from Collingham *et al.*, submitted).

The version of MIGRATE used in this investigation is an adaptation of the original version which is used to simulate the migration response of sessile organisms on large spatial scales to climate change. This project did not consider climate change and was working at a finer spatial scale and so the model had to be adapted to work with a grid with a large array of small cells and a plant whose biological characteristics required the model to be age-structured into cohorts. Thus the parameters given above and their descriptions are not exactly in accord to the original version of the model.

The equations used in the model can be found in Collingham *et al.* (submitted).

To simulate the spread of a specific population in a specific geographic area, the model also requires a "map" of the proposed initial distribution of the species being studied.

The accuracy of the model in predicting spread from the initial focus or foci of introduction will be judged by comparing model output of distribution and abundance to that mapped in the field for the present day, and to that of past distributions through the use of aerial photographs (Fuller and Boorman, 1977; Thomson *et al.*, 1993; Lonsdale, 1993).

1.3.3.3 Structure, simplifications and limitations of the model.

The model is structured into cohorts with age spans equal to the maturation time (*T*) to allow for differential seed productions with age and differential survivorships. This structure represents a balance between trying to represent change in plant characteristics with age as opposed to all plants being classified as having the same attributes, and the computationally demanding effort required to keep tabs on all individuals and their attributes separately as opposed to the attributes of groups of similar individuals.

The relative carrying capacities (*K*) of grid cells, which represent the landscape over which the plant spreads, are assigned values through the use of "habitat maps". These can be constructed according to the observed patterns of the plant in relation to features of the landscape to be modelled (as described in the methods section). Changes in the habitat through time in its ability to allow for colonisation by the plant can be modelled by a GIS as a set of habitat maps. These can be inputted to the MIGRATE grid - whose cells are referenced to the corresponding cells of the habitat maps - at the beginning of each generation. Thus the cohort structure of the model not only limits the temporal resolution of the biological data, but also limits the resolution at which habitat changes through time can be modelled. Habitat changes within the period of an active cohort cannot be instigated and the year of the habitat change must be rounded up or down to the onset of the nearest cohort, whence it can begin to have its effect on the dynamics of spread. Thus the model does not have the structure to deal with short-term changes in habitat, and these will only be incorporated into habitat maps if they are thought likely to affect the spatial dynamics of the species at the spatial scale of study, the change being expanded to the length of a cohort.

The model represents self-thinning by restricting newly established plants to a proportion of the area that would be required if all seeds grew to maturity, i.e. it uses the measure of the area occupied by a mature specimen. This is not a valid representation of the self-thinning process which is much more progressive, and will have progressive effects through time. Therefore, to overcome this simplification the data representing the size of a mature individual can be collected from stands that are not fully mature but have 100% cover and thus are at maximum carrying capacity.

Another simplification of the model with regard to its interaction with the environment is that the environment is only allowed to exert its influence on the biotic potential of a species by affecting the carrying capacity of grid cells for mature bushes. The e~~a~~ffects of environmental heterogeneity on other biological /e attributes are not considered and can only be accounted for by averaging the measurement of these attributes across the different habitat types present.

produced ?

The model calculates the number of seeds outputted by a given cohort dependent firstly on the number of individuals within that cohort (a variable dependent on cohort number, carrying capacity, and stochastics of earlier cohorts if cohort number is >1), and on the seed production value characteristic of individuals belonging to that cohort (one value). The model assumes that all plants within a cohort have the same character and these characters can only be allowed to change through "movement" into another cohort. Each member of a cohort is thus given one value of seed production which means that care has to be taken that this value is representative of the total production of an individual for one cohort length. Estimation of the parameters is outlined in the methods section.

The model makes calculations based on a discrete cohort structure, one calculation being made for each generation. Seed productions are subject to dispersal according to one or two dispersal functions which can be exponential or normal in character. The seeds are then subject to carrying capacity constraints and survival probabilities.

The cohort structure represents a method of summarising the temporal information required about the species being modelled. In the spatial sense the model cuts down the amount of memory needed for positional information by assuming all plants are at the centre of their grid cells. This could result in inaccuracy if the cell size was a lot larger than the half-distance or root-mean-square of dispersal (*H* or *R*), so that plants have difficulty leaving the initial cells. Also if the cells of the grid are large, assuming plants to be at the centre of each cell is a gross approximation of the probable real world distribution.

Throughout the methods section it is important to bear in mind that the model works on data collected from the field or from the literature. Constraints imposed by the timing of fieldwork and the limited extent of specific literature available mean that there will be necessary simplification of real world biological heterogeneity to get at the parameters required by the model. Many methods are those of averaging or using small datasets to obtain rough approximations, which is often a procedure of modelling as opposed to "simulation" (in the sense of Maynard Smith, 1974), although this must be remembered when interpreting results and applying them to new situations.

Chapter 2: METHODS AND MATERIALS.

Firstly the methods section details how age data were obtained from the measurements taken in the field. The second section elaborates on the methods used to calculate the parameters required by the model (as in section 1.6.2). The only parameter not treated in this second section is the relative carrying capacity *(K)* of the grid cells, which is not strictly a biotic attribute of the plant although it is related to the character of the plant. The methodologies used to calculate *K* are treated in the third section and include the GIS techniques and packages used. The third section also outlines methods used in the construction of the initial distribution map.

2.1 Laboratory and field methods used for data collection.

2.1.1 Preparation of specimens for tree ring chronology.

The sections collected in the field were sawn from as low down as possible on the stems, without cutting into the root or bole structure. Sometimes for smaller specimens it was possible to obtain sections using loppers, but in all cases the use of an axe was avoided because it produced very uneven cuts. Sections were recut at a later date in the lab if this was necessary to give a flatter surface with which to work. The surfaces were then sanded with coarse grit sandpaper to remove the roughest parts of the cut and to reveal areas of the section with least blemishes and imperfections such as splits and cuts. Having selected the areas with the best potential for ring counting, especially in the zones where the rings are tightly packed, the sections were then sanded with progressively finer sandpapers so as not to clog the finest grades and to get a smoother finish. The sections were finally polished with a buffer cloth. An initial inspection and trial count usually revealed if more work was going to be necessary.

Specimens too young for ring counts were judged according to the table produced by Cross (1981) for 1-7 year old seedlings. The parameters of 3 and 5 year old plants were used as the starting point data for most graphs.

The centre of each section was usually found to contain a region of 1-2mm of softwood in which the rings were not discernible. This width of material represents the initial growing period of about 5 years and so all counts quoted have an addition of 5 years to the age discerned from the rings counted. This was justified because simply ageing stems from the number of tree rings present, the age of a plant section could be given as 7 years even though it was obviously older than this. This conclusion was drawn from comparison of the size of the bush with the findings of Cross (1981) for the dimensions of seedlings and from the counts of annual stem terminations evident on the plant.

The rings of most sections could be counted by eye and it was only in areas of confusion that examination under low power of a light microscope was needed. Rings were marked as they were identified using a soft pencil. This made later counting and recounting much easier. It is advisable to get the two flat faces of the sample section parallel to one another as this makes the microscope work a lot easier, also the sections should have some depth as this gives something to grip them by in the sanding process which is especially useful for smaller specimens. Otherwise a vice or other grip can be used.

2.1.2 The measurement of bush dimensions.

Bushes sampled had measurements taken for stem circumference, bush width and bush height using a flexible tape. The measurements for circumference were taken as low down on the stem as possible, but above the bole structure, this often required the removal of dead vegetation surrounding the stem to ease access and to make sure only the circumference of the stem was being measured without the inclusion of other grass stems. Bush width was for the longest lateral axis of the canopy, and height was measured from the top of the root structure to the highest bud tip on the canopy. Measures of bush canopy and height were taken to the nearest centimetre, and for stem circumference to the nearest millimetre.

Stem circumferences were transformed into estimates of stem area using the equation:-

$$A=C^2/4\pi$$

where A =the stem section area (cm^2), and C = the stem circumference (cm).

The areas of all the stems present on a bush were calculated individually from their respective circumference measures, and then totalled to give a single value for the area of stem section material present. Simply using the total circumference measured would not give an accurate representation of the actual stem area present.

Stem area was chosen as a necessary calculation and representation of production with age because a property of circles is that small increments in area produce disproportionately large increases in perimeter length, thus stems differing only slightly in area may have large differences in their circumferences. Therefore, area provides a better representation of actual wood production than circumference.

The relationships found between age and the other physiognomic characteristics of the bushes were used as tools for getting at the parameters required by the model. The equations for these relationships were used to assess the age of bushes where stem sections were not collected due to time and labour constraints (a method used by Cross, 1981).

2.2 Estimation of the parameters required by the model from the field data collected.

2.2.1 The area occupied by a mature individual (a).

The model requires the area occupied by a mature bush to calculate the maximum potential carrying capacities of a grid cell for *Rhododendron* considering the cell's relative carrying capacity (*K*). To calculate the average area occupied by a bush in the field, areas of *Rhododendron* with 100% canopy cover were selected, and if necessary felled using a chainsaw. Rectangular areas were marked out within three stands, the size of which depended on the extent of the canopy cover and how accessible the stand was to measuring. Sample areas were delimited using sticks according to measurements taken using a 35m flexible reel tape. In each area, the number of stumps or specimens were counted. Areas were selected for their completeness of cover and for their apparent homogeneity in age. The actual ages of a sample of the individuals from each stand were calculated using the tree ring chronology technique or from other parameters, as outlined above.

Density estimates from different aged stands were averaged to produce an average bush size that represented partial self-thinning although not that definitely associated with maturity. This averaging method was used to overcome a simplification in the assumptions of the model as outlined in section 1.6.3.

2.2.2 Time to reproductive maturity (T).

The number of years until maturation is quoted as 12 years in the literature (Cross, 1975 and Shaw, 1984). This value was to be compared to that obtained from the field.

2.2.3 Number of seeds produced per individual in one generation length (S).

Estimates of seed production combined field data with that given in the literature. The quantitative data on seed production was taken from Cross (1975). Cross' data came from 10 racemes collected from a bush 10m in circumference in a semi-open situation, the results were as follows (figures given = means±standard errors): seeds per capsule 268±88; capsules per raceme 18.3±3.4; seeds per raceme 4900±1900. Cross went on to state that the same bush bore 233 buds and that if seed production was similar for these, then well over one million seeds could be produced.

Although the mean figure given for seed production has a large standard error and was obtained from analysis of only 10 racemes from one bush, in one situation, it is the only data available in the literature. Seed production data for bushes was not collected during the fieldwork period of the current project because capsules had already released their seeds. The figure given by Cross (1975) is not representative of extremes but is probably a closer approximation to an average in that it is described as coming from a semi-open situation and is from a bush of about 3m in width. Although the use of this figure is not wholly satisfactory it is the best available.

The mean seed production value of 4900 was used to calculate seed productions from individuals passing through a cohort by combining it with estimates of flower production taken from the field. The number of flower buds per bush were counted for all individuals within two areas of open habitat. The collection method used to obtain these data was to gradually cut the bush down using loppers, counting the number of buds on each section removed. At the same time the number of capsule structures representing last year's flower crop were also counted to see if there was any relationship between the number of flowers produced this year and the numbers produced last year. All bushes for which these data were obtained were aged directly through the tree ring chronology technique outlined in section 2.1.1 above.

2.2.4 Distance over which seed is displaced (H *or* R).

The time of year and the time available for the fieldwork phase of the project meant that the ideal of seed trap studies for investigation of the patterns of seed dispersal was not feasible. Therefore an approximation of the dispersal function was obtained by selecting three discrete sub-populations (i.e. separate from the main populations), from the three main habitat types, which had potentially distinguishable parents and population development histories (a method akin to that used by Johnson, 1988). The populations were selected according to their clustering and visible separation from other possible seed sources. Thus the following results are biased against older bushes without populations around them and against populations developing in more competitive environments. Also potential outliers representing long-range dispersal at the stochastic tail of the dispersal function will not be included in the data because it is often not clear whether these are attributable to the parent in question or to other mature individuals or populations nearby.

Stem sections for definitive ageing were only taken from the riverside population studied. The individuals of the other two sub-populations in the ride and open environments were aged according to the habitat specific exponential relationships of age to width, height, and stem section area.

In the open and ride situations all plants sampled were numbered and labelled with sticky tags and their positions in relation to the hypothesised parent and seed source noted in a sketch diagram. In the more precarious sampling environment of the riparian habitat, sections were collected first before distances of the plants from the parents were measured, the section, and its corresponding stump, being labelled with a unique identifier using a waterproof marker pen. All distances were measured to the nearest centimetre from the stem base of the plant sampled to the base of the probable parent as directly as possible considering the topography of the habitat.

The data on plant distributions in the three habitats was grouped into 3m interval, distance cohorts.

To decipher which plants had been produced by the hypothesised parent it was necessary to truncate the age distribution.

2.2.5 Probability of seed survival between generations (P).

The data collected on the three sub-populations was also used for the calculation of establishment rates from seed productions, by combining it with the results of the calculations on the potential seed outputs of individuals within age cohorts (see section 2.2.3). The entire dataset collected for the sub-populations could be utilised because there was no need for the truncation applied to assess dispersal distances (as in section 2.2.4) from a *single* source, it being assumed that all plants old enough could contribute equally to young plants within the same sub-population.

The number of seeds contributing to the plants of a cohort was calculated by totalling the individual seed productions of the other plants in the population which had reached reproductive maturity.

The age of a plant is passed through the relevant equation relating age to seed production (as calculated from the methods outlined in section 2.2.3) for the period over which it could contribute to the younger plants in question. The whole process of calculation of who contributes to who follows the population back through time until the population dwindles up to the point when the original parent arrived at the site.

The proportion of seeds contributing to the plants recorded was to be averaged across cohorts and between habitats, taking the shape of the habitats into account and thus the amount of the actual dispersal "plume" (assuming dispersal is equal in all directions through time) sampled by the habitat. For example, a corridor habitat only receives seeds from part of the circular dispersal area, sampling the areas on the two sides of the parent bush. Thus the actual number of seeds out of the whole seed production actually contributing to the seedlings observed within a distance cohort will be a fraction of the total seed production. This fraction will be proportional to the area of that habitat available for colonisation out of the total available in a circular annulus for that distance class to which they belong.

2.3 Mapping the distribution and abundance of the *Rhododendron* through time.

Initially it had been hoped to use two bearings obtained from the alignment of a compass clinometer with two landmark features such as the high points of mountains or buildings in the glen to position bushes within the study site. This method proved to be very inaccurate though, especially in windy conditions, and was impractical in heavily vegetated areas which reduced the field of view. Thus the distribution was mapped onto a 1:10000 map of the area on which positions along rivers or rides could be easily followed. For the more contiguous areas of cover, the distribution was mapped by gaining high vantage points from which to sketch in the distribution, and where sketching was not practical due to other constraints photographs were taken. High vantage points were chosen to reduce the distortion of the view.

Aerial photographs at a 1:10000 scale for May 1946 were used to ascertain the past distribution of *Rhododendron* in the glen and the probable sites of introduction as well as any other information on environmental history of relevance, such as the presence of sheep pens and other enclosures seen at the present day, forestry blocks, rides or tracks.

Other information on the past distributions of the *Rhododendron* was obtained from the ageing of the samples in the field, with all single plants come across away from the main distribution being aged either directly through stem sectioning or through estimates based on the other measures of bush dimensions described previously.

Also the stalker on the estate was able to give an impression of the rate of spread, including a probable date of introduction to the gardens of the Lodge of about 1910 when the Lodge was built.

2.4 The construction of habitat maps for relative carrying capacity *(K)*.

All factors of physical and biotic relevance to the spread of *Rhododendron* in the environment of the glen were digitised initially as GIS 'coverages' (a spatial and attribute data layer representing one or more habitat features). Coverages were produced using the ARC/INFO package developed by the Environmental Systems Research Institute, ESRI, for the handling of spatial and attribute information, respectively.

Streams and rivers, rides, roads, fences and contours were digitised as linear or 'arc' features, their attributes being associated, in an INFO table, with the unique identifiers of these lines. Streams and rivers were digitised from two 1:25000 OS maps covering the area, as were the 25m contour intervals. Roads, rides and the fence line surrounding the forestry were digitised from 1:10000 maps as were features extending in two dimensions such as lochs and forestry blocks. These features with aerial extent were digitised as 'polygons', the character of these polygons being associated with their label identifiers in a database. The species types of forestry block sub-compartments and their dates of planting and fencing were also obtained from the 1:10000 Forestry Commission map.

The grazing regimes characteristic of the area were assessed from the field evidence of fencing history and from the aerial photographs, and these had to be digitised as polygons with differing attributes such that their effects on carrying capacity could be changed through time.

The arc coverage representing the contours was used to construct a digital terrain model (DTM or 'tin') using TIN (an ARC sub-environment containing its own characteristic set of commands for the creation of three-dimensional models from contour information through interpolation). It was intended to use this 3d-model to extract information on the actual area of the cells of a grid draped over, and thus warped, by the major topographic features of the habitat. This was not computationally possible. The mapped present day distribution covers a greater area than the planimetric horizontal distances of the MIGRATE grid suggest. This effect is due to the vertical extent added by the topography of the area compared to the area of cells had the habitat been flat. The MIGRATE simulations are therefore underestimates of the true distances present in the glen because the grid on which it runs does not take account of the topography of the habitat. This inaccuracy must be borne in mind when comparing the mapped distribution with that predicted by the model which is for a uniformly flat habitat. It was hoped that this problem of comparison could be overcome by overlaying a graphics file containing the predicted distribution maps onto the tin and comparing this with the real situation, but again this was not possible.

Therefore, the continuous surface of the tin was "sliced" to create the discrete contour classes of a 'lattice' (a representation of a surface by regularly sampled points from a common origin, with a constant sampling distance in the x and y dimensions) sampled at a 25m interval resolution from 0-500m, with altitudes >500m being classified as one value. A similar classification to this is shown in figure 2.4a), although here, height divisions above 500m are shown. This altitudinal classification allowed for the effects of altitude gradients in carrying capacity to be simulated. The structure of the 'tin' as modelled from the digitised contours allows different surface features of the glen to be analysed, such as slope angle and aspect if necessary (Fig. 2.4b)).

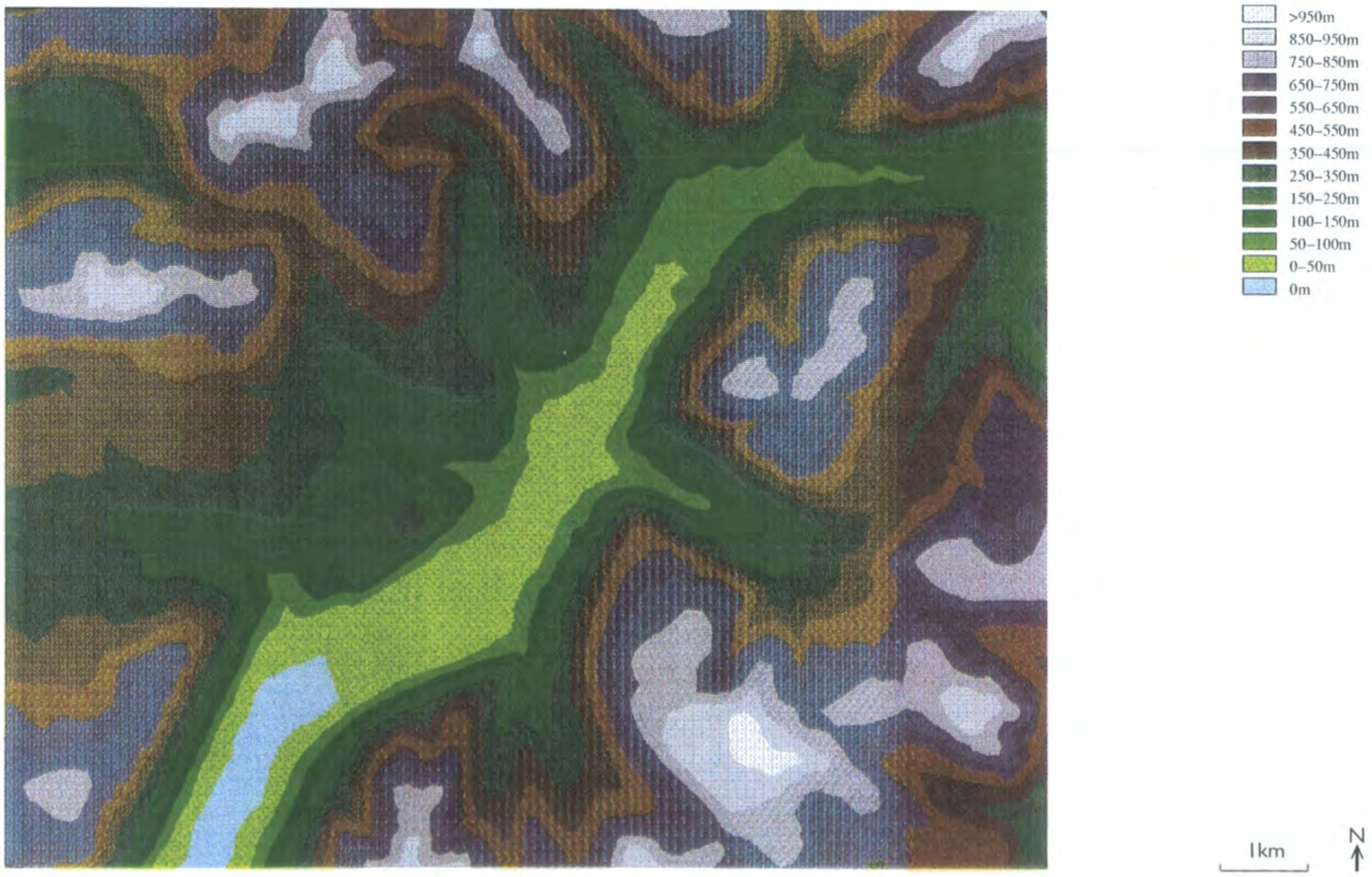


Fig. 2.4a) An altitudinal classification of the Glen Etive study site.

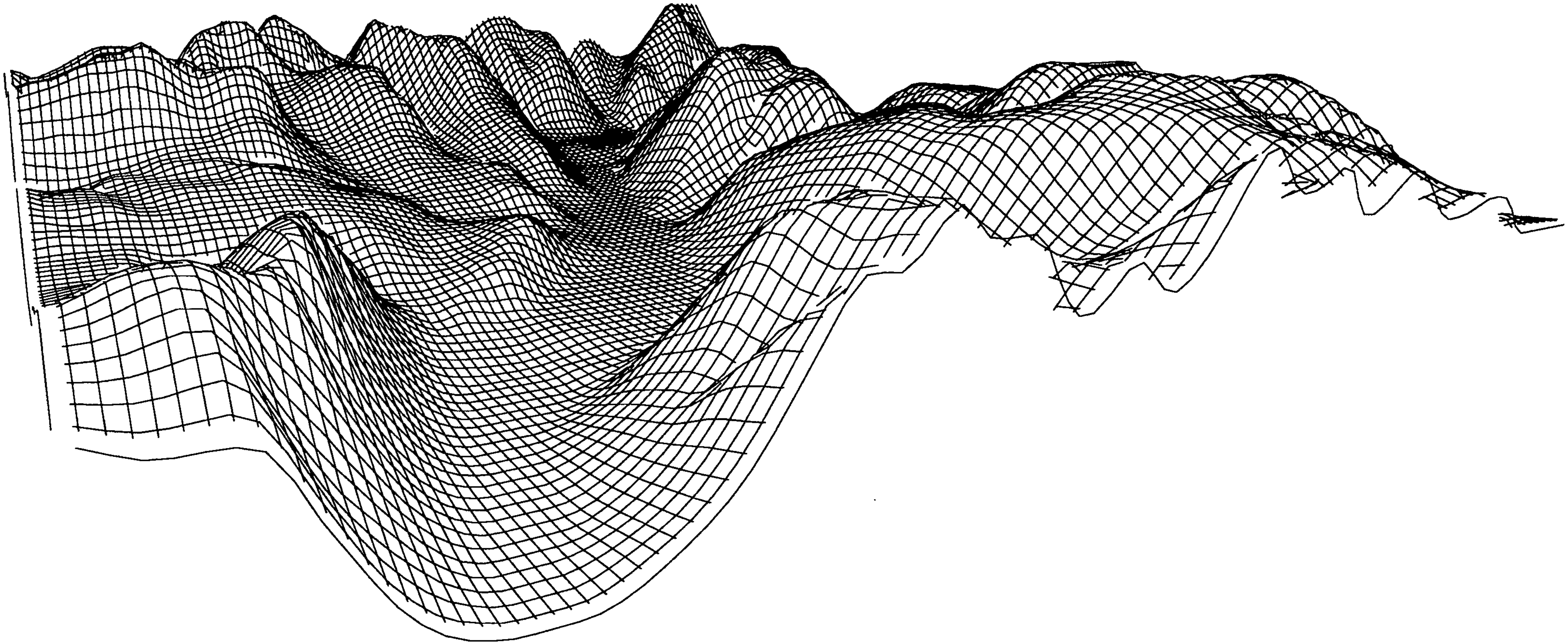


Fig. 2.4b) The digital terrain model viewed north–eastwards from the head of Loch Etive.

Both the lattice and the coverages generated by the GIS were converted to gridded images at a 10m (length of the side of a cell) resolution using GRID (an ARC sub-environment that creates grids of equally sized rectangles to represent map data, including polygon, line and point features, each cell being referenced in space by its row and column number). This avoided the complications that would be caused by using an independent grid overlaid on all the coverages made and assessing the unique percentage contributions of each coverage to each cell. Instead, GRID can be used to convert all coverages to a rasterised (information converted to cellular form) image georeferenced to the same in the real world and thus exactly overlapping one another such that each cell can easily be assigned a unique measure of its relative carrying capacity (*K*). Using this method each georeferenced cell has presence/absence data for the coverages used.

The gridded coverages are converted to ASCII file format and then read into a conversion program which creates a combined ASCII file. This file combines the information from the separate ASCII files into a file simply containing the co-ordinates of the grid cell followed by presence/absence data for the number of coverages used. If the cell contains part of a coverage, for instance all cells contain altitude information, the value present in the cell is also important since this represents a classification code. To demonstrate the nature of the file a few lines are given below:

```
208000 743000  0  0  0  1  0  2  0  1  11
208010 743000  0  0  0  1  0  2  0  1  11
```

For example, the "1" values represent the presence of road and river in the cell, whereas the "2" represents the code for the grazing regime. The altitude code in this case is "11" which represents a height of 250-275m.

The data converted to this form is easier to manipulate in the construction of the actual habitat maps containing *unique* carrying capacity measures for each cell. A second conversion program called "make_k" uses input files containing information on the number of coverages to be used in the creation of the habitat maps, the number of cells to be combined to form the output grid, and the carrying capacity values (as a proportion of 1) which the code values of the coverage features were to receive. Also the program allowed the carrying capacity values in the grid cells to be multiplied or replaced by the next coverage value given in the input file if this existed within the same cell as the previous value. Due to the replace feature the order in which the coverages are combined is important. This order is based mainly on considerations of how these coverages relate to one another in the glen and thus their possible utilisation by *Rhododendron*. For example, roads are built over the top of streams and rivers, and so this is the way the coverages should relate to one another in the model, because the *Rhododendron* will not be able to utilise these portions of river corridor habitat. Although these effects may seem of negligable importance to the dynamics of the model, at a larger scale it would be self-defeating to place the effect of the grazing regime coverage on carrying capacity over the forestry block coverages. Coverage order can also compensate for inaccuracies occurring at the digitising stage and changes in the spatial data resulting from the GRID process. For example, the edge of a forest block may have been digitised overlapping the arc digitised for a fence line because the gap between the two in real terms is less than ten metres. Therefore the fence line coverage data can be inputted later into the "make_k" program so that it replaces forestry information for a grid cell containing aspects of both coverages. This overlap effect may be especially exaggerated by the GRID process which converts the line (and point) features of coverages into features with two-dimensions because each occurrence now occupies a 10m cell. Thus all linear features having virtually no real area are expanded to cover a line with a width of ten meters, which can lead to overlap with the edges of polygon features whose irregular edges are expanded to fill 10m cells. Therefore the order of coverage input is based on the observed sequence in the field, with considerations for the digitising and gridding processes of data capture and manipulation.

Grazing regimes form the underlying template to the area, followed by, in order of overlay, the forest blocks, fences, streams and rivers, lochs, rides, roads, and finally altitude. Altitude effects on carrying capacity were simulated through multiplication. Other coverages, if present in the cell, simply replaced one another.

The "make_k" program, through the format of the input file, can be flexible as to:

1. The number of cells it can combine and thus the resolution of the gridded output;
2. The number of coverages considered from the overall ASCII file;

3. The number of code values within these coverages to be used;
4. The way the codes are combined (i.e. the order of input of the coverages and whether the replace or multiply option is used); and
5. The actual carrying capacity measures assigned to these item values.

The habitat maps produced by the "make_k" program were produced in accord with the timing of probable changes in the habitat of the study site through time, and were produced for each generation, their resolution in the temporal dimension being defined by the cohort structure of the model. Habitat changes have to be expanded to the length of cohort or ignored altogether.

Both conversion programs referred to above were written by Dr. Brian Huntley specifically for the problems encountered in converting the GIS grids into a format which the model could "understand" and utilise.

The habitat features deemed to be of relevance to the spread of *Rhododendron*, with regard to their measures of relative carrying capacity, were assessed from observations made in the field, and from quantitative data collected on the habitat associations of *Rhododendron* seedlings and of the saplings other woody taxa.

For each *Rhododendron* seedling for which measurements were taken or observations made, i.e. all those encountered in open habitats, a 10×10cm quadrat was placed around the plant centring on the stem base. The physical features within these quadrats and the dominant vegetation types (>50%) within them were noted. Also for each case the average slope of the quadrat site was estimated using the dip feature on a clinometer (Cross, 1981).

A similar procedure was used to measure the associations of the tree species, although here an extra measure of the vegetation type present within a 1m quadrat was noted if there was no particular association of the root structure with a particular physical feature.

The categories for vegetation were broad in some cases, such as for fine mosses and grasses other than *Molinia* where individual identification was difficult, it being assumed that these groupings of different species with similar forms was justifiable in terms of their probable effects.

For the tree species in the sample there were often many seedlings that had germinated this year and had their cotyledons still intact. These were not included in the sample as they had not been acted upon by the selection pressures characteristic of the full yearly cycle in the glen. Also the multitude of suckers arising from mature *Populus tremula* (aspen) were not counted as independently established individuals in relation to habitat features because it was thought that they would bias the sample. The uncertainty in identifying suckers and freely establishing plants of this species prohibited its inclusion in the sample.

Chapter 3: RESULTS.

3.1 Relationships of the parameters of bush physiognomy to age.

The parameters of bush physiognomy collected in the field were found to be correlated with age. The nature of the overall relationship of stem section diameter to age is shown in figure 3.1. The other figures presented are those for habitat specific relationships which represent a breakdown of the overall dataset. The data were divided into habitat types representing open, ride and riparian habitats, because of the different plant forms associated with these habitats and because of the patterns shown in the data collected.

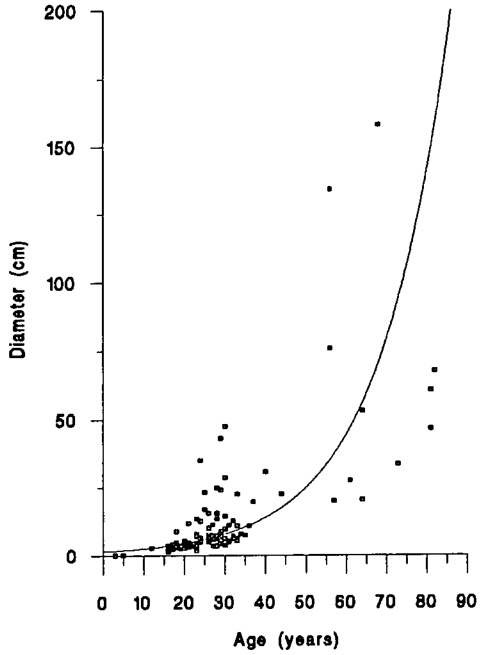


Figure 3.1a) Fitted exponential (r^2=0.98, $p<0.01$) relating age to stem section diameter for all *Rhododendron* samples collected in the field and aged through tree ring chronology. The measure of stem diameter was calculated from stem circumference.

The relationships of radius, circumference and area to age are not shown for the overall dataset because these relationships were not used in calculations of age and because these measures are obviously correlated to one another. Also the relationships of bush width and height to age are not given for the overall dataset because these too were not used in calculations. The plot of stem section diameter against age shows that the underlying relationship between the two approximates to an exponential. Thus the exponential relationship of stem section area to age is not simply an artefact of the method of calculation.

In all of the graphs shown, a simple linear fit did not produce such a high degree of correlation, and the residual plots showed similar patterns of scatter to those for the exponential fit. The data in all cases are probably better represented by a different set of equations, but the correlation coefficients and the residual plots suggest that the exponential is sufficient for the purposes of this project.

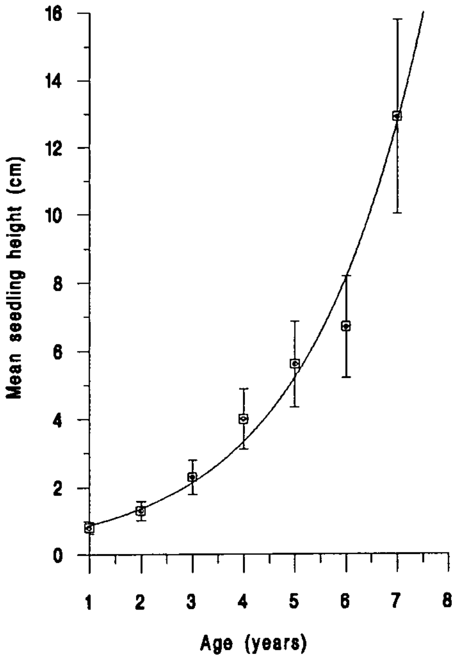


Figure 3.1b) Mean height of *Rhododendron* seedlings ± standard error bars, calculated from data given in Cross (1981) ($r^2=0.98$; $p<0.01$). The equation derived from the fitting of the exponential was used to calculate the ages of seedlings found in the field.

The fitting of exponentials is not only justified for the data collected from the field. The measurements of *Rhododendron* seedling height with age given by Cross (1981) demonstrate a clear exponential relationship (Fig. 3.1b)). The growth of individuals has often been shown to follow this pattern of exponential increase, although it is only a phase after which there is a levelling off in growth rate, the equation describing this process being known as a logistic (e.g. for *Zea mays* and *Pinus sylvestris* in Evans, 1972). There is evidence for logistic relationships of growth parameters to age in this project, and in figures 3.1d)-3.1f) "logistic lines of best fit" have been drawn in to estimate the age at which the levelling off phase of growth occurs.

The affects of habitat type on the dimensions of the bush "canopy" are shown in figure 3.1c). Pairwise comparisons of bush dimension ratios between habitat types using the t-Test statistic showed significant differences between ride and riparian habitats (p<0.01) and between open and riparian habitats (p<0.01). Differences in the ratio of width:height for canopy dimensions were not found to be significantly different between the open and ride environments. Figure 3.1c), plus figures 3.1d), e) and f), tie in well with the observation of more compact, domed shaped bushes with small leaves in the open situation, and the larger leafed, more etiolated and lanky specimens with single emergent stems found in the shaded ride and river habitats.

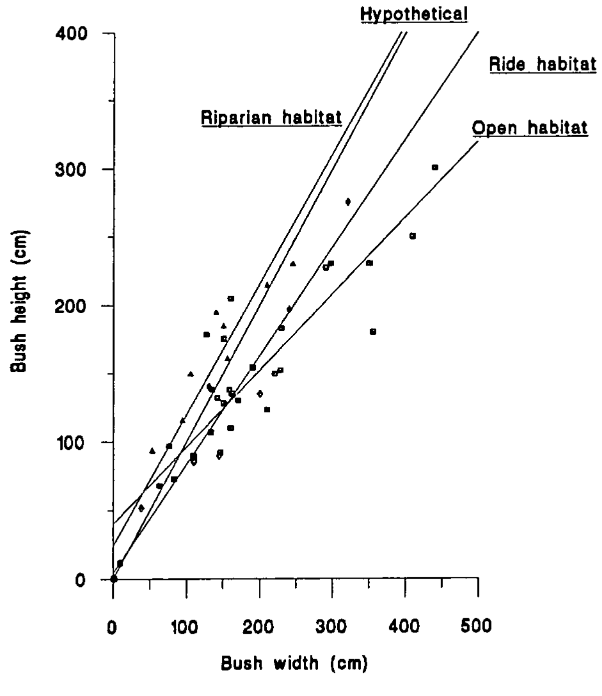


Figure 3.1c) The change in bush dimensions with habitat. Open habitat plants (■) tend to have width:height ratios of >1, as do ride plants (◆), although ride plants have a closer approximation to the equal dimension curve (the hypothetical). Plants of riparian habitats (▲) tend to lie above the line, having width:height ratios of <1. The graph also shows a tendency for all plants to start off taller than they are wide.

From the positions of the curves in figures 3.1d)-3.1f), the observed differences in growth form become apparent. For plants of the same age, bush widths, are greatest in the ride habitat and lowest in the open habitats (Fig 3.1d)).

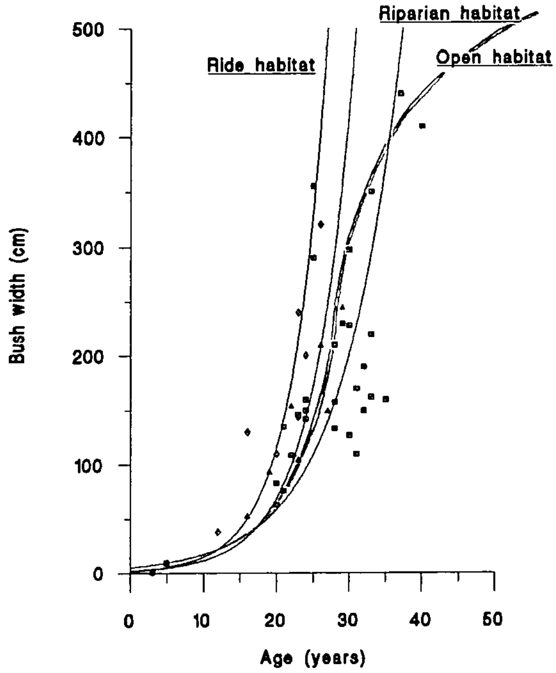


Figure 3.1d) Habitat differences in bush width with age ($r^2=0.72$ $p<0.01$; $r^2=0.88$, $p<0.01$; $r^2=0.89$ $p<0.01$ for open (■), ride (◆) and river (▲) data respectively). The line fitted through the whole dataset is a logistic used later for calculations of seed production (see section 3.2.3 for explanation).

A similar pattern is seen for height with age, it being roughly the same in both riparian and ride habitats whereas a plant of the same age will be shorter in a more open environment (Fig. 3.1e)).

From the fitted exponentials it can be seen that both height and width approximate to the curve fitted, the lines of the curves averaging differences within the dataset. The collective datasets for all habitats for width and height do not actually represent all specimens collected and aged. This is because some plants were too unwieldy or inaccessible for such measurements to be taken or the foliage was found to be severely damaged. For example, with older specimens with high canopies in dense stands it was impossible to distinguish the boundary between one specimen and the next or to obtain accurate measures of height. For these specimens, as for those with badly damaged canopies, the only measure taken was of stem section circumference which was later used to calculate area and radius.

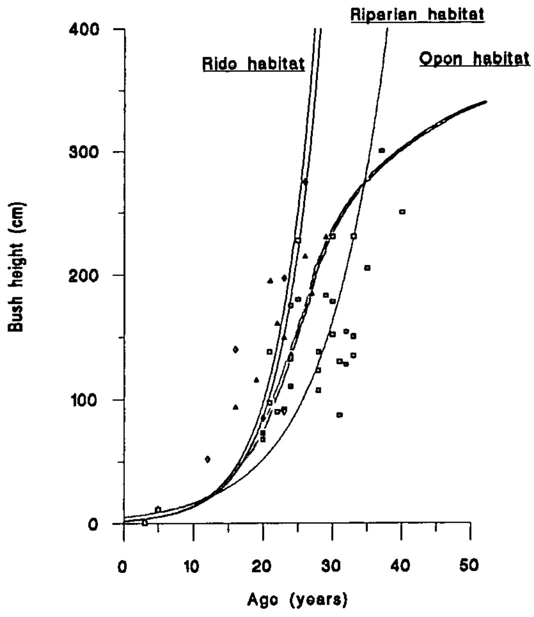


Figure 3.1e) Habitat differences in bush height with age ($r^2=0.69$ $p<0.01$, $r^2=0.78$ $p<0.01$, $r^2=0.82$ $p<0.01$ for open (□), ride (◇) and river (△) data respectively). The line fitted through the whole dataset is a logistic used later for calculations of seed production (see section 3.2.3 for explanation).

Thus overall it seems that plants of the same age will have smaller canopy dimensions in more open situations. This conclusion though is only based on the width and height measures of the canopy and it is possible that plants of open habitats have greater canopy volumes. Therefore any inferences drawn from these data must be rather tentative.

Stem section area gives a better indication of wood production by the plant. The relationship of stem area to age is therefore of greater interest as it infers levels of biomass production and thus qualitative differences in habitat. Figure 3.1f) shows divergence, of the exponentials fitted, from similar initial starting points, according to the habitat type.

Overall these graphs suggest an effect of environmental heterogeneity on the physiognomic characteristics of bushes and their patterns of biomass production. This realisation was important in establishing the methodologies for the sampling regimes required to estimate the parameters required by the model. Also these differential phenotypes (Cross, 1975) of *Rhododendron* must be remembered when the process of averaging across habitat types is carried out.

These apparent differences in bush form due to habitat will probably also feed through to other parameters such as flower and seed production, although this was not tested.

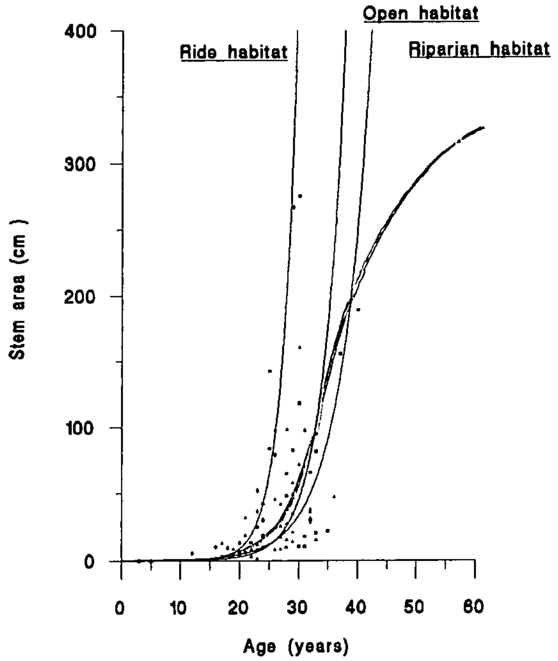


Figure 3.1f) Habitat differences in stem section area with age (r^2=0.72 $p<0.01$; r^2=0.87 $p<0.01$; r^2=0.64 $p<0.01$ for open (□), ride (◇) and river (△) data respectively). The logistic fitted to the whole dataset is used in later calculations of seed production (as in section 3.2.3).

These results consistently show that width is the parameter that is the best predictor of age, not only between habitats but also within habitat types compared to the other parameters used. Even so, age predictions were made from an averaged total produced from the habitat specific equations of age in relation to the *three* parameters of width, height and stem area. This method was used for two reasons: firstly it was thought that all parameters measured correlated well with plant age and could thus even out measurement inaccuracy that might occur if only a single parameter was used; and secondly, because some parameters were not collectable, for instance some bushes had stem circumference but no width or height or appeared distorted due to severe damage. Others had so many stems arising from a single bole that it was far easier to estimate age from measures of width or height or a combination of the two.

3.2 Data required for the model parameters.

3.2.1 The area occupied by a mature individual (a).

Direct estimates of self-thinning rates could be assessed from examination of *Rhododendron* stand densities with differing average ages. Although the data collected were limited to three samples there does appear to be a trend in the average area occupied by an individual bush through time (Table 3.2.1). These data, though, are not used by the model which instead calculates carrying capacity according to the area occupied by a mature bush.

Table 3.2.1: The mean age, and number of individuals in different sized quadrat samples. These data were used to calculate average canopy areas of *Rhododendron* at different survey sites which were then totalled and averaged to give a measure used by the model for estimates of self-thinning rates.

Quadrat site	Mean age (yr)	No. of stumps	Area (m^2)	Average area occupied (m^2)
Area 1	32	110	150	1.37
Area 2	24	16	10	0.63
Area 3	75	12	100	8.33
			TOTAL	10.32/3
			AVERAGE	=3.44

Thus the average area occupied by a bush can be considered to be $3.44m^2$. Although habitat carrying capacity was not be measured directly, this average bush size for plants in dense and competitive stands places an upper limit on the number of bushes that can be fitted into a grid cell of the modelled habitat, depending on the cell resolution.

3.2.2 The time taken to reach reproductive maturity (T).

Age of first flowering is recorded in the literature as being not before the twelfth year (Cross, 1975). No plants aged in the field that were less than 12 years old showed signs of reproductive maturity, only plants older than 12 had flowers or had flowered in the past. Therefore the age of reproductive maturity was taken as 12 years.

3.2.3 Number of seeds produced per individual in one generation length (S).

The model was structured according to the 12 year maturation period into age cohorts with 12 year spans. Each age cohort is fixed and each individual within a cohort is assigned a fixed seed output that can only change on progression (through ageing) into a later cohort. Using the average values of seed production for a flower head given in the literature by Cross (1975) the probable outputs of each cohort were calculated according to some further assumptions. Firstly, considering the relationship between the number of old flowers and the number of new flowers it seemed appropriate to structure total flower production in terms of a two-year cropping cycle. Figure 3.2.3 suggests a pattern of high production of flowers this year with low production last year and vice versa, such that total flower production is actually for a two year period.

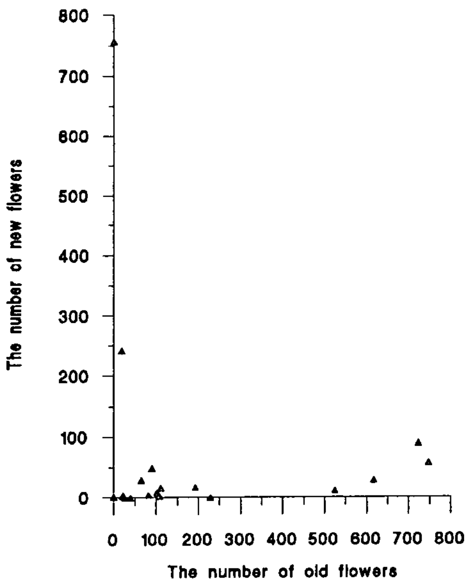


Figure 3.2.3a) Production of old and new flowers from a sample of plants taken from two areas in an open habitat. The points of the graph, it is tentatively said, point to a two-year cropping cycle.

Although the data set and the time scale used to make this assumption are both small and of little statistical significance, it was observed that stems producing flowers last year generally did not have flowers this year and were instead producing new shoots from just below the base of the dried capsule structure that represented last year's flower head. Those having buds for this year showed evidence of having flowered one year ago, the buds coming from the new shoots arising from these terminations, the dried capsules still being in place. Also it was observed that very few plants were flowering this year, with flowering plants standing out against the green mass.

Using the combined (old plus new) bud data as total flower production and comparing this with the production of new shoots measured, it can be seen (Fig. 3.2.3b)) that there is probably a fairly constant "failure rate" for shoots developing into buds. The discrepancy between hypothetical and that observed could be due to the data for flowering having been collected in an open environment whereas that collected for shoots was from a riparian habitat. Also the "lag effect", just described and observed in the field, of the inability of new shoots to flower the same year of production must be taken into account. Even so this disparity between the number of new shoots and the total numbers of flowers produced seems large and evidence for a certain degree of shoot failure was observed in the field, with some buds appearing brown and shrivelled and some shoots not developing bud terminations at all.

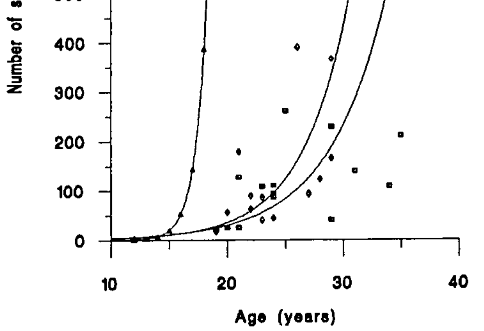


Figure 3.2.3b) Total flower (■) and new shoot production (◆) with age, all samples being aged using the tree ring chronology technique. The hypothetical curve of new shoot production (▲) was calculated from a field estimate of the bifurcation of growing apices with age.

Figure 3.2.3b) demonstrates the huge discrepancy between the number of shoots observed in the field and the hypothetical number produced by "model" plants, which suggests shoot failure is a real phenomenon. The hypothetical was calculated using data collected from the field which suggested an average shoot production per stem apex termination of 2.7 new shoots (= total new shoots/bud terminations producing those shoots, i.e. 664/246 = 2.7). Thus, although it was initially intended to use a model of the exponential increase in the number of shoots, and hence flower production, to give an idea of seed production with age, it seems that this idea would have produced unacceptably inaccurate results and was too simplistic to represent the real world situation with its additional complications. Using this average measure of shoot production with increasing age, and with bud termination during each year and thus the production of new shoots from every apex, would, apparently, have produced an artificially high estimate of flower and thus seed production. This is because such a simple model of seed production does not include failure rates of shoots once produced, of flower buds and of each apex to produce the average number of shoots.

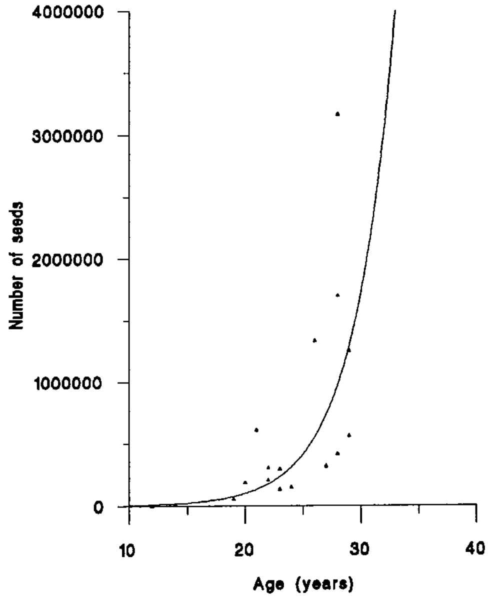


Figure 3.2.3c) Seed production with age, calculated from seed production data per flower head obtained from the literature and estimates of total flower production measured in the field.

Seed production *per cohort* was calculated firstly by multiplying the total flower production data up into seed production (Fig. 3.2.3c)) using Cross' data, and then by using an exponential equation fitted ($r^2=0.77$ $p<0.01$) to seed production with age, total seed output for discrete cohorts was calculated., it being remembered that seed output is probably for a two-yearly period.

This total seed output per individual per 12 year cohort period was then divided by 6 (because each seed production tallied to give the total was calculated by rounding ages down to the nearest "even" age, with an age of first flowering at 12 and seed production after this being for the hypothesised two-year cropping cycle) to give an average total seed production per cohort. This measure was used rather than the total because I believe that it came part way to overcoming a simplification of the model whereby all individuals within a cohort are adjudged to have the same age. This is not a true reflection of the field situation where a cohort is more likely to have an even age distribution, and so to impart this reality, upon the model, of differential seed productions from plants of differing ages within the same cohort class, the average was used. This average represents the yearly seed output per plant of a cohort present in the model.

A problem that is apparent in many of the relationships so far expressed is the tendency, with the fitted exponentials, on the steepest parts of the curve to get unrealistically high increases in width, height, stem area, flowers or seed production with small increments in age. Looking at the graphs in this light it can be seen that there is evidence of deviation from the exponential and often a closer approximation to a logistic function. Also in the field it was apparent that bushes seemed to reach a certain size and with ageing did not seem to be getting "infinitely" bigger as the exponential suggests. The idea of logistic growth of individuals is not new in biology and has been shown in many case studies. Although logistic curves may have fitted the data more precisely, the difficulty of fitting logistics meant that the exponential approximation was used. The exponential was still used for the calculation of ages, because this represents the start of a logistic curve and would be ample for measuring young populations. The levelling off associated with a logistic curve of growth and production for older plants would be implemented on the seed dispersal data as a threshold ceiling level to the exponential, which is somewhat unrealistic but is the best approximation available. The threshold was to be accessed through the calculations of the average width of a mature bush, which assumed bushes with square shaped canopies that fitted into the rectangular quadrat areas studied as in table 3.2.1. Therefore from these "square" areas occupied by a bush, the average width a bush could extend to was denoted by the square root of the area. The value used as the maximum hypothetical width obtainable was thus 3m, but when this is fed into the equation generated by the exponential fitted to figure 3.1d) it produces an age of maximum spread at about 30 years. From the graph this is obviously too young since width measures greater than this were obtained from older specimens in the field. Also in the stands sampled cover was 100% and so these bushes may not represent those in less competitive situations, and also it was observed that bushes were extending vertically rather than horizontally with the age of the stand.

Using logistic curves fitted to the data sets by hand (as shown in the figures), the tail off in production seemed more closely associated with the 50-60 year age group, and so the start of the 60-72 year cohort was assigned as the threshold beyond which seed production could not increase, it staying the same as the previous cohort.

Seed productions per cohort, shown in table 2, were calculated using the equation relating age to seed output, the equation had the form:-

$$y = 337.84 \times 10^{(0.124x)}$$

where y = seed output and x = age in years (up to 58 years, because 59 rounded down).

Table 3.2.3: Average individual seed output totals for the discrete age span cohorts used in the model.

Cohort number	Age span (years)	Seed output
1	0-12	0
2	12-24	123074
3	24-36	1432212
4	36-48	16666608
5	48-60	36726555
6	Cohorts > 60	36726555

3.2.4 Distance over which seed is dispersed (H *or* R*).*

Figure 3.2.4a) shows the establishment histogram for seedlings with distance from the hypothetical parent. This shows the combined datasets from the discrete populations from the three differing habitat types identified, with truncation of the individuals according to age.

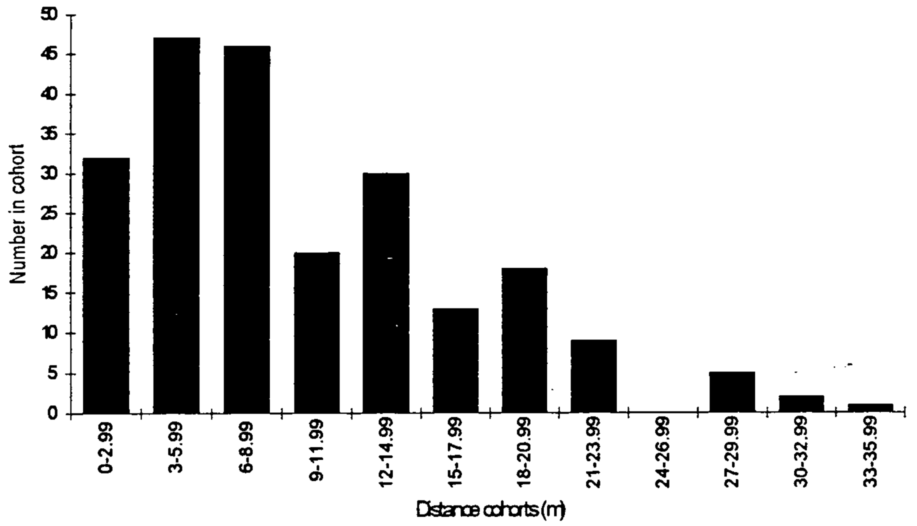


Figure 3.2.4a) The combined datasets from the three habitat types for seedling distributions with distance from the hypothetical parent/seed source. The distributions are age truncated.

The data for established seedlings with distance from the parent plant was assumed to reflect the pattern of seed dispersal and so the curve fitted to this distribution would be used as the function - in terms of its half-distance (*H*) or root-mean-square distance (RMSD) (*R*) - for seed dispersal.

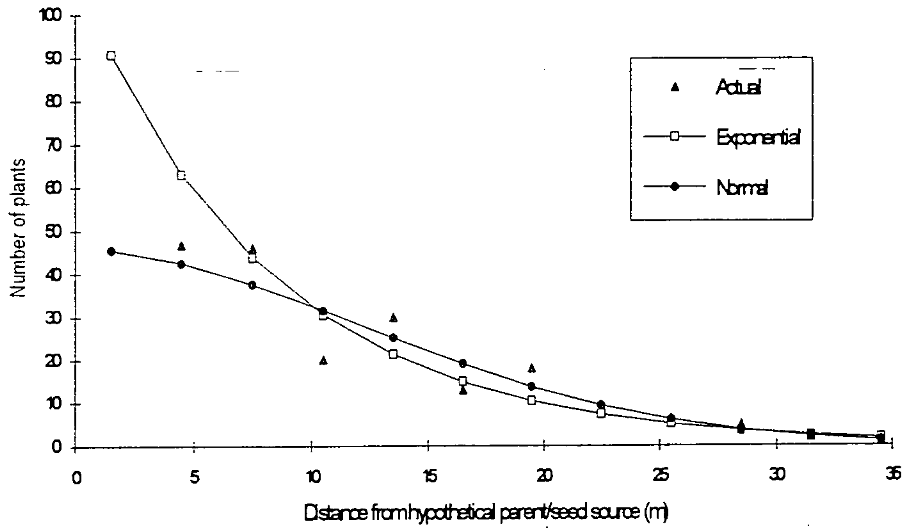


Figure 3.2.4b) Exponential and normal curves fitted to the seedling distribution data truncated for age.

The numbers of plants established in each distance cohort were plotted against the median distance values in each class, and curves fitted using 'Curvefit'. The 0-2.99m cohort values were not used in the fit because it was thought that the lower value compared to the next distance class probably represented the influence of the parent plant on the establishment rate of seedlings. The fit achieved by the exponential was high, $r^2=0.92$ $p<0.01$, although the fit achieved by the normal function was higher. The fitted normal and exponential functions are shown in figure 3.2.4b).

The values for the intercepts of the curves are given in table 3.2.4 as are the general forms of the equations fitted.

Table 3.2.4: The intercept and slope values of the curves fitted to the field data for the dispersal function.

Equation type	Formulae	'A' value*	'B' value*	'C' value*	r^2 value
Exponential	$Y=A.e^{(B.x)}$	108.74	-0.12	0	0.92
Normal	$Y=A.e^{[((xB)^2)/C]}$	44.23	0	-326.22	0.96

* the 'A' value is the y intercept for both curves, the 'B' value is the gradient of the slope of the exponential and the 'C' value is the gradient of the slope of the normal fitted.

The values given in table 3.2.4 can be used to calculate the half-distance of dispersal for the exponential function or to calculate the root-mean-square distance of dispersal (RMSD) for the normal distribution of seedlings. To calculate the half-distance the equation needed is:-

$$-(B) = \ln 2/d$$

where 'd' = the half-distance; therefore the half-distance = 5.73m.

For the normal curve the equation needed to calculate the RMSD value is:-

$$-(C) = R^2$$

where R = the RMSD; therefore the RMSD = 18.06m.

3.2.5 Probability of seed survival between generations (P).

The population is structured in terms of twelve year periods for the number of plants established, as shown in table 3.2.5, but the seeds contributing to the number of plants establishing in these cohorts was calculated from the sum of singular hypothetical seed productions with age for each older plant able to contribute to the cohort in question. This seed output being for two-yearly periods, the output value being calculated from one age value (which if odd is rounded down to the nearest even number, because the process starts at 12 years of age) being passed through the relevant equation (as used above for the calculation of average seed outputs for cohorts) to count for the whole production during the two-year period. The whole process of calculation of who contributes to whom follows the population back through time until the population dwindles up to the point when the original parent arrived at the site.

Table 3.2.5:-The number of established plants in discrete sub-populations of three habitat types as a proportion of the number of seeds hypothesised to have contributed to these individuals.

Habitat type	Cohort span (yr)	Plants	Seeds contributed	Proportion established
Riparian	(0-11)	67	7785724	8.61^{-06}
	(12-23)	26	1919637	1.35^{-05}
	(24-35)	21	155748	0.000135
	(36-47)	1	12748	7.84^{-05}
	(48-59)	1	unknown	-
Open	(0-11)	62	14994787	4.13^{-06}
	(12-23)	29	489560	5.92^{-05}
	(24-35)	6	unknown	-
Ride	(0-11)	108	1150314	9.39^{-05}
	(12-23)	118	26369	0.004361
	(24-35)	2	unknown	-
			TOTAL	0.004754/8
			AVERAGE	=0.000594

The average value for the proportion of seeds contributing to the number of plants within a cohort was calculated by dividing the total by 8 (the number of calculations made) as shown in table 3.2.5. This gives the average proportion developing through time within and between habitats.

It had been hoped that a similar method to that suggested for calculating the actual number of seeds contributing to the plants in a linear as opposed to a circular feature could be worked in reverse, so as to calculate the number of bushes that should actually be present in a distance cohort whose area covered a circular annulus rather than two segments of this annulus as represented and sampled by the corridor habitats. Thus the data was to be multiplied up to give an idea of the numbers of plants that would have been present had the ride or river habitats been circular, allowing direct comparison and merger with the open habitat data. This method though was found to exaggerate single finds at longer distances and to exaggerate the difference between the find of one bush as compared to none within a distance cohort. This method destroyed any resemblance of the curves obtained to any describable dispersal function and so it was not used.

The data in table 3.2.5 was to be used to calculate the probability of survival from one cohort to the next. This idea though would suggest that the proportion of seeds apparently establishing should decrease with cohort age, but an initial survey of table 3.2.5 reveals that the opposite trend is observed in all 3 habitat types, with the proportion of seeds becoming established decreasing through time to the present. It is suggested that this general trend represents the decreasing availability of suitable establishment sites around the parent bush through time due to intrapopulation competition for space and resources, and possibly to some sort of environmental change through time that has affected the establishment rate.

Thus it was decided that the probability of initial establishment and the entry of plants into cohort 1 was the only "cull" point to possible plant production, there being no further death with plant maturation past the age of 12. This was decided predominantly on the basis of 2 main observations. Firstly, seedlings between the ages of 3 and 7 were observed to suffer desiccation stress when in moss on the tops of hummocks and from trampling or top removal through grazing. Secondly, even with a complete survey of the whole site, no bushes past the age of reproductive maturity were observed to have died. Some growing in bog environments showed signs of deficiencies, but they were still able to flower.

3.2.6 Observations leading to the construction of habitat maps (K).

The differences between unfenced and fenced or otherwise protected habitats was at the crux of the decisions made as to the carrying capacities of different parts of the overall study site through time, and it was thought that in general *Rhododendron* establishment was highly correlated with grazing patterns in the area. The reason for this conclusion was based mainly on qualitative observational data although the limited quantitative data collected is in accord with these observations.

Quantitative data were collected in support of the observations made during the fieldwork period, not only for the microtopographic and habitat avoid the confounding effects of habitat change through time in vegetation due to shading by more mature individuals), but also for the saplings of other woody taxa found during the fieldwork period. This data is not only of use for making valid carrying capacity judgements for certain habitat types included as model parameters (in habitat maps), but is also of interest to the more applied side of this project. Tables 3.2.6a) and 3.2.6b) show the relationships of *Rhododendron* seedlings to certain habitat features and vegetation types in open habitat types and the relationships of tree saplings to habitat features, and perhaps more importantly to *Rhododendron*.

Table 3.2.6a): The micro-scale associations of *Rhododendron* seedlings with certain features of the open habitat environment, which is freely grazed by deer.

Physical feature		Number of plants	Evidence of damage *
"*Molinia* tussock"	Top	24	18
	Base	17	0
Drainage ditch		28	9
Slope angle (°)	0-30	28	20
	30-60	7	3
	60-90	34	4
Plant associates			
Finer mosses		36	9
Sphagnum spp.		19	17
M. caeruleus		9	0
Bare soil		5	1

* Damage includes that which appears to be due to grazing or trampling (assumed in the cases where the growth point has been removed and growth has become sympodial prematurely) and that due to desiccation (defined by leaf wilt and/or browning and drying). Damage due to nutrient deficiencies (excluding water), disease or wind blast is not included. Damage includes death of a plant, this simply reflecting an extreme.

Table 3.2.6a) shows *Rhododendron* seedlings have a high association with the base of *Molinia* tussocks as opposed to the flatter tops, no doubt due to the damage inflicted, predominantly on seedlings, on the more exposed tops. Some plants were suffering desiccation stress and others had become sympodial at an early age on as many as four different occasions because of the removal of growing apices. The cause of this damage was not clear though, and could have been due to grazing or trampling. Considering the observed proportion of the habitat surveyed accounted for by drainage ditches, there was a high proportion of seedlings establishing in these microditches, there was a high proportion of seedlings establishing in these micro-habitats. This effect was probably due to selective exclusion from other more exposed habitats due to grazing, trampling or desiccation. Rooting of seedlings in *Sphagnum* rendered them liable to desiccation, especially during a two-week period of dry weather at the end of May. Although frequency data for the various biotic and abiotic parameters at random points within the study site were not obtained, it was obvious that the largest portion of the habitat was made up of the "flat" tops of *Molinia* tussocks, the runnels and drainage ditches running between these, as assessed from aerial photographs, made up less than 30% of the habitat. Many of the habitat variables identified in table 3.2.6a) are interrelated such that the best way to describe the micro-habitat associations of *Rhododendron* seedlings observed is through diagrammatic representations of the typical ecological associations of *Rhododendron* to habitat features noted in the field:

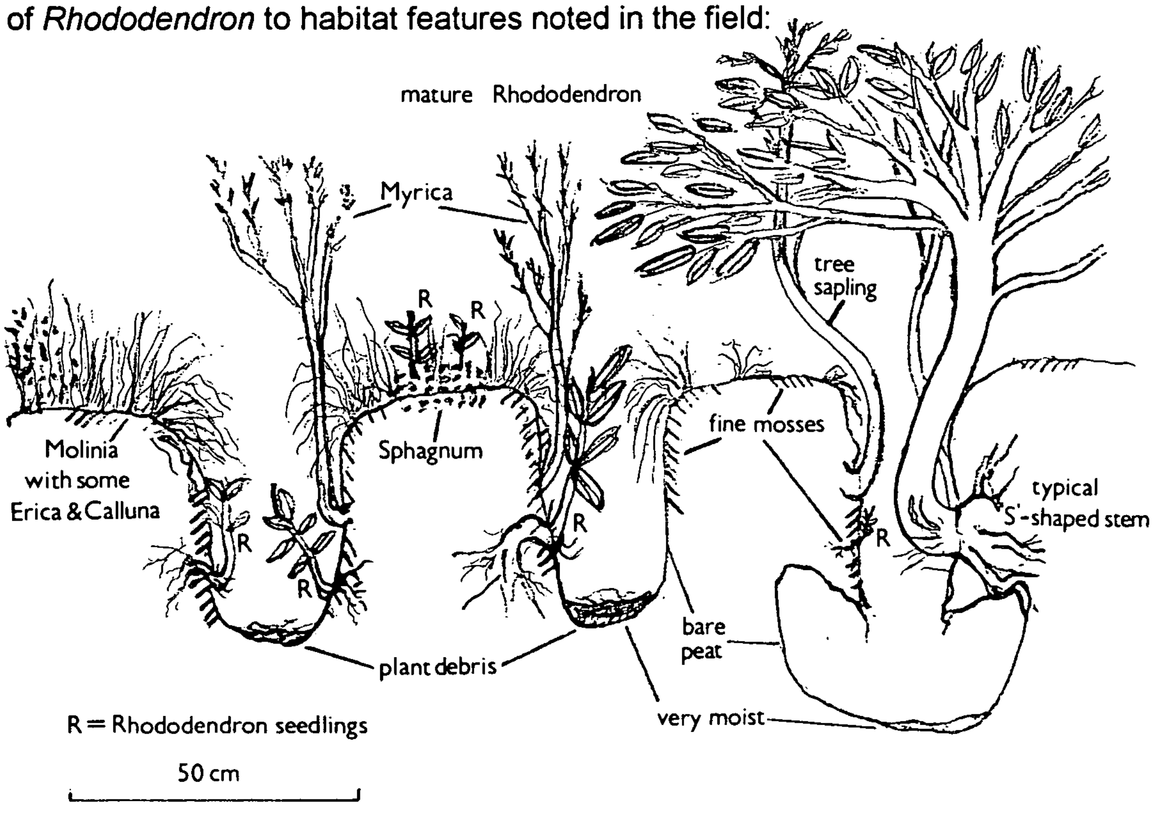


Figure 3.2.6a) Typical micro-habitat associations of the seedlings of *Rhododendron ponticum*, observed in the field, showing the importance of microtopography to *Rhododendron* establishment and the importance of the vegetational composition of the "gap" exploited.

The physical and vegetational features classified in table 3.2.6a) and shown if figure 3.2.6a) have underlying features in common. For instance, the habitats are probably highly disturbed by water which could create gaps for the establishment of *Rhododendron* directly, or indirectly through the formation of a safe site for fine mosses. Also the environments utilised have features offering protection, not only by being inaccessible to grazing and trampling but also by providing a moist microclimate for seedling survival.

Habitat information collected on older plants followed the patterns suggested at the seedling stage, with many being rooted to the sides of drainage ditches or coming from the bases of boulders in dry stone walls and in the gravel outwash environment of river and stream floodplains, and from between the pebbles of finer screes. Again these physical features of the habitat represent a minor component compared to the vast amounts of open grassland habitat.

A pattern observed in open habitats between mature and immature plants was that seedlings suffered much damage whilst adult bushes only showed slight damage. Damage of adult plants was never entire and included bark fraying or mechanical damage of shoots, leaf spotting, and leaf death on the windward sides of bushes, probably due to wind blast. A different pattern of vulnerability was observed in the riparian environments where large plants were snagging the dead plant material carried by rivers and streams at times of flood and were thus suffering mechanical damage. Compared to similar aged plants in ride habitats, plants in riparian and open habitats were characterised by much regrowth and suckering from the bole.

It was interesting to note that the youngest plants growing along rides often grew on the flat amongst the grasses and other herbs and mosses, on disturbed banks, with the older founder plants rooted in the sides of drainage ditches or between the boulders of stream channel banks. The seedlings as shown in figure 3.2.6b) were profuse and showed none of the signs of damage observed in the open habitats. The populations these older plants had produced made sections of ride impassable.

Figure 3.2.6b) The associations of seedlings in ride habitats with the moss cover of disturbed banks. Little damage of seedlings in ride habitats was observed.

The sample used for table 3.2.6 included virtually all singular plants come across in the mapping phase of the project in the open habitats, especially in the sampling of the open habitat sub-population described in sections 3.2.4 and 3.2.5 above. The habitat relations of all other isolated plants were also noted for river and ride habitats, again especially at times of sub-population examination. I believe, therefore that the results are a good representation of the affinities of *Rhododendron* for certain features of the landscape and of the selection pressures exerted by the environment on the establishment of *Rhododendron*.

Whilst surveying the site observations were made on other woody species in the area, which seemed to follow many of the same patterns as *Rhododendron*.

Table 3.2.6b): The associations of the saplings of tree species in the glen with physical features and other features hypothesised to offer protection from grazing.

Habitat feature	Height class of sapling* (m)		
	0-1	1-3	3-6
Grass	67	0	0
Grass/*Calluna*	5	0	0
Molinia	15	0	0
Molinia/Pteridium	5	3	0
Molinia/scree	6	0	0
Rhododendron	3	39	21
Rhododendron/Molinia	0	1	1
Rhododendron/Pteridium	0	1	0
Rhododendron/scree	0	1	1
Pteridium	15	2	0
Fence line/wall	8	15	8
Boulder	6	4	0
Rock face	2	14	7

* sapling species and their percentage contributions to the sample: *Betula* spp. 39%: *Quercus petraea* 15%; *Sorbus aucuparia* 12%; *Alnus glutinosa* 8%; *Acer pseudoplatanus* 7%; *Fagus sylvatica* 6%; *Ilex aquifolium* 3%; *Salix caprea* 3%; *Pinus sylvestris* 2%; *Fagus sylvatica* 'purpurea' 1%; *Aesculus hippocastanum* 1%; *Larix* sp. 1%; *Fraxinus excelsior* 1%; *Picea sitchensis* 1%.

Data was collected on the habit associations of tree saplings at the more micro-spatial scale (table 3.2.6b)), because it was thought that this might shed some light on the reasons for the similarities in distributional patterns. The relationship of tree sapling height to the progression of the invading front of the *Rhododendron* population and even to the canopies of individual bushes was of particular interest.

The tree species, when analysed individually, show significant affinities for habitat features, and when analysed as a whole there is a statistically highly significant association between sapling heights of all species encountered and certain habitat features ($\chi^2 = 186.72$; $p<0.001$).

In particular, larger tree specimens (1-6m in height) were associated with the rock faces sampled and the *Rhododendron* population. Larger specimens were underrepresented in fine grass and *Molinia* environments, which along with bracken (*Pteridium aquilinum*) harboured the smallest height class of sapling, there being many more observed in association with these vegetation types than expected. *Rhododendron* also supported smaller saplings at a frequency higher than expected.

Larger saplings are also common along fence lines, especially with *Quercus petraea* (sessile oak), and dry stone walls and coming from the base of large boulders, as was particularly observed for *Ilex aquifolium* base of large boulders, as was particularly observed for *Ilex aquifolium* (holly). These specific correlations are somewhat superficial in that they often represented proximity of a likely seed source. The general correlation, though, between these physical features and *Rhododendron* in allowing the establishment of larger trees suggested to me that they were all performing similar roles and had some underlying feature or features in common. The nature of this parallel is enforced when it is realised why the saplings of other habitats, such as those of the open grasslands, are so small. It is not that all of these saplings are younger but rather that they have been heavily grazed. *Rhododendron*, in common with the natural and artificial physical features described in table 3.2.6b), it seems, provides a niche for escape from grazing pressures. For example, one bush of little over a metre wide in an open situation was observed to have a specimen of *Betula*, *Sorbus* and *Picea* growing under and just through its canopy, it also harbouring larger specimens of *Myrica gale* (bog myrtle) than the surrounding area (the typical growth form of protected saplings is shown in figure 3.2.6a)). This phenomenon, on a larger scale, was particularly visible in the birch trees growing on the hillside behind the Druimachoish Post Office as shown in figure 3.2.6c).

Figure 3.2.6c) The relationship of tree sapling height to the "front" of the *Rhododendron* invasion on Creag Dhubh behind the Druimachoish Post Office and Lodge gardens. The majority of the sapling trees seen in this picture are *Betula pubescens*.

Here a clear gradient in height of birch from large to small at the edge of the main *Rhododendron* encroachment is visible. Judging by the gradient in height of the *Betula* it seems plausible to suggest that the date and rate of invasion could be calculated from a knowledge of the age of these trees obtained through stem sections.

Patches of *Pteridium* near potential seed sources were observed to contain some larger sapling specimens, although these again showed evidence of grazing damage. *Pteridium* also had an associated under storey of relict woodland flora plants such as *Hyacinthoides non-scripta* (bluebell), *Primula vulgaris* (primrose), *Oxalis acetosella* (wood sorrel) and *Anemone nemorosa* (wood anemone).

From the general observations and semi-quantitative data analysed above 5 general conclusions can be made as to the nature of probable *Rhododendron*/habitat interactions taking place in the glen:

1. The exploitation of linear features of the habitat by *Rhododendron* followed the patterns of utilisation by other woody taxa in the area. This does not suggest to me that the other habitats are unsuitable to the autecology of these plants but that the grazing pressures characteristic to the glen prevents their establishment. Also this is only an observable pattern at a distance, closer examination reveals the presence of many tree species saplings in a "bonsai" state due to grazing, and also an abundance of newly germinated seeds. Table 3.2.6 demonstrates the associations of the saplings of the tree species in the glen with physical features such as the ledges of rock outcrops or fence lines or other features providing protection from grazing. Therefore I would not propose that *Rhododendron* is confined to these linear habitats due to its requirement for disturbance to become established or because of some other feature of these environments, but rather, as for the other woody taxa, that grazing pressure confines *Rhododendron* to these habitats. If the autecology of *Rhododendron* required disturbance to become established then intensively grazed habitats should represent an ideal.
2. Areas fenced for sheep pens and with high stocking rates and thus intensive grazing, had no *Rhododendron* in them, even though the areas juxtaposing the fences often had a 100% cover of mature specimens. Rather than this representing some fluke of alignment of the fence along the

threshold of a habitat gradient in some vital resource, I suggest this represents the repressive effects of intensive grazing on a woody taxa.

3. In connection with point 2, fencing of forestry permitted establishment and encroachment of *Rhododendron* into habitats between the fence and the forestry, although not into the same habitat beyond the fence which was freely grazed.
4. The *Rhododendron* was also found in associations with more microtopographic features of the landscape characteristic to other woody taxa and other evergreen shrubs such as *Ilex aquifolium* (holly), *Ulex europaeus* (gorse) and *Cytisus scoparius* (broom) and yet the habitat preferences of these species for these particular habitats would not be considered as the true reason for these species being where they are.

Therefore, overall it was decided to map areas of suitable habitat rather than areas of unsuitable habitat, because from the field evidence at the Glen Etive study site it was impossible to say which habitats were suitable or unsuitable outside of their grazing regimes.

It was thought initially from the findings reported in the literature that the positions of bog features would be important and detrimental to the spread of *Rhododendron*, but it was found that *Rhododendron* could grow quite well in these environments and that the bogs were not of sufficient extent to significantly affect the dynamics of invasion at the scale of study in question. Also the initial survey of the site just after winter pointed to the possibility that bracken (*Pteridium aquilinum*) patches were not utilised by *Rhododendron*, but this was hypothesised from the pattern of the brown remains of the bracken which were thought to represent the extent of the extant bracken patches. In the spring it was revealed that these patterns of accumulated remains bore little relation to the actual pattern of distribution of the bracken in the habitat where this phenomenon was seen and bracken is in fact less clumped and more evenly distributed than initially suspected.

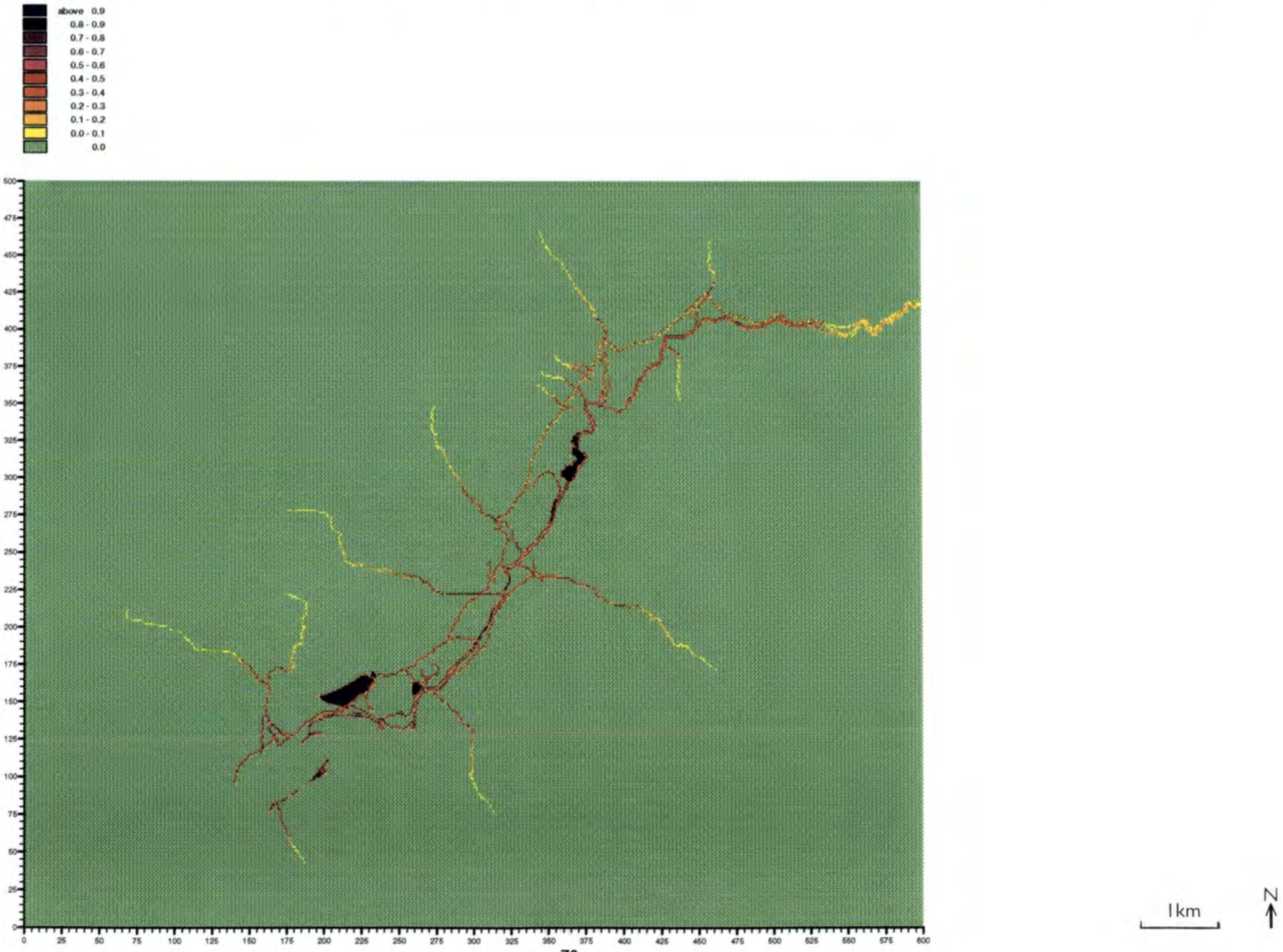
Therefore, overall, the only features of interest to be digitised into GIS coverages included linear (or arc) features such as fence lines, roads, rivers and rides, and area (or polygon) features including forest block compartments, lochs and areas with different grazing regimes or histories. From observations there was little to suggest that *Rhododendron* was limited by altitude with healthy plants being found to heights of 300m. Grazing regimes formed the underlying coverage on which all else was overlaid.

Roads, rides, fences and lochs were characterised as being of only one type, each having one possible estimate of carrying capacity. Rivers were divided into two types based on their major or minor character (>3m wide and <3m wide respectively) and each code was given a representative measure of its carrying capacity. The digitised forest blocks were divided according to three definitions of their species character, i.e. whether they were *Picea*, *Larix* or *Pinus*, with more minor species being characterised as the closest type in terms of density of the canopy cover. The sub-compartments of the forestry block were also grouped according to their planting dates into cohorts of 12 years starting from the initial planting date of the *Rhododendron*, such that planting, thinning and/or felling regimes could be simulated through time in the habitat maps.

Some of the changes in habitat carrying capacity through time in the glen are shown in figures 3.2.6d),e) and f). These show static features in the landscape and those of a more dynamic nature, and also the mosaics of habitat suitability through time and their associated measures of carrying capacity. The dynamic aspects mainly represent fencing histories, for example figure 3.2.6d) shows the areas fenced initially around the Lodge, this fencing protecting the ornamental shrubs planted and the vegetable patch seen on the aerial photos from grazing. These fences degrade through time having a negligable effect by 1958. Forestry fence construction in 1960 is simulated as a change of habitat suitability in 1958. At this time large lengths of ride became suitable for colonisation.

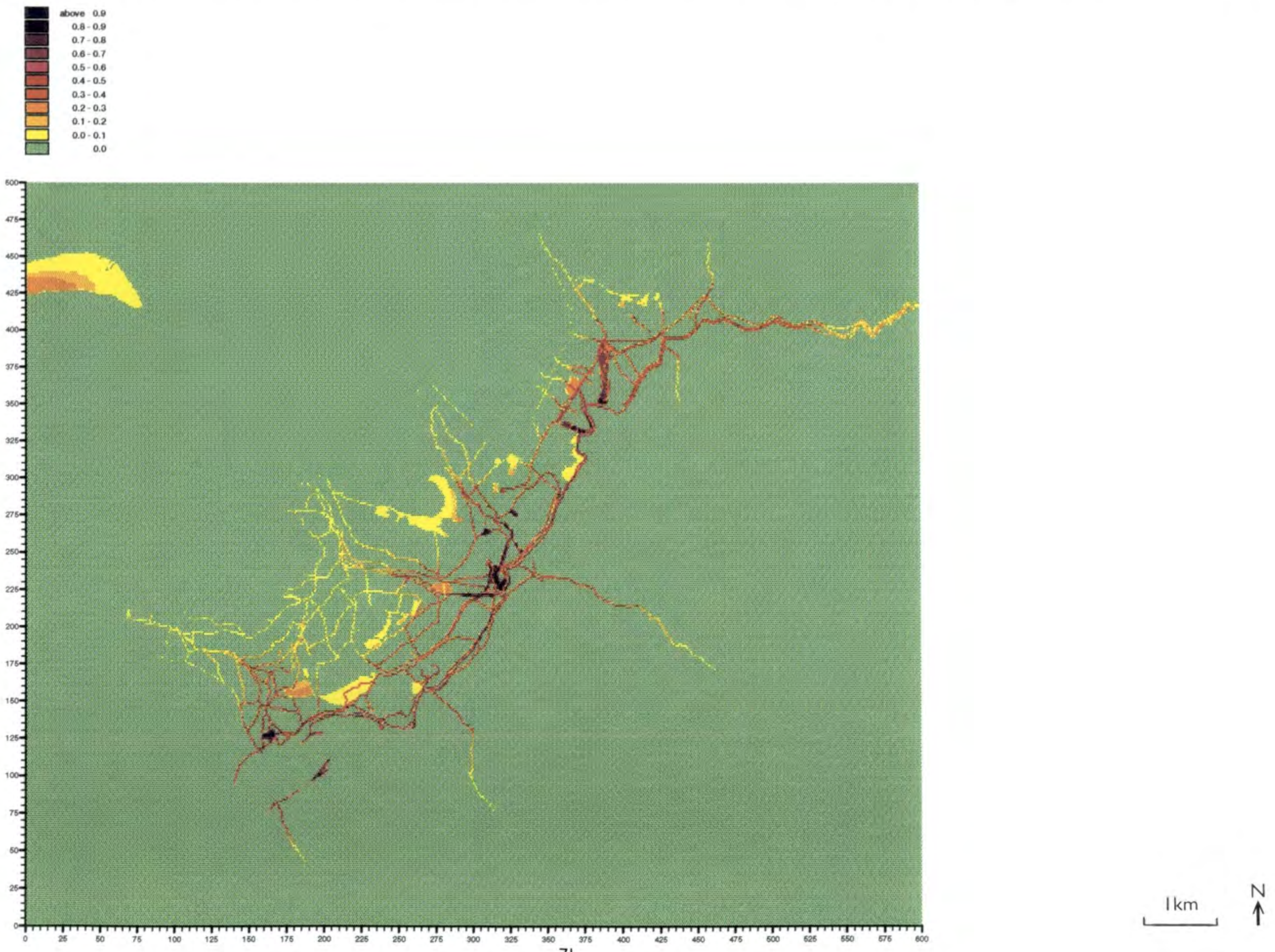
The initial carrying capacity map for the Glen Etive study site.

Fig. 3.2.6d)



The mosaic of habitat suitabilities in the glen by about 1958.

Fig. 3.2.6e)



Relative carrying capacity (K) map for the present day.

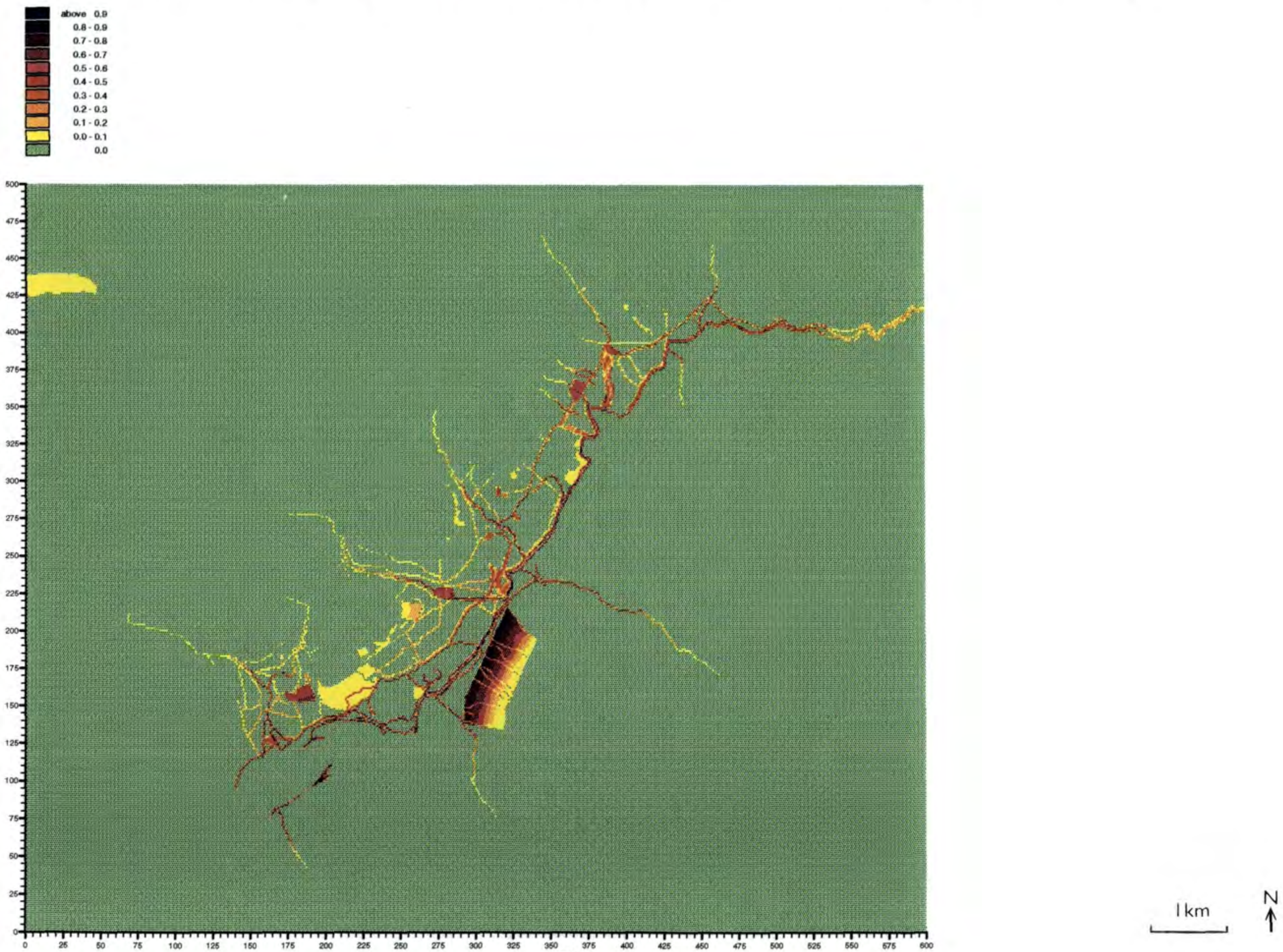


Fig. 3.2.6f)

When previous fieldwork in the area was carried out in August of 1992, the forestry fence was still intact, by the time of the current project the fence had mainly been taken down to allow grazing access on rides. Thus the habitat map for 1994 (figure 3.2.6f)) shows this decrease in suitability of fence line, ride habitat, and areas occupied by mature forest blocks, where they are not independently fenced. The map for 1994 also shows a new rectangular area of high suitability where a new deer fence was erected this year around a patchy hillside stand of deciduous trees.

Unless otherwise stated, the code for lochs was assigned a value of 0, as were areas exposed to grazing. Fenced or otherwise protected areas, such as river gorges were assigned carrying capacities of 1, as were rides and fence lines, when the Forestry Commission fences were erected. Roads were given a value close to 1 because although the tarmac surface is inhospitable to colonisation the drainage ditches dug alongside appeared highly suitable. Fence degradation with time was introduced as sudden changes in grazing pressure although not down to 0 carrying capacity as the plants established were seen to create their own impenetrable barriers. Maturation of forestry blocks was represented as a gradual increase in carrying capacity after 36 years, it being observed that mature stands had an under storey of *Rhododendron* whereas thicket stage blocks had none. Altitude was represented by a gradient of 10% decreases in habitat suitability with each 25m interval from 50m.

3.2.7 Initial points of introduction for Rhododendron ponticum.

The foci of the initial introductions of Rhododendron into the study area were determined from aerial photographs in conjunction with tree ring chronology of samples collected from the most mature stands. Two areas of initial introduction were identified, the grounds of the hunting lodge, where specimens up to 82 years old were collected and the peninsulas jutting into Lochan Urr where 81 year old samples were recorded. This represents an initial introduction to the glen of about 1910, the year suggested by the stalker for the completion of the hunting lodge. Attempts to determine ages were hampered in many cases by the apparent control cutting that had been undertaken. The number of plants introduced initially was set at 38, 30 along the drives to and from the Lodge, and 8 at the Lochan Urr site on the two peninsulas (see figure 1.3).

3.3 The present-day distribution and abundance of *Rhododendron* in Glen Etive.

The survey of the site revealed three primary types of cover, singular plants, areas of 90-100% cover and areas of intermediate density. For a 10m grid working in terms of bushes per hectare, it was suggested that density classes be assigned according to order of magnitude increases in numbers of plants present from single individuals to areas of 100% cover. Figure 3.3 is the present–day distribution of *Rhododendron* in the three density classes as determined from the field survey of the area. The area was intensively surveyed, with every ride and water-course being investigated, often to its mountainous source. The area covered on foot often went well beyond the last individual encountered. Forest blocks were surveyed from high vantage points using binoculars, and likely patches of *Rhododendron* distinguished were investigated on the ground. The distribution can be compared to the transparent overlay of 5 of the coverages digitised for the area (Fig 3.3).

A map of the landscape attributes used as initial coverages in the GIS.

3.4 Output from the model.

The figures presented to demonstrate the actual predictions made by the model are arranged in an order representing the logical development of the project. The main changes made to the model input were ones involving the habitat maps with the biotic parameter values determined being kept constant. By keeping as much information as possible the same, and changing very few other variables the causes of effects observed are easier to pin down. Many specific combinations that were tested are not produced, the results only showing a representative sample to get a feel for the modelling process. All but the last simulation use the same biotic parameter values given in the results section, as determined by the field methods used. A summary of these values is given as part of the header information in each figure for each model run. These figures are rounded for the first P_{survive} value and for the value of H0 in the header display, although the values actually used by the model in its computations are those given in the results section.

Except in certain cases, the final picture seen in a model run is reproduced in the next figure at a larger scale, so that the detail of the pattern can be examined and comparisons to the actual present day distribution made. The header information for the whole model output in each case also contains additional information to the parameters outlined in section 1.7.2, including:

Notation	Description
H1	Half-distance displacement of seed via the long-distance dispersal function (km) (H0 being the half-distance of short-distance dispersal determined in section 3.2.4).
P(H0)	Probability of seed dispersal according to the short-distance dispersal function (H0).
P(H1)	Probability of seed dispersal according to the long-distance dispersal function (H1).
k_mod	A habitat modification parameter, available, which it was unnecessary to use during this project.

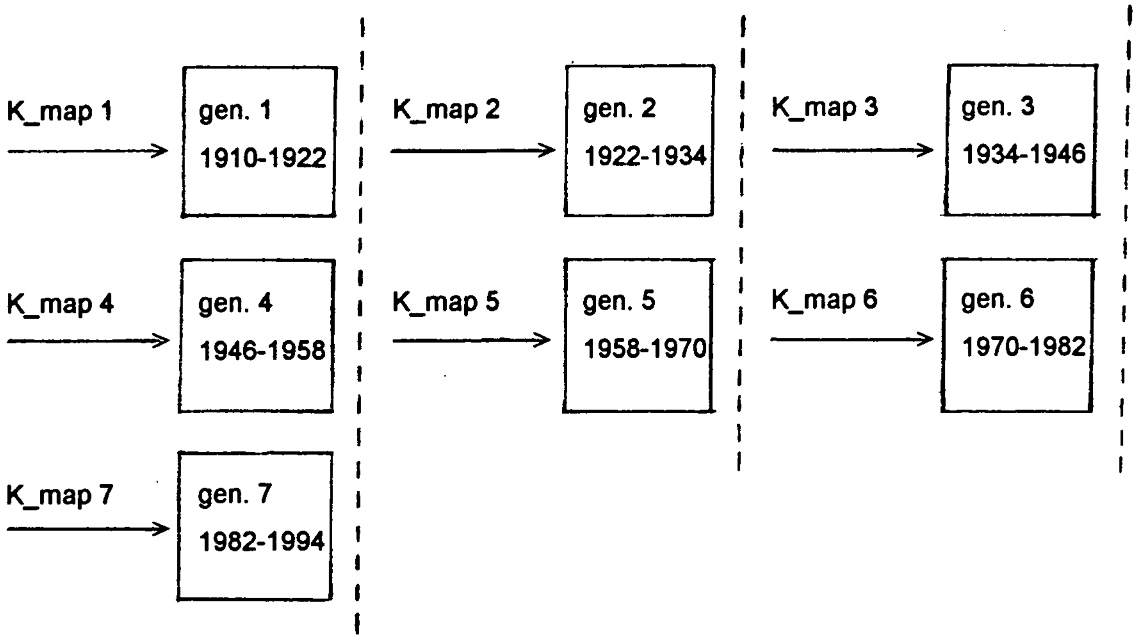
The dispersal of seeds according to a long-distance dispersal function in terms of its half-distance and probability of occurrence is set in all but the last figures given. The values for these parameters arrived at for use in the other simulations will be discussed. These values could not be determined from the field and were added through a process of trial and error.

The term *'L'*, which denotes the length of a cell side of the MIGRATE grid is very important and is assessed in relation to the dispersal distances characteristic of the plant and to the detail of the pattern of spread required. Cell size also affects computation times. Thus a cell size of 0.01km was chosen for all simulations, giving a value for *A* of $100m^2$, which means that the presence of one individual in a grid cell would give a density measure of 100 bushes per hectare. The maximum permissible density, whatever the cell size of the MIGRATE grid is 2900 bushes ha^{-1}, i.e. 10000/3.44.

The density measures given for whole model outputs show 10 density classes, whereas the GIS conversions for generation 7 of the model output, and the other single generation outputs presented, show 3 density classes. This is because the 10 classes have been "sliced", using GRID, into the 3 density classes used to classify the present-day distribution.

Other terms shown in the header information such as "Amalgamation", "Furthest cell" and "Dispersal sums" relate to the structure of the model and are of little importance to the results of this project. Suffice to say that these measures were kept constant, allowed rapid computation times (because cells too far away to receive seed input were not considered), whilst allowing for rare dispersal events to be "captured". The model amalgamates grid cells into larger cells working with larger scale processes to save on computational effort. The closer the total dispersal sum is to unity the greater the efficiency of the model grid set-up in relation to the dispersal distances used. The "Random number of seed" measure given in the simulations represents the only stochastic process taking place in the model, and is used to create whole numbers in cases of fractional production.

The layout of the print outs are mainly as follows:



Variation on this set up of generation interval output for 7 generations occurs when "predictive" runs are used which span 10 generations with output at 2 generation intervals. For these "predictive" runs, future habitat maps are made based on that constructed for the present-day, according to the rules of change already established for the normal simulations. The term "predictive" is used here to denote simulations of possible *future* changes, although all runs of the model can be considered predictions of a sort.

Titles for most figures are brief due to constraints imposed by the graphics output page. Full descriptions of the figures used will be given in the text.

The aerial photos for the area were for 1946 and so could be compared directly to the model output for the end of generation 3. Generation 1 represents the initial maturation period of the *Rhododendron* seeded in at 1910. The 12 year cohort periods from this time lead up to 1994 and so this predicted distribution can be compared directly to the distribution mapped in the field for the present-day. The initial habitat map (K_map) inputted into the model is shown in figure 3.2.6d), that for the beginning of the model calculations for generation 5 for 1958 is shown in figure 3.2.6e). Figure 3.2.6f) shows the habitat map for the present-day (of use to the predictive runs of the model) representing K_map 8 in the above diagram.

3.4.1 Conventions used in the map and model graphics.

It is important to note that all axes on all output are the same:

one unit = 2km; sub-divisions = 400m in 7 generation outputs and 200m in 10 generation outputs.

Similarly, for all output, including GIS grids (unless otherwise stated), as with map convention, north is towards the top of the page.

The behaviour of the model under different scenarios of parameter values for the components of the habitat maps, and in one case for the biotic parameters measured, is described in the following sub-sections.

3.4.2 Spread of Rhododendron *through a homogeneously suitable habitat.*

Figure 3.4.2a) shows the slow build-up of the *Rhododendron* population until the third generation. The core areas of introduction have produced dense populations, but have yet to spread. The distribution of *Rhododendron* seen at the end of generation 3 is similar to that in the aerial photographs of the study site. Thus, even in perfectly suitable habitat, the biological characteristics of the organism given, limit it to a certain period of virtual range stasis.

After 1946, through the period of generation 4, the population begins to spread, with small satellite populations forming up to 2.5km from the main populations. These satellite populations gradually become more dense with an aura of low density neighbourhood spread around them. Satellite populations send out their own propagules causing further spread of the population as a whole.

Generation 6 shows the phenomenon of range coalescence beginning, with sub-populations merging into the populations spreading from the two main core areas, representing the sites of initial introductions. It is interesting to note how the structure of the sub-populations is subsumed within that of larger population bodies.

The larger scale copy of generation 7 produced in figure 3.4.2b), shows the white "shadows" of the inhospitable loch environments. Generation 7 also shows a high amount of scatter of individual bushes about the study site, although these still have a circular structure to them in relation to the initial areas of introduction. Using the model with these habitat maps in which all values (except for lochs) were set to 1, allowed for the "structure" of the model to be set, i.e. the cell amalgamation values and the furthest cell values, so that artificial box patterns were not produced due to a short cut-off point to dispersal.

The unrealistic assumption of a perfectly suitable habitat is also useful in acting as a null model for habitat effects, it represents a simple case, and if the biotic parameter values calculated are accepted, this model does not fit the observed distribution. Therefore changes to the relative carrying capacity of the habitat need to be made.

Figure 3.4.2a) shows that after 84 years some plants have established up to c.8km from the nearest initial foci planted in 1910. This represents a migration rate, according to the biotic parameters alone, of 95m yr.$^{-1}$.

Figure 3.4.2b) demonstrates the idea of the importance of scale, and the principal idea arising from research into fractals, that patterns discernible at one scale are also found at another. At first it appears from the whole run that only the pattern of sub-population build-up is clear, with a single propagule becoming established and then forming a dense population which spreads initially by small increments into the surrounding habitat. This phenomenon of local spread is due to the short-distance dispersal function. At the larger scale the main population appears to contribute randomly to the formation of satellite populations, and the idea of stochastic long-distance dispersal events is simulated. The pattern of spread seen at the level of individual sub-populations is taken on by the two main populations forming, only taking over at the larger scale after considerable population build-up and the beginnings of range coalescence in the two core areas at generation 6. Now, both the main populations and the sub-populations have annuli of progressively lower densities around them, an effect especially evident by generation 7.

Even within contiguous areas of high density cover, there are still areas of lower density where range infill has yet to be completed.

This initial run of the model, although simplistic, creates very interesting outcomes. The tendency of the population to create these patterns should be borne in mind when analysing further output from the model.

Figures 3.4.2a) and b) are encouraging for two main reasons. Firstly, because they tie in well with the observations of discrete sub-populations in the field, and old individuals scattered at great distance from the initial points of introduction. The sub-populations measured in the field for the parameterisation of the dispersal function, when truncated for age, also revealed clumpings and a spatial structure more akin to a small-scale "metapopulation". This finding agrees with the idea of pattern repetition on moving up or down through the scales of a spatial hierarchy. Secondly, the results suggest that the two-dimensional version of the MIGRATE model is performing correctly, in that it produces circular invasion fronts from point sources, and is, to a certain degree, producing stochastic output from deterministic beginnings due to the random number feature.

Although the title for figure 3.4.2a) suggests that this run of the model is a simulation of the likely spread of *Rhododendron* in a homogeneously suitable habitat, it in fact shows a low estimate for possible spread in such a uniform environment, because, most importantly, establishment probabilities ($P_{(survive)}$) were derived from the field situation of differentially suitable habitat mosaics.

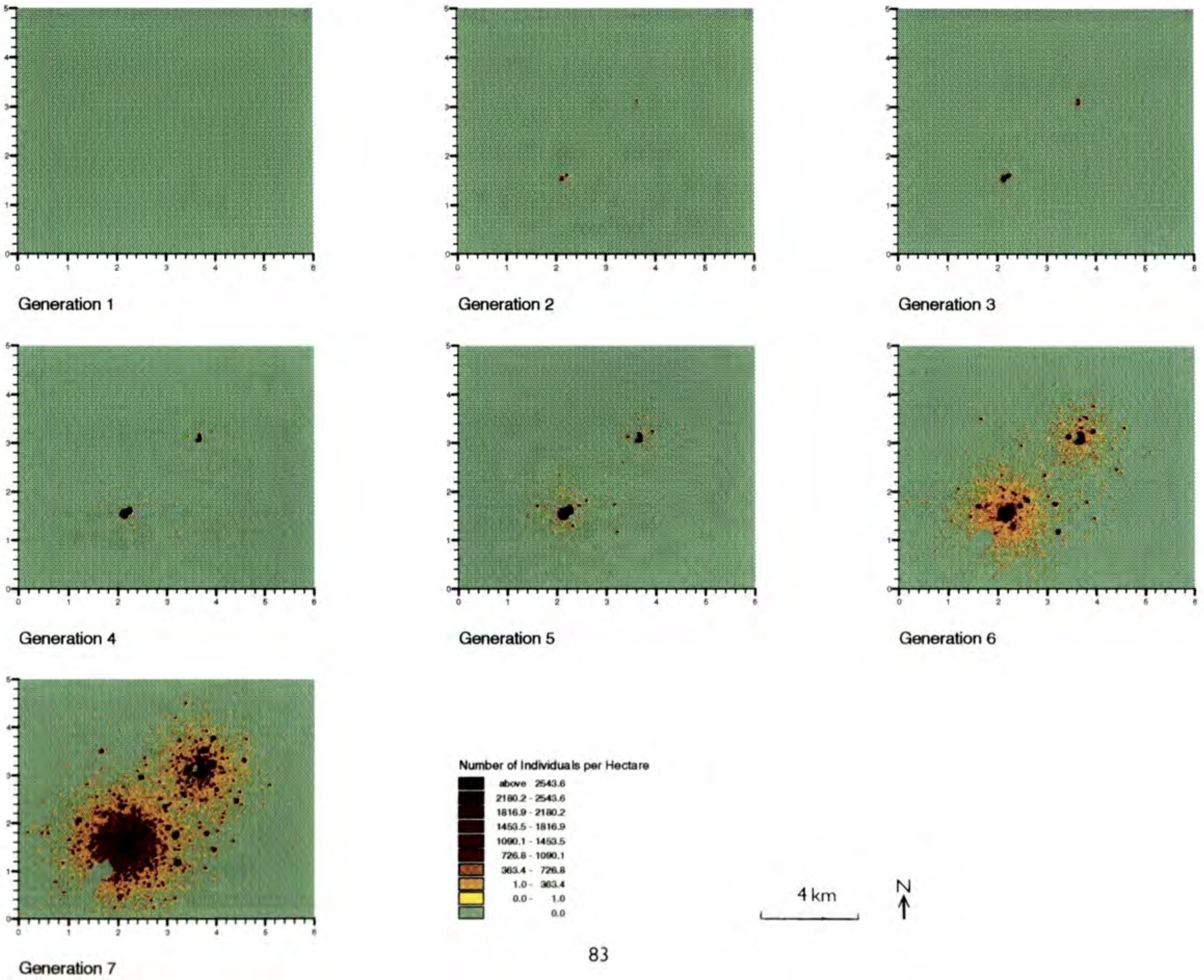
The density banding apparent in all figures is somewhat abrupt due to the rather arbitrary assignment of plants to three density classes differing in orders of magnitude. Such discrete banding though, is not totally a result of this classification procedure. Abrupt changes in density of the likes shown in figures 3.4.2a) and b) are also seen in the field (figures 3.4.2c) and d)). The density classes to which individual cells are assigned helps to clarify subtle differences in densities, elucidating the major underlying patterns apparent in the data.

The next step towards achieving more accurate simulation of distribution changes through time, is to introduce habitat restrictions to reduce the overall extent of spread, because both the distribution and abundance of *Rhododendron* shown in figure 3.4.2b) are far in excess of that observed in the field.

Fig. 3.4.2a)

The spread across an homogenously suitable (except lochs) habitat.

L = 0.010 km; a = 3.44 m^2; T = 12 years; $P(survive)$ = 0.0006, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000; F = 0.0, 123074.0, 1432212.0, 16666608.0, 36726556.0, 36726556.0, 36726556.0, 36726556.0;
H0 = 0.01 km; P(H0) = 0.999000; Amalgamation = 1; Furthest cell = 5;
H1 = 0.19 km; P(H1) = 0.001000; Amalgamation = 20; Furthest cell = 20; Dispersal sums = 1.0462, 0.0010; Total = 1.0472;
Random number seed = 8; k_mod = 0.000;



Generation 1

Generation 2

Generation 3

Generation 4

Generation 5

Generation 6

Generation 7

Figure 3.4.2c) The abrupt changes in density class seen in the spreading population on Creag Dhubh, developed from the initial introductions at the Lodge, produces a "steep" invasion front with scattered peripheral individuals ahead of it.

Figure 3.4.2d) The extent of spread around the Lochan Urr invasion site, again showing the discrete nature of the patches developing, and the contiguous coverage within these areas.

3.4.3 The effect of selected habitat restrictions on the pattern of distribution.

The simulated spread of *Rhododendron* when it can exploit all river types and all altitude ranges equally, is shown in figure 3.4.3a). The title (which is worded relative to later output rather than in its own right) suggests that all grazing regimes are also treated equally, and although this is not strictly the case, the values for all grazing types are kept high. This is the cause of the "regular" structure seen in the pattern of spread around the Lodge. The restrictions imposed on the habitat used compared to figure 3.4.2a) are in the areas of forestry blocks, the thicket stages of all conifer species being highly unsuitable to the light requirements of *Rhododendron* for germination and establishment. Roads, rides and fence lines had *K* values of 1.

The development history of figure 3.4.3a) is basically the same as that described for figure 3.4.2a), and the same patterns of spread are still visible, even though the population front has been channelled into ride and river corridor habitats. These links between sub-populations growing on suitable areas mainly develop after the separate colonisation events.

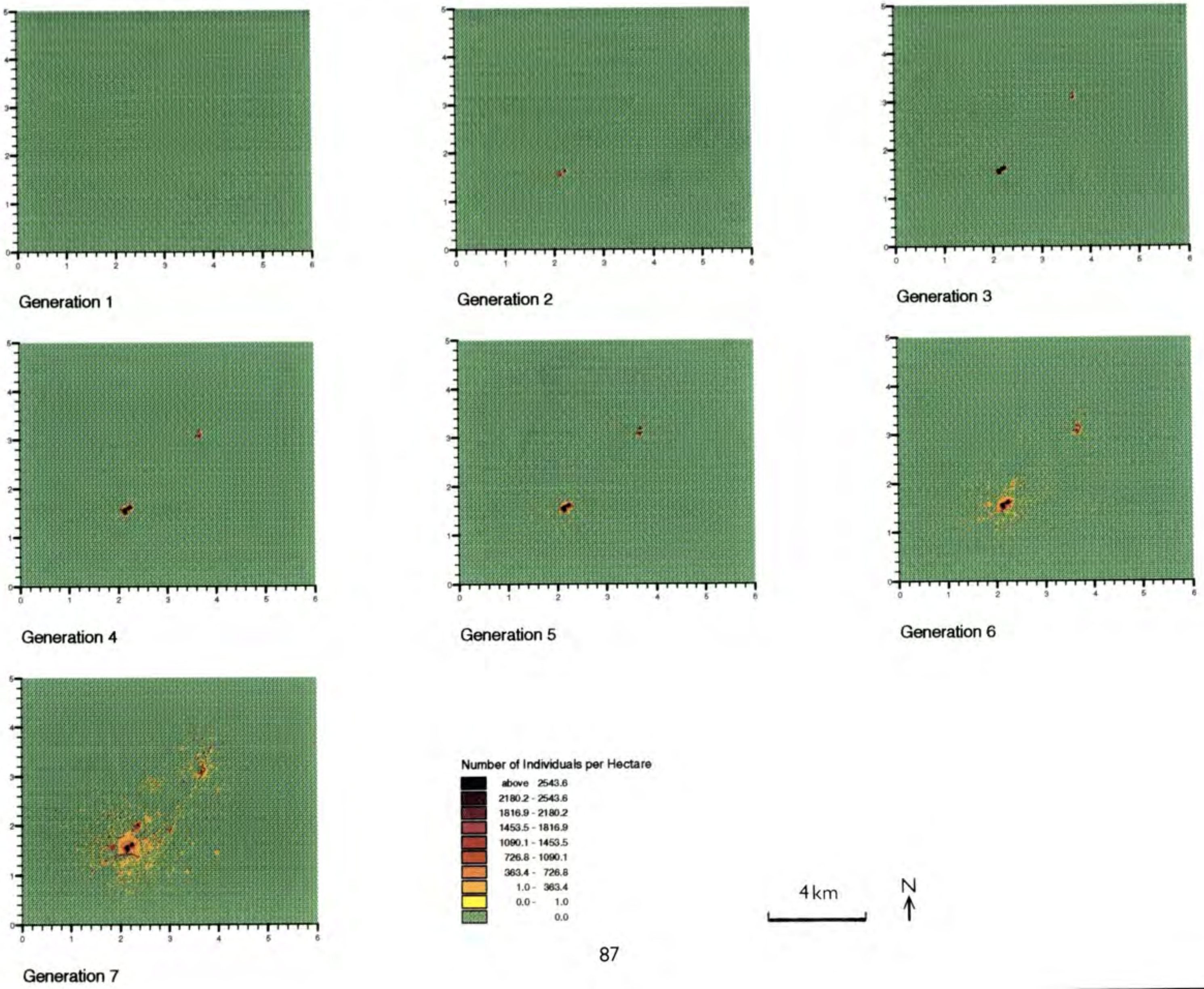
In comparison to figure 3.3, figure 3.4.3b) still shows a wider pattern of overall spread, and the development of discrete satellite populations with a discernible structure of spread. Compared to figure 3.4.3a), though, the degree of spread has been limited, and population expansions in the two core areas have been "brought in" to produce a pattern of spread in the final generation with elements in common with that mapped for the present-day in the field (figure 3.3).

Further grazing restrictions were implemented in the next run of the model, such that areas accessible to deer and/or sheep were given *K* values of 0. Areas protected from grazing had *K* values of 1. These values were not necessarily constants through time and often depended on the fencing history discerned for the area. This produced a pattern more akin to that seen in figure 3.3, although there were still many plants exploiting river and ride habitats at great heights (this figure is not shown). Therefore it was thought necessary to introduce altitude and stream size restrictions, even though there was little evidence for an effect of altitude in the field.

No altitude restrictions ;partial suitability of all habitat types.

L = 0.010 km; a = 3.44 m^2; T = 12 years; $P(survive)$ = 0.0006, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000; F = 0.0, 123074.0, 1432212.0, 16666608.0, 36726556.0, 36726556.0, 36726556.0, 36726556.0;
H0 = 0.01 km; P(H0) = 0.999000; Amalgamation = 1; Furthest cell = 5;
H1 = 0.19 km; P(H1) = 0.001000; Amalgamation = 20; Furthest cell = 20; Dispersal sums = 1.0462, 0.0010; Total = 1.0472;
Random number seed = 8; k_mod = 0.000;

Fig. 3.4.3a)



Generation 1

Generation 2

Generation 3

Generation 4

Generation 5

Generation 6

Generation 7

3.4.4 Altitude, grazing regime, forestry block cohort and stream size restrictions to spread.

Figure 3.4.4b) shows the relation of the spread of *Rhododendron* to the vertical relief of the area. The shaded overlay (Sun position: 215° azimuth, clockwise from north; 30° altitude above the horizon) provides visual and positional information. Produced from the DTM, it shows *Rhododendron* reaching greatest heights in the dark, shaded, river valleys, as in figure 3.3.

Figure 3.4.4a) shows the model run used for prediction of distributions in the years 2006 and 2030 having achieved a simulation (figure 3.4.4b)) approximating to that seen for the present-day (figure 3.3). Thus figures 3.4.4b), c) and d) were produced from the same model run, although figure 3.4.4b) is not seen on the overall simulation plan (figure 3.4.4a)) because this is generation 7 whereas the overall model output is for two-generation intervals.

Figure 3.4.4b) shows a predicted pattern similar in many respects to that produced in figure 3.3. Both show exploitation of linear features, similar overall patterns to the limit of spread and areas of high density. These are general similarities of pattern produced mainly through the structure of the habitat maps as in figures 3.2.6d) and e) which "direct" the growth of the *Rhododendron* population into specific areas.

There are many instances where the specifics of the two figures (3.4.4b) and 3.3) do not match up, although some of these would be removed if the patterns were viewed at a larger scale. For instance, there is greater utilisation of habitats to the south and west of the Lodge foci and a lesser use of suitable habitat to the far north-east in the model simulation. The real world distribution shows more discrete, medium density patches, especially of a linear nature. Overall, the actual distribution of *Rhododendron* shows more contiguous patches of the two highest density classes and a less particulate and heterogeneous structure to populations than the model simulation. The reasons for these specific differences will be discussed.

It had been hoped to compare the predicted and real world distributions using the spatial κ statistic (Prentice, *et al.*, 1992) on the patterns resampled at a larger scale. The κ statistic gives a value based on a relative scale drawn up from experiments conducted in the field of cognitive psychology on the spatial comparison of patterns (B. Huntley, personal communication). Due to time constraints though, this method was not used, and the patterns were simply compared visually.

Having produced an acceptable simulation of the present-day distribution, the pattern of spread was extrapolated into the future producing the results seen in figures 3.4.4c) and d). Figure 3.4.4c) shows a likely scenario for the year 2006 by which time there has been some range infill in areas of lower density and extension of the range into the area east of the Lodge, fenced in 1994. This area of newly available habitat and that of decreased suitability due to the removal of the forestry fence surrounding the conifer plantations is shown in figure 3.2.6f). Basically the distribution in the year 2006 appears little different to that in 1994.

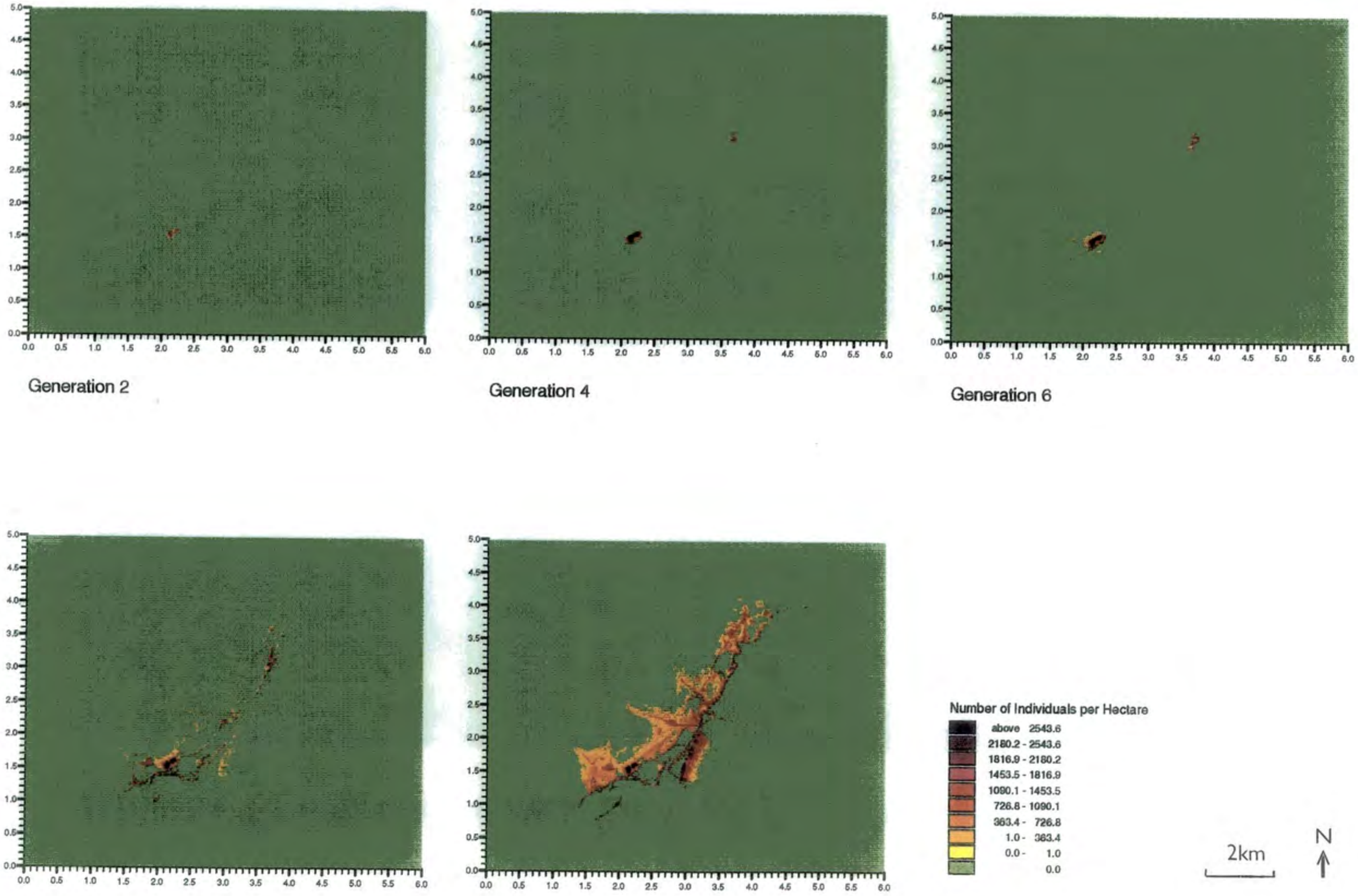
A dramatic, and somewhat disturbing, increase in the distribution and abundance of *Rhododendron* is seen by the year 2030 (figure 3.4.4d)). By 2030 it is predicted that there will be infill of corridor habitats and of the majority of forest blocks (planted in 1968) as they mature and thin. This assumes, though, that the large forestry area will again be protected during establishment of new tree crops in clear-felled areas. The patch of hillside fenced to permit establishment and regeneration of old stands of broadleaved trees now has virtually 100% cover of *Rhododendron*.

Obviously, all predictions are for potential patterns of spread under the conditions given. By changing certain parameters different scenarios could be produced, such that a range of possible outcomes could be produced. All predictions will need to be adjusted if significant control programs are implemented in the future.

The predicted spread of Rhododendron by the year 2030.

$L = 0.010$ km; $a = 3.44$ m²; $T = 12$ years; $P(survive) = 0.0006$, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000; $F = 0.0$, 123074.0, 1432212.0, 16666608.0, 36726556.0, 36726556.0, 36726556.0, 36726556.0, 367265
H0 = 0.01 km; P(H0) = 0.999000; Amalgamation = 1; Furthest cell = 5;
H1 = 0.19 km; P(H1) = 0.001000; Amalgamation = 20; Furthest cell = 20; Dispersal sums = 1.0462, 0.0010; Total = 1.0472;
Random number seed = 8; k_mod = 0.000;

Fig. 3.4.4 a)



Generation 2

Generation 4

Generation 6

Shaded relief map showing the structure of the DTM used to extract the 25m resolution contour lattice.

Fig. 3.4.4 b) The simulated distribution and abundance of Rhododendron in three density classes.

Fig. 3.4.4c) The predicted distribution and abundance of Rhododendron in Glen Etive by the year 2006.

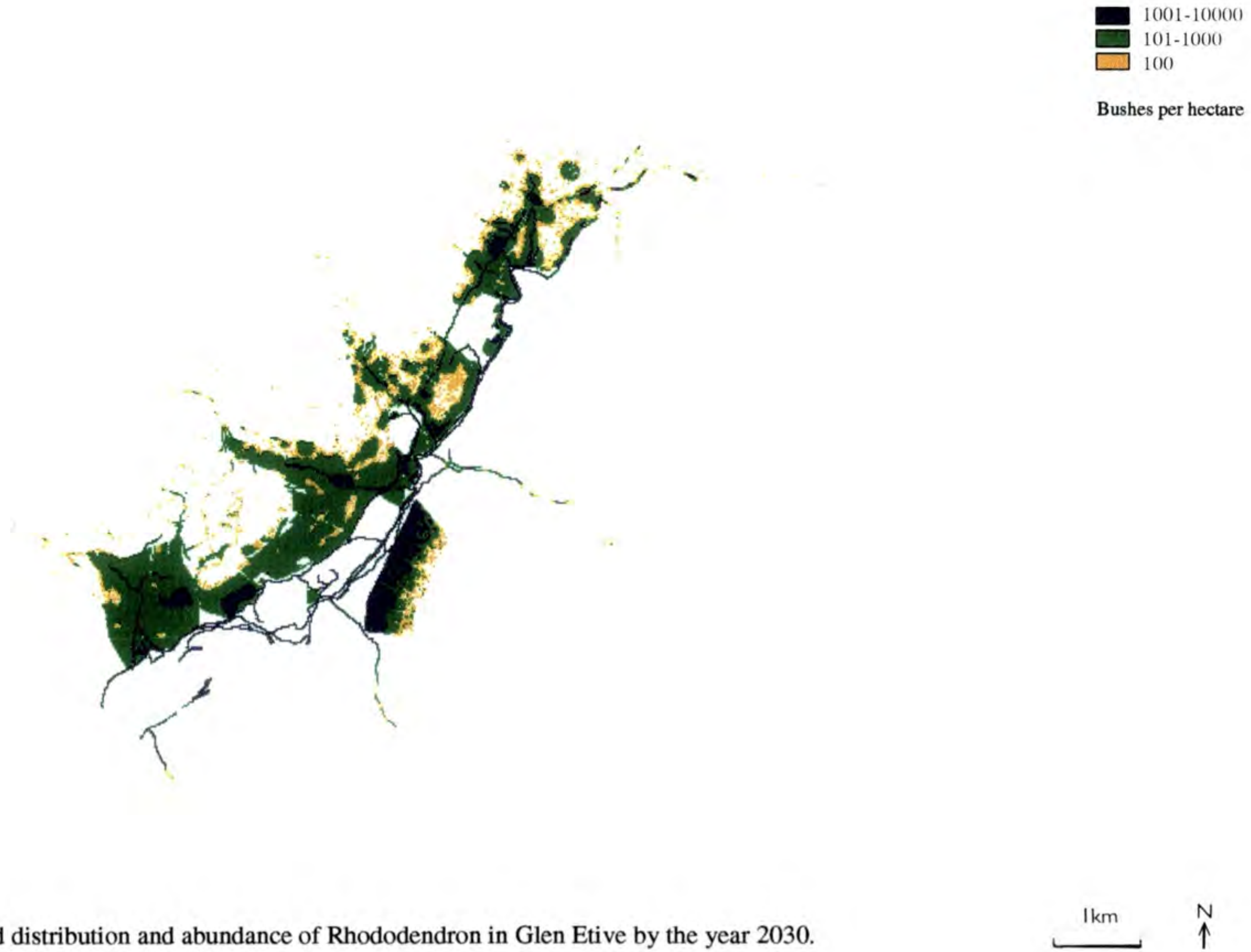


Fig. 3.4.4d) The predicted distribution and abundance of Rhododendron in Glen Etive by the year 2030.

3.4.5 The use of prediction to management techniques.

Using an older version of the MIGRATE model, which culled established individuals if the carrying capacity of the environment changed to a lower level, it was possible to produce a rough estimate of the effects of two different control strategies.

Lowering the level of K to 0 in the habitat maps in the positions of the core establishment areas, culled all individuals in these areas, i.e. the dense populations developed from the initial foci of introduction as shown in figures 3.4.2c) and d). This change to the habitat maps was the only change made to the parameters as compared to previous runs shown in section 3.4.4. The cull was conducted in 1994 at the end of generation 7. It left the plants established in peripheral ride and riparian locations. These peripheral plant populations have mainly refilled the core areas by the year 2030, and spread is very extensive in the mature polestage areas of conifer and the newly fenced hillside area (figure 3.4.5a)).

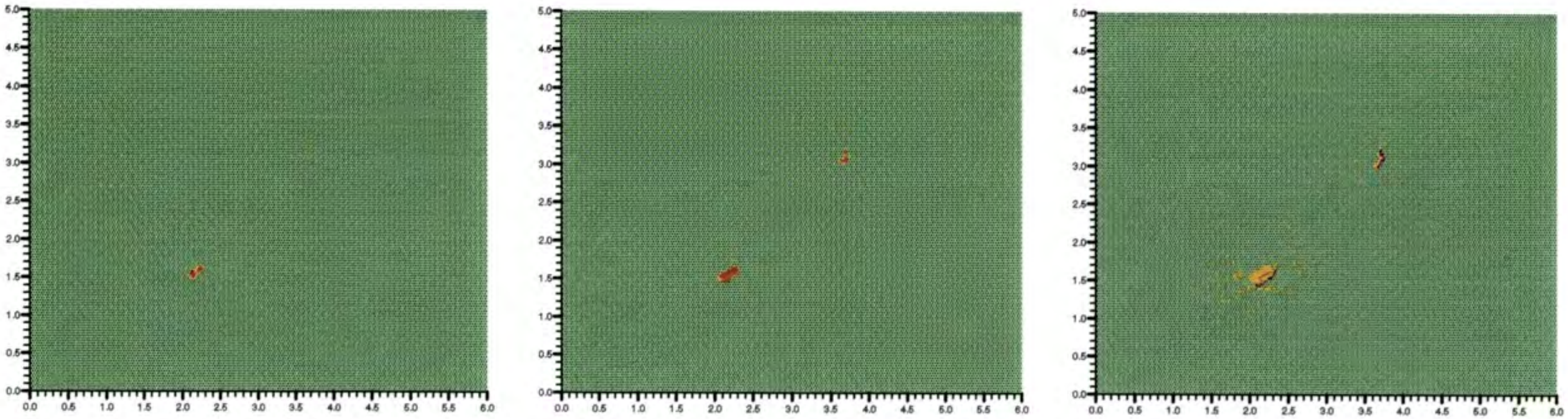
Culling the peripheral individuals at the end of generation 7 leaves the core areas intact (figure 3.4.5b)), and a comparable number of individuals to that left with the core cull. In the case of the peripheral cull the extent of spread into new areas by 2030 was much reduced, and so this management plan would be the best to implement on the basis of the patterns of spread alone. The design of management plans is based on many considerations, and patterns of the predicted spread effects of different control scenarios may be of low priority, as will be discussed later.

The results shown were not expected because throughout the simulations it had been the core populations derived from the initial foci of introduction which had contributed to the peripheral patterns of spread. The predictions produced from culling regimes suggest this trend can be reversed and peripheral populations can act just as well as sources of propagules and are more "dangerous" in that they can soon produce infill of these core areas cleared nearby as well as further spread into disjunct regions. This suggests containment of the core areas is the best strategy for preventing wide-scale spread.

Spread by the year 2030 with a cull of the core populations in 1994.

L = 0.010 km; *a* = 3.44 m^2; *T* = 12 years; *P(survive)* = 0.0006, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000; *F* = 0.0, 123074.0, 1432212.0, 16666608.0, 36726556.0, 36726556.0, 36726556.0, 36726556.0, 367265
H0 = 0.01 km; P(H0) = 0.999000; Amalgamation = 1; Furthest cell = 5;
H1 = 0.19 km; P(H1) = 0.001000; Amalgamation = 20; Furthest cell = 20; Dispersal sums = 1.0462, 0.0010; Total = 1.0472;
Random number seed = 8; k_mod = 0.000;

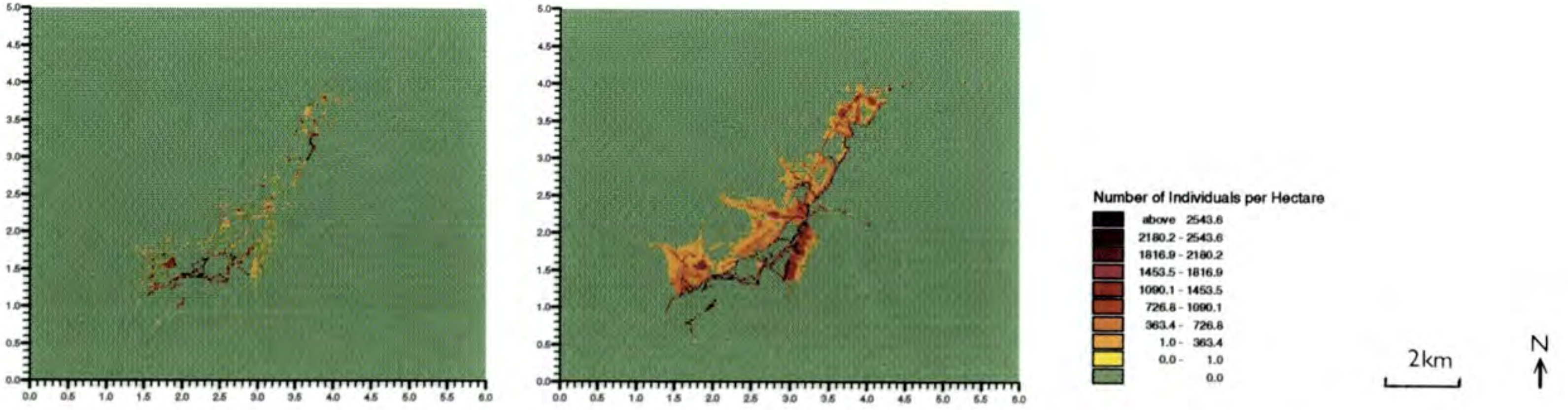
Fig. 3.4.5a)



Generation 2

Generation 4

Generation 6



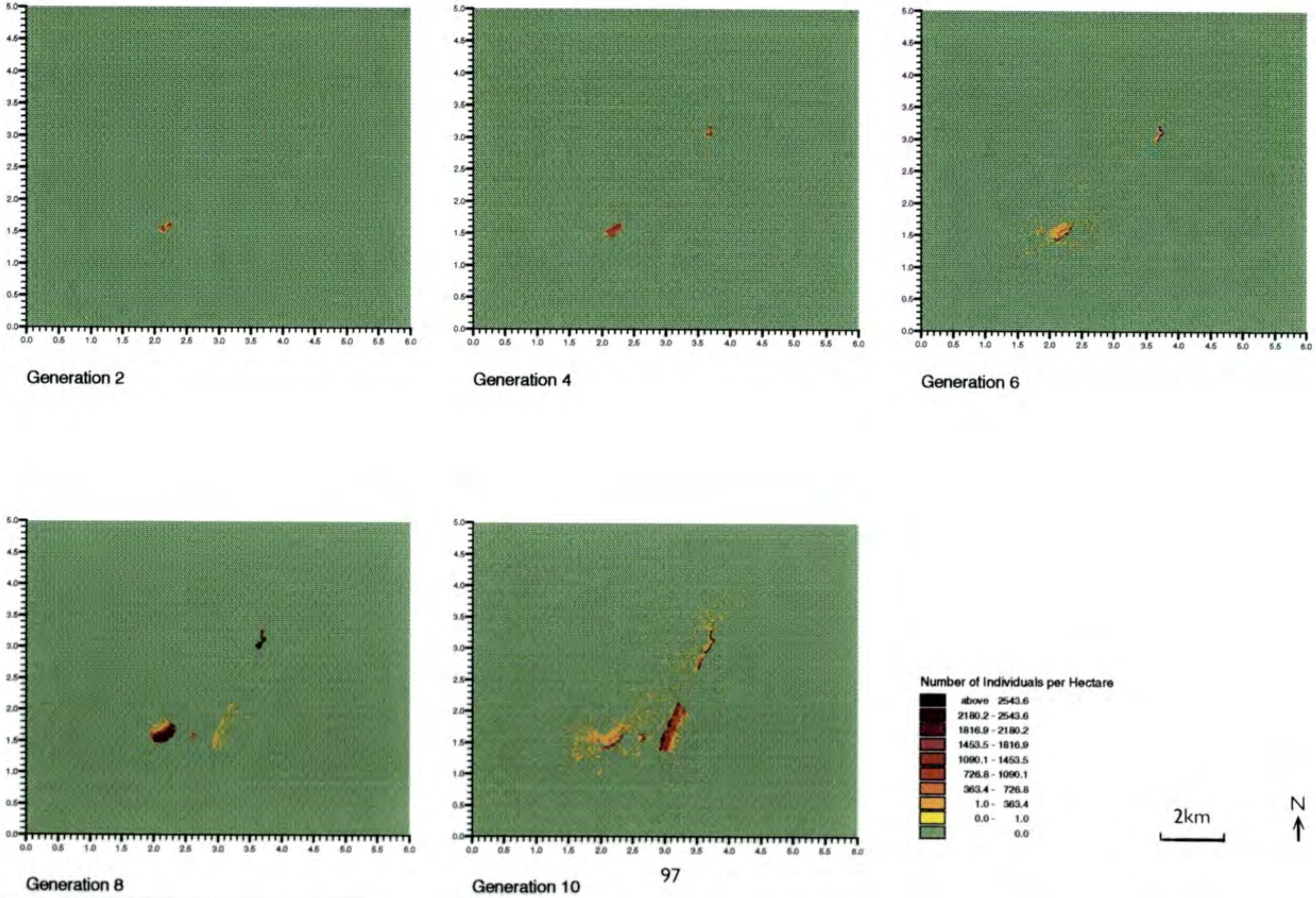
Generation 8

Generation 10

Spread by the year 2030 with a cull of the peripheral populations in 1994.

L = 0.010 km; a = 3.44 m^2; T = 12 years; *P(survive)* = 0.0006, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000; F = 0.0, 123074.0, 1432212.0, 16666608.0, 36726556.0, 36726556.0, 36726556.0, 36726556.0, 367265
H0 = 0.01 km; P(H0) = 0.999000; Amalgamation = 1; Furthest cell = 5;
H1 = 0.19 km; P(H1) = 0.001000; Amalgamation = 20; Furthest cell = 20; Dispersal sums = 1.0462, 0.0010; Total = 1.0472;
Random number seed = 8; k_mod = 0.000;

Fig. 3.4.5 b)



Generation 2

Generation 4

Generation 6

Generation 8

Generation 10

3.4.6 Behaviour of the biological parameters of the model.

This section will attempt to qualify what has gone before with regard to the values for the long-distance dispersal function half-distance and the probabilities of dispersal according to the two dispersal functions used.

A long-distance dispersal function was deemed necessary because of the very limited spread resulting from the short-distance function (H0) derived in the field. Simply using the H0 value of 0.00573km produces patterns of spread for 1994 equivalent to that seen in generation 3 of figure 3.4.6a). Therefore a long-distance dispersal function had to be introduced to allow for scattering of individuals into areas beyond the initial foci. This parameter was not measured in the field and was not contained within the dispersal function derived from the field data due to the reasons outlined in section 2.2.4 of the methods section. Also long-distance dispersal events are difficult to study because of their low, stochastic occurrence rates. The half-distance for dispersal according to the second dispersal function (H1) was given as 0.19km. This value was arrived at through a process of trial and error, in combination with the dispersal probabilities, through the comparison of model output with that seen at the present-day. As such, this aspect of the modelling technique is based on circular derivation through a "tuning" process. Considering the important effects of the implementation of the second dispersal function (H1) and of the probability values to the dynamics of the invasion, this aspect of the modelling process is perhaps the weakest in that the values have not been independently derived. Although, it should be realised that the values for long-distance dispersal and the probabilities of dispersal could not be determined in the field and so in a sense the model presents an opportunity for calculation of these parameters. If these parameter values can then transferred to another instance of *Rhododendron* invasion successfully, then they can be classed as independently derived and a good representation of the real world values. The best validation for these values available during the present project was obtained by combining them with the parameter values determined in the field from sub-populations and individuals to predict a population pattern of spread seen at the present-day and for 1946. The slight distinction I make here is that the values are derived from the population pattern of spread, and yet are applied to the individual, whose properties combine to produce the population pattern of spread again.

An example of the effect of changing the number of seeds dispersed according to the long-distance dispersal function (H1) is shown in figure 3.4.6b). Here the probability of dispersal according to H1 is increased by an order of magnitude from 0.001 to 0.01. The distribution developed by 1994 is similar in terms of maximum extent to that in figure 3.4.4b) primarily due to habitat restrictions. Within the areas of suitable habitat though, this increase in the prominence of dispersal according to H1 produces a closer match to the distribution of figure 3.3 in the middle regions between the two core populations. With an increase in the accuracy of this aspect of the pattern of spread come decreases in accuracy in other areas due to trade-offs.

There is little loss in the accuracy of prediction of neighbourhood spread in the area due to H0. There is considerable discrepancy between the predicted (figure 3.4.6b)) and observed (figure 3.3) distributions in the degree to which ride and river habitats are exploited. Increased prevalence of long-distance dispersal results in faster colonisation rates of distant areas and more rapid infill of disjunct ranges. This occurs because H1 does not only produce rare, propagule dispersal, to great distances. The value for the half-distance represents an exponential curve with an extended tail. There are still high rates of seed deposition at distances less than the half-distance, it is just that the dispersal function is shallower, and so deposition is more even and less concentrated near to parental sources. Thus the long-distance dispersal function is the main contributor to intermediary patterns of density spread and to neighbourhood diffusion. The short-distance dispersal function merely acts as a sink in the modelling process to the vast number of seeds produced, reducing that which can be dispersed over further distances.

Decreasing or increasing the half-distance for H1 has little effect on the overall pattern within certain limits, although in accord with the above, increasing the value begins to reduce the local spread of populations and range infill is less enhanced. Reducing the distances to which seeds can be dispersed reduces the accuracy of longer distance simulation back towards that produced in figure 3.3.4b).

The value given to the probability of dispersal according to the two dispersal functions is the biotic parameter most sensitive to change. It has the greatest effects on distribution *and* abundance simulation for the smallest increments. This conclusion is based on experience with the model in other simulations, behaviours being observed in relation to changes in the other parameters, the products of which are not shown.

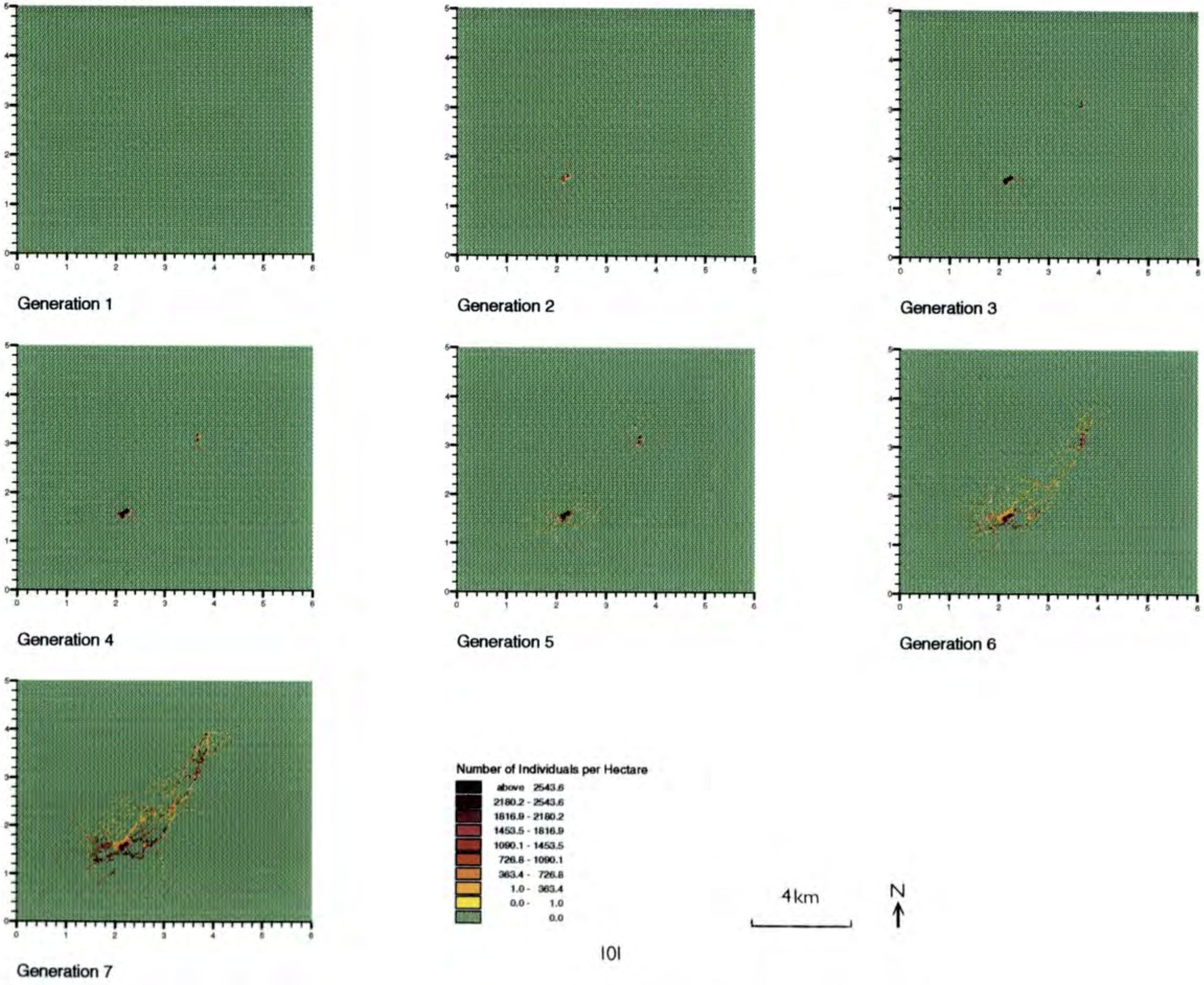
Conclusions based on sensitivity tests must be tentative though as many parameters are not strictly comparable, for instance some are proportions and others are real values and thus small changes can have vastly different consequences. Conclusions as to the behaviour of individual parameters of the model therefore require further empirical testing.

Although the probability of dispersal is quoted as a biotic parameter, it is really an artefact of model structure. The use of two dispersal functions is an attempt in itself to model the dispersal process. If seed trap studies were conducted on discrete individuals, only data for one dispersal function would be found, and that would probably be an average between the two used in the simulation, that would change from year to year within certain bounds according to prevailing climatic conditions. Thus again, the values derived for the probabilities of dispersal must come from the model simulations themselves, because, unless seed trap studies are carefully conducted in the field for many years, and a single dispersal function produced, no such values actually exist.

An order of magnitude change in dispersal via the 2 dispersal functions.

L = 0.010 km; a = 3.44 m^2; T = 12 years; *P(survive)* = 0.0006, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000, 1.0000; F = 0.0, 123074.0, 1432212.0, 16666608.0, 36726556.0, 36726556.0, 36726556.0, 36726556.0;
H0 = 0.01 km; P(H0) = 0.990000; Amalgamation = 1; Furthest cell = 5;
H1 = 0.19 km; P(H1) = 0.010000; Amalgamation = 20; Furthest cell = 20; Dispersal sums = 1.0368, 0.0101; Total = 1.0469;
Random number seed = 8; k_mod = 0.000;

Fig. 3.4.6a)



Generation 1

Generation 2

Generation 3

Generation 4

Generation 5

Generation 6

Generation 7

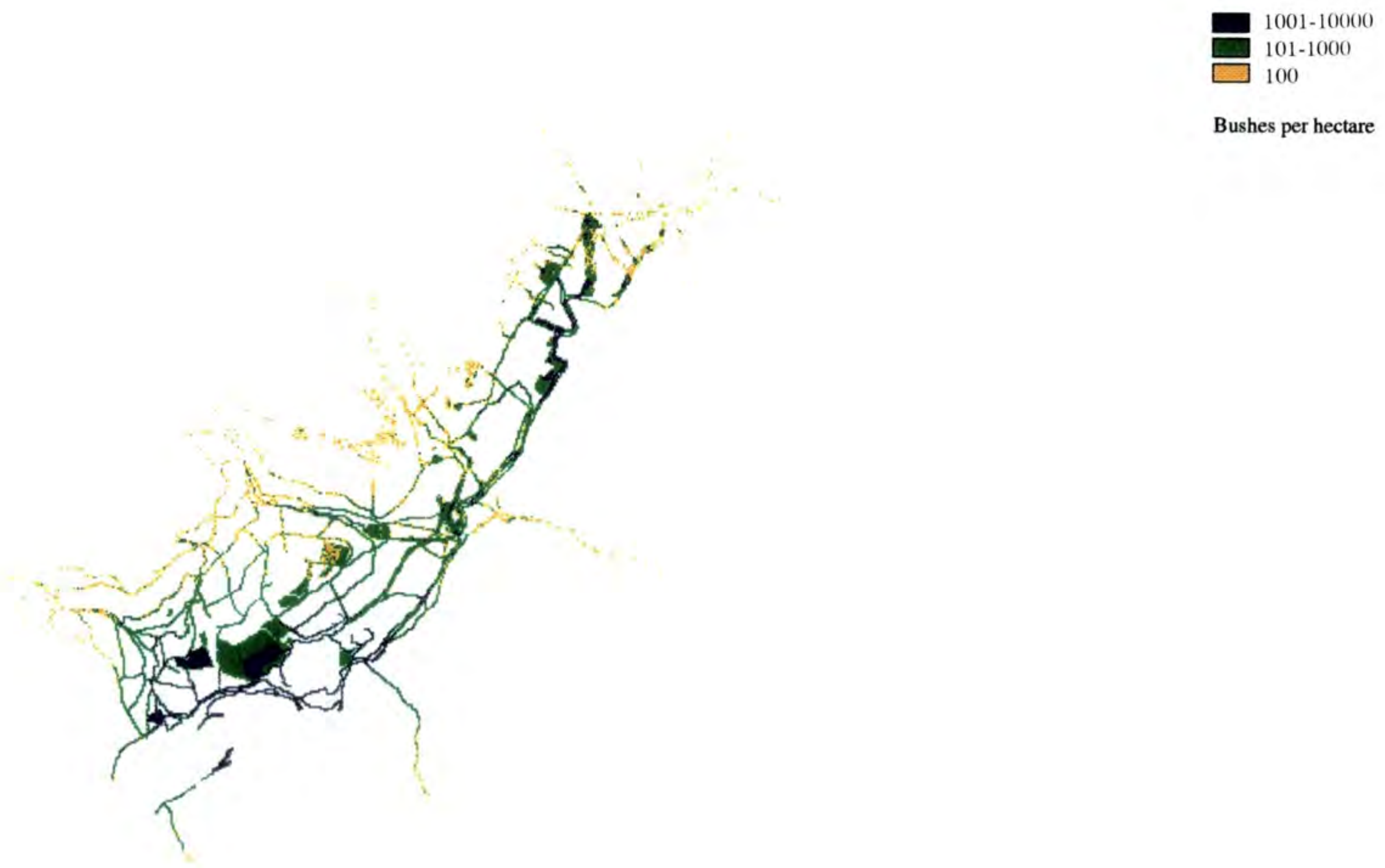


Fig. 3.4.6 b) Simulated spread when the probability of long distance dispersal is increased by an order of magnitude.

Chapter 4: DISCUSSION.

4.1 Performance of the model.

Comparison of the present-day distribution and abundance of *Rhododendron* (figure 3.3) to that modelled (figure 3.4.4b)), shows many similarities. Both the pattern of distribution and abundance of *Rhododendron* are "predicted" for 1946 and for 1994 with good accuracy. Plants were seeded in at 1910 at the two main locations for the initial introductions, and spread was modelled from these foci. The model only made calculations of seed output, seed establishment and subsequent survival at 12-yearly cohort intervals and did not make yearly calculations. The seed output from a cohort was also dispersed at the end of a cohort period of 12 years. The model incorporated habitat heterogeneity through time, finding habitat heterogeneity to be of great importance as suggested by the findings of Dwyer (1992) and Tilman (1994). The model produced these simulations at a fine spatial scale (10m resolution). Extrapolation from predictions of the past and present gave a picture of the likely extent of future spread in the glen, and was used in conjunction with culling regimes to predict the possible effects of two broadly different control strategies. Thus the project covered all of its main aims and represents a successful integration of modelling, GIS and field techniques in a manner analogous to that suggested by Thomson *et al.* (1993).

Prediction was achieved at a temporal resolution of 12 years using simplified biotic and habitat data. Simplification of the data was made under necessary assumptions which intend to highlight generalities and avoid specifics.

4.2 Model implications to the importance of dispersal.

The model demonstrated the link between distribution and abundance, and the patchy pattern of population development even in homogeneous environments. This establishment pattern of populations derives from the dispersal function in itself without the need for spatial variation in habitat quality.

The migration rate of *Rhododendron* was shown to increase rapidly in all cases between the fifth and sixth generations (1958-1982), i.e. in the last 20-35 years. This was probably due to the population moving on to the steeper part of an exponential growth curve (Shaw, 1984) and to the increase in availability of suitable safe sites for establishment with increased forestry activity in 1958. The establishment of conifer plantations in areas adjacent to the initial introductions increased the amount of disturbed ground available through its creation of drainage ditches, bank cuttings along rides and newly tilled soils. These features were often observed to act as seed beds and seedlings establishing in these areas were offered protection from grazing by the fences erected at the time of tree planting. Thus the two further reasons (the possible importance of the withdrawal of the lime subsidy and the genetic adaptation of *Rhododendron* to the British climate) given by Shaw (1984) for the dramatic increase in *Rhododendron* over the last 15-20 years are not needed. The expansion can simply be explained in terms of the logistics of population growth and the specific environmental changes that occurred in the area. It would be interesting to investigate whether these two processes could be disentangled in the present study, so that the greater contributor to the population increase could be determined. This would not be difficult if they differed significantly in the timing of their effects, because GIS distribution coverages could be produced at generation intervals. The MIGRATE program could be altered to give actual numbers of individuals in grid cells as opposed to density measures and so the conformity of the population to a logistic curve could be tested. If it was found that significant levelling off in population numbers occurred before the population "explosion" then this would point to the importance of habitat changes. If on the other hand a logistic was found this could suggest a predominance of demographic processes on population build-up, although the steepness of the curve may be influenced by the habitat changes. The fact that the pattern of spread conforms to certain distinctive habitat types, though, suggests habitat change has been of great importance in determining the rate of spread and has "released" the population through time.

Therefore the conclusions reached by Shaw (1987) to explain the countrywide pattern of increase have little applicability to the increase of *Rhododendron* in this specific case. I would suggest that the increase in forestry and thus fencing activities have been of greatest importance, as have changes in grazing regime intensities.

When habitat restrictions to the migration rate of *Rhododendron* are removed it becomes apparent that dispersal in this species is very effective and has the potential to reach values analogous to those calculated for other woody taxa in the Quaternary, being in the range of 100myr^{-1} (Huntley and Birks, 1983). This disagrees with the findings of Thomson *et al.*, (1993) who suggest that *Rhododendron* has "limited powers of dispersal". I say this because, although the statement in itself is correct, it is suggesting a characteristic of *Rhododendron*, that is different from other wind dispersed species. The difference of opinion probably lies in the use of the term dispersal, because Thomson *et al.*, (1993) actually use it in the sense of migration basing their assumption on patterns of *spread*. This is not a correct usage of the term "dispersal".

Manipulation of the biotic data so that the proportion of seeds dispersed over greater distances was increased (figure 3.4.6a)), demonstrated the importance of the long-distance dispersal function to the overall pattern of spread in terms of distribution and abundance (Hengeveld, 1989). The long-distance dispersal events determine the rate of invasion, whereas local seed fallout results in population build-up (Hengeveld, 1994). The idea of differential roles for the dispersal function is demonstrated by the model. All simulations show the build-up of populations for the first three generations and then, with a large combined seed crop, the chance of a successful long-distance dispersal event with establishment is increased and peripheral colonisations begin to take place.

The large distances quoted for the migration rates of trees as deciphered from the Quaternary record have allowed for species survival in the face of environmental change. Therefore, one might expect there to be a premium on the evolution of dispersal strategies resulting in long-distance dispersal. Possible strategies developed could include the production of the seed crop at the top of the tree in wind dispersed species or the production of vast amounts of seed, both of which would give a longer tail to the dispersal function.

The evolutionary hypothesis suggested, for the benefits of a long-tailed dispersal function to migration and how it might be achieved is not supported by the findings of Augspurger and Kitajima (1992) who conclude that in *Tachigalia versicolor* selection on dispersal should act to increase the uniformity of the seed distribution, but not increase dispersal distance. Although they go on to say that the increase in distance is only detrimental if it dilutes the seed shadow.

With a large production of seed this need not necessarily be the case. The field data for *Rhododendron* suggested a negative exponential form to the seed dispersal curve, and Johnson (1988) suggests that curve height increases with increasing seed production, although this may or may not be accompanied by a significant change in slope. Again though, this should not be seen as going against the proposed hypothesis as descriptions of changes in slope do not tell us very much about the length of the tail to the dispersal function. Measures of half-distance are much more informative.

The output from the model suggests to me that local dispersal represents more of a failure of long-distance dispersal than a strategy in itself, although the local establishment events do result in population build-up which allows for further long-distance events. This highlights the linkage of abundance to dispersal and thus distribution.

The pattern to migration shown by the model is most closely analogous to that described by Hengeveld (1989). There is evidence of stochastic long-distance dispersal events and the co-occurring process of neighbourhood diffusion. Even in an homogeneous environment, though, the process of neighbourhood diffusion results in a slightly patchy and stochastic distribution to the population fronts and is no more deterministic than the patterns of long-distance dispersal. The separate models of migration hypothesised by Woods and Davis (1989) are evidently part of the same process, and are largely subsumed within the effects of spatial scale of the study on apparent distributions. In figure 3.4.2b) it can be seen that outlier populations have established and that gradual infill is occurring which is separate from the main population fronts. This process, under magnification, is found to be occurring within the population front. The outlier model is contained within the continuous front model and if the spatial resolution for viewing figure 3.4.2b) was decreased the outliers would merge into the population front. The outliers at all distances create the population front. A frontal and outlier structure can be seen at many higher resolution spatial scales and is thus a valid description of the patterns of migration. What is disputed, though, is that they offer *alternative* explanations for patterns of migration.

4.3 The implications for research into the effects of environmental change.

The comparison of figure 3.3 with figure 3.4.2a) demonstrated the need for the incorporation of environmental heterogeneity into the model simulations to account for the dynamics of spread of this invasive species. Any models based purely on biological data and which do not allow for interaction with the environment through time are lacking in this fundamental dimension and can thus not be applied to real world situations at a fine spatial scale.

The data used in model simulations can provide "null models" for future predictive attempts because they represent known combinations of biotic variable values under the influence of a certain environmental history (Hengeveld, 1994). The impact of changes in abiotic conditions, for example due to climatic warming, could be assessed in relation to the performance of the population not experiencing these conditions and the differences noted. This point can be elaborated to express the applied importance of the model itself.

Possible climatic warming scenarios suggest that sessile and mobile organisms alike will face the danger of extinction due to the rapidity of the rate of predicted change. Organisms will find themselves unadapted to their current spatial locations and will attempt to migrate in response to the geographical shift in the environmental space to which they are adapted (Huntley, 1989). Highly altered, anthropogenic landscapes such as ploughed fields or urban developments are inhospitable to most species and act as a barrier to migration. To facilitate migration it has been suggested that reserve areas should be linked through a network of corridor habitats (Huntley, 1991). The current model shows the important effects of environmental heterogeneity on the rate of spread and of its importance in determining patterns of spread. The model output supports the ideas of both Huntley (1991) and Simberloff (1992) in that it shows the use of corridor habitats for the migration response of a sessile woody taxon, which is also a weedy exotic deemed a threat to the British flora and fauna (Usher, 1986; Usher 1988). In this specific case the inhospitable habitat through which the *Rhododendron* is spreading is one influenced heavily by grazing, and so it seems that even the apparently natural or semi-natural habitats of Britain could also pose a threat to the migration response of organisms, especially those of a more palatable nature. Basically the model demonstrates, very graphically, the important effects of the unconscious activities of humans on the realised rates of migration. The grazing regimes of many habitats have been highly altered by man, due to his introduction of non-native species, as with *Cervus nipon* (Japanese sika deer) in Ireland (Cross, 1981), sheep and rabbits in the glens of Scotland, and due to the supplementation of foodstuffs during periods of hardship as with *Cervus elaphus* (red deer) to provide increased numbers of game. Man has also elevated numbers of grazers by removing agents of natural control such as disease or predators.

Although this project highlights more of man's activities which may be detrimental to the dynamics of species' ranges, it does also demonstrate a more encouraging aspect of species dispersal. The long-distance dispersal events tend to establish populations beyond the main centres, and corridor habitats are only utilised later in the process of range infill. Therefore the construction of integrated networks of reserves mat not be necessary if sufficient patches of habitat are left available for colonisation within the dispersal distance. Corridor features may not necessarily be of greatest importance in permitting the migration response.

y/

Of course the probability of successful long distance establishment depends on the qualities of the habitat provided and the number and areas of suitable habitat patches compared to the extent of the inhospitable habitat. Thus there may be scope for the integration of migration models with models of patch dynamics as suggested by May (1994).

Using the MIGRATE model at a larger scale in the "null" manner suggested previously would highlight discrepancies between the rates of migration of the species and their "environmental space" under climatic change scenarios. As such the model may be able to provide insights into which species will need human assistance to disperse and the likely dynamics of spread of newly introduced species. Combined with the findings outlined above it is probable that human interference could be limited to establishment of outlier individuals or populations beyond the main population fronts. Therefore the scattered exotics found in many regions of the world, well outside their natural ranges could be of use to management plans to facilitate migration.

If wildlife corridors were to be used as a conservation strategy then there may well need to be control of weedy exotics now. Corridors designed to naturally control the "passers-by" are highly unlikely to succeed because as demonstrated in this case, the unwanted exotics often have many characters in common with other members of the native flora.

The conclusions drawn from the model outlined above refer to its general performance. The conclusions are discussed under the assumption that the biotic and habitat data used are accurate and valid. Having said this, it is important to realise that the general behaviours exhibited by the model would probably still be in evidence if significant changes were made to these parameters. The next section discusses many of the simplifications made to the data used by the model. This is followed by a synthesis of the implications of the output from the model to the particular species studied. The discussion then considers the relationship of *Rhododendron* to other members of the communities in which it is found and the importance of GIS to this project.

4.4 Assumptions and simplifications made during the modelling process.

Although habitat carrying capacity maps were derived mainly from observations, these were observations that had an historic component, and as such, could offer more insight into probable habitat effects than present-day, short-term experiments. The large effect of habitat on the pattern of spread suggests that quantification of the effects of altitude, grazing and other disturbance regimes would be desirable as this would narrow down the range of possibilities for values assigned to habitat types for relative carrying capacities. Long-term field experiments on the effects of grazing by different herbivores in different habitat types would give greater rigour to the values chosen as would seed establishment trials carried out on an altitudinal transect. Without th~~is~~ ese quantitative data, it was necessary to assign values to physical parameters of the habitat, which were subsequently modified to achieve greater accuracy of prediction. With quantification the inaccuracies in the data used in other areas of the model could be tracked down and their effects observed. The more variables that become unknowns the greater the risk of circularity in the modelling process.

Simplification of habitat data and of environmental history, only represents one aspect of the modelling process, analogous procedures are used to establish biotic parameters. All parameters are derived from an individual or set of individuals in one or more habitat types, and these are used to represent the traits of all individuals. This avoids the impossible task of assigning each individual their own set of traits, which would still suffer from inaccuracies and assumptions of methodology and could not possibly cater for variation in these traits through time. Instead, the great variability is taken into account through the use of average measures so that the data, as much as possible, do not represent extremes. This is not to say that running the model using data derived from a single habitat type or based on single individuals would be misleading. In fact this would be very informative, as it would show not only how sensitive the biological parameters of the model are with regard to its overall behaviour, but also it would provide output representing the biotic bounds of possibility.

The assumptions made in the collection of biological data were numerous, although necessary considering the time available for field work. Some of those deemed more important considering the behaviour of the model are outlined below, as are suggestions for further field work.

The seedling distribution data were used to infer the likely shape of the seed dispersal function. This method was found to be lacking in that it needed to be supplemented by a hypothetical long-distance dispersal function. Seed trap studies conducted on isolated individuals or populations would probably provide better dispersal data and may reduce the need for the addition of an extra long-distance parameter. The pattern of seedling establishment in open habitats followed the lines of drainage ditches and so the numbers and spacing of individuals were affected by the spatial distribution of these features. This could have created bias in the overall dataset, although it is assumed that they did not because the ditches had regular straight shapes and so should sample from the dispersal plume in a regular way. It certainly created bias in the calculation of the proportion of seeds becoming established in that it sampled a plant with a population of seedlings around it. Most open habitat plants were not in areas where drainage ditches were present and so had no populations around them. The common occurrence of isolated bushes without sub-populations could not be sampled. Thus the estimate of seed establishment rates is probably high.

Perhaps one of the most important assumptions made was that the seed data collected from one bush was representative of the likely seed productions from any bush regardless of age and habitat type. This is a gross simplification of observed patterns of flowering, and this aspect would also benefit from further detailed field study and quantification. In ride and riparian habitats it was observed that few plants in shaded habitats were flowering or had flowered. Thus during model simulations these plants would be contributing to spread in a disproportionate way. The combination of this assumption with that made on the two-year flowering cycle in *Rhododendron*, when multiplied up, could create discrepancies with real world figures in orders of magnitude. The two-year cropping cycle was based on limited data that was only obtained from one habitat type and from one time. Detailed study over a longer time course should be carried out to assess the accuracy of this assumption. Therefore the seed output parameter is in need of further quantification, especially between habitats and age groups, so that better average values could be obtained.

Having noted the numerous simplifying assumptions made in abiotic and biotic parameters it was still interesting to observe the behaviour of the model.

The biological data derived from the field measurements were kept constant during runs of the model. This demonstrated the importance of making habitat changes through time and of changing biotic variables not measured in the field, such as the value given to the half-distance of the long distance dispersal function or the probability of dispersal according to this function.

The accuracy of the biotic data may be disputed on the grounds that they are generalisations made from limited data sets and are not representative of the whole. Throughout the results section, though, it was stressed how it was important to get average data for parameter values to allow for simplifications in the model. This ideology also limits the impact of individual heterogeneity.

The combination of biotic quantities used highlights important behaviours of the model overall and other areas of great importance and in need of further investigation. This general property of models, as with theory, to suggest further areas in need of research, conforms to the sentiments expressed by Levin (1981).

Habitat maps only affected the relative carrying capacity of grid cells for mature bushes, and in this way affected the modelled process of self-thinning. Habitat maps also simplified patterns of physical heterogeneity. For example, roads, rides and rivers were all given high values for carrying capacity even though these features in themselves are mainly inhospitable. The high values refer to the habitats directly associated with the edges of these features, such as road or ride cuttings or the steep banks of the rivers. Due to digitising constraints it was not possible to differentiate spatially between the inhospitable middle aspect of these habitats and their highly suitable edges.

Thus there have been many simplifications of biotic and abiotic patterns of heterogeneity, and yet it can be seen that good correlation between observed and expected results can be achieved.

The similarities between observed and expected distributions mainly lie in general aspects of the distribution such as overall extent and the exploitation of linear features such as roads, rides and river corridors. Specific details match to a lesser degree, although this is not discouraging considering the small-spatial scale of the study and the time over which the pattern of spread has developed. If the spatial scale of sampling of the real world and simulated distributions were increased, the patterns would conform more closely, because the details would be lost.

A simplification made to the real world distribution shown in figure 3.3 compared to figure 3.4.2c) is that areas of *Rhododendron* cleared for control are classed as having 100% cover. This was based on the observation of numerous shooting rootstocks in these particular areas around the Lodge. This simplification avoided the need to incorporate small scale human developments into the habitat maps.

There are two respects in which the model probably gives a more accurate idea of the present-day distribution than the actual data mapped. Firstly the output from the model is more patchy and less contiguous, especially along the linear features which is a good approximation to that seen in the field. When mapping the distribution, as in figure 3.3, areas of sporadic cover with intermediate densities were very hard to classify. The impossible ideal would be to lay a 10m resolution grid over the whole area, counting the number of plants in each cell. When assessing density it was often very hard to decide when cover had ended and when it was still part of the same population. Within the populations it was very difficult to assess density, and all areas of 100% cover were assumed to have maximum densities. Secondly the simulated distribution treats first year seedlings the same as mature individuals in terms of presence/absence data. These tiny seedlings are obviously much harder to find, and thus map, in the field.

Areas where the present distribution and that simulated do not match up mainly includes the south-east part of the distribution. The reason for this, and other mismatches is that the detail incorporated into the habitat maps is mainly derived from OS maps rather than from field survey. Rides, roads or rivers are all classified individually as one type whatever their true character. This homogeneity of physical features is not a true reflection of the real world, and where, for example, *Rhododendron* is shown as colonising the lower reaches of the River Etive in the simulation, this is not found in the mapped distribution. This is probably because this area levels out into a floodplain and the steep, protected river gorges are no longer evident. Red deer were observed to cross the river freely at this point and utilise the grazing on the spits and bars. Another limit to *Rhododendron* growth on this part of the river system, is that it is periodically flooded and thus highly disturbed, the lowest reaches being inundated with sea water. Similar flat banks adjoining the river occur in other reaches and on other tributaries resulting in the patchy mapped distribution in many places. The lack of *Rhododendron* colonisation in the south and in the north in the actual compared to the simulated distribution, suggests an affect of the prevailing winds on seed dispersal. This affect of a predominant wind direction is not taken into account in the dispersal equations of the model.

The model could be made more complex to capture the differences in establishment rates between habitat types or differences in the dispersal function. It could also incorporate habitat specific growth rates and seed and flower productions because it is likely that a young plant could have seed productions an order of magnitude different to those of an adult plant. This added complexity would probably result in a greater accuracy of simulation of specific aspects of the pattern of spread because the habitat, in effect, would be exerting a greater influence upon the dynamics of spread.

The fine spatial and temporal scales of habitat heterogeneity are not taken into account by the habitat maps used. For example, in the open habitats the carrying capacity was set at zero, even though it was evident that some colonisation was taking place. Seeds were exploiting small-scale drainage ditch features not shown on maps and so were not digitised. This highlighted the main weakness of the model which bases habitat interactions on relative carrying capacities. The evidence in the field suggested no particular differences in carrying capacity between different habitats, but rather it showed differences in establishment rates. Habitat maps for relative establishment rates would allow for greater accuracy in prediction and this is a change I would recommend for the overall structure of the model. At present, changes in relative carrying capacity are used to represent changes in establishment rates.

Short-term historic events are not taken into account by the model, for example stochastic events such as forest fires, wind throw of forest blocks or chance colonisation of particular places in the order of their occurrence in the actual pattern of spread. Thus the model in the present form cannot hope to capture the specific details of the invasion. To simulate all of these details would require a model with a finer temporal resolution and access to detailed historical data, the collection of a greater amount of data through more detailed survey, and the implementation of vastly more complicated habitat maps with numerous different carrying capacity measures. Such specialisation of the model inputs to a specific situation though would be in vain unless the model's structure could be changed to work with finer scale habitat maps and MIGRATE grids which in turn depend on computational capacity.

Moves towards specialisation occurred during earlier runs of the current model, as the model was tuned to produce output in accord with that seen for the present-day. With a greater amount of time and using different parameter values and different combinations, I have no doubt that increasing accuracy of simulation could have been be achieved. The question one must then ask though is whether this increase in accuracy would represent a significant departure from that achieved with simplification of variable structure. For example, the habitat measures used in the simulations are, in themselves, an attempt at modelling physical heterogeneity. Although contours were turned into a 3-dimensional model of the habitat showing topographic attributes, this was not a specific model, it was produced to give the generalities of the landscape. It gave the same amount of information for the resolution used as a similar although far more detailed model would have given.

Moves towards specificity represent a move away from the overall aim of modelling, which is to capture the main determinants of a process. It is important to gauge the general applicability of a model according to the changes actually made during the simulation process and the level at which they occur.

Basically the MIGRATE model works at two main resolutions, and changes can be made at both levels. The MIGRATE model has generality and yet can be made to incorporate the specifics of a particular situation.

Firstly at the level of the model structure itself, no changes were made except in the way carrying capacity measures affected the die-off of established *Rhododendrons.* Initially carrying capacity had affected established bushes whereas it was obvious from the field situation that it was only immature individuals who were to be culled by habitat effects. Once mature, all individuals should survive because there was no evidence of death in the field.

In simulating control regimes this earlier version of the model was useful for simulating the cull of established populations. Overall though, the adaptation of the MIGRATE model only differed to that used for larger spatial scale simulations in that it was able to utilise a grid composed of a greater number of cells and was able to produce ASCII files for conversion into GIS coverages. The intermediary conversion programs between the GIS stages of the project and the model itself simply represent conversions of input into readable forms. Thus the biotic parameters needed for prediction at the large scale are also applicable to smaller scales. This shows the general nature of the model.

Secondly there are the values derived from the field study and from the literature and the parameters included in habitat maps. These values and parameters will be species specific to a large extent, although it would be interesting to test the current set up of the model on a different population of *Rhododendron* for which similar knowledge of environmental history is obtainable. The results of this test could verify the general applicability of the values derived from this particular field situation and the methodologies used. Thus this level of the model structure has attributes which are more variable, especially between species, and allows the model to specialise on a particular species in a particular location.

4.5 Implications of model predictions of likely future changes in the patterns of spread.

Having achieved fairly accurate simulations for past and present distributions the model can be used for prediction. Prediction of the future assumes the biological parameter values will stay roughly the same and that the patterns of habitat change observed up to the present time should continue into the future. For example, it can be assumed that plantation forestry will continue to mature and be felled. Similarly it can be hoped that fences erected will be maintained for a certain period of time.

Prediction of future changes is obviously dependent upon the nature of the habitat feature considered. Those features with biological properties and/or tied directly with human activities such as forestry and grazing regimes are often more dynamic and can be subject to future socio-economic and political factors which influence man's decisions. Such factors are notoriously difficult to predict although change in these areas are also often slow. Relatively static physical features of the habitat such as rivers, lochs and altitude can be predicted with greater certainty. Intermediate structures of the habitat would include features such as roads.

The habitat maps constructed for future prediction assumed that an area fenced on the hillside east of the Lodge in 1994 to protect native tree species and to encourage regeneration will remain intact for the next 40 years or so. This gives it a similar lifespan to that observed for the fence around the main forestry block. In the context of the above this event would not have been predictable a few years beforehand and has been erected through the use of grant money provided by SNH. This new policy means that there will be planting of hardwoods in the area presently occupied by the coniferous plantation, and so it was assumed that forestry fences in this area will be repaired within the next 12 years. The disrepair of the forestry fence in 1994 meant that habitat maps had to include a lowering of carrying capacity in ride environments and along fence lines, as well as in the overall area now accessible to grazing. The values were not reduced to zero though because many sections of ride were rendered impassable by the growth of sub-populations. This aspect of spread not only negates the reasons behind the construction of rides, but also highlights an aspect of spread probably peculiar to this woody taxon that is very difficult to model. It was observed in the field that *Rhododendron* could exploit natural and man-made linearities in the landscape to block off areas - because the growth formed an impenetrable "fence" to large herbivores - which it was then infilling.

The spread until the period of 2030 is described in section 3.4.4. It is somewhat ironic that the establishment of the fenced area to encourage regeneration of relict woodland stands will apparently lead to their extinction as regeneration is prevented in the long-term due to shading out by *Rhododendron* encroachment (Cross, 1981). The extent of spread predicted also shows the Ard Trilleachan SSSI to be under threat and so these areas will need to be monitored in the future and necessary control programs carried out. Any control strategies implemented in areas of *Rhododendron* invasion will obviously affect the dynamics of spread and thus the patterns predicted.

Overall, the contiguous character to the pattern of spread will significantly reduce biodiversity in the area because of the evergreen and exotic character of *Rhododendron*.

The dense shade cast year round by *Rhododendron* will significantly reduce the diversity of the ground flora in all habitats, which in some instances is quite rich (especially in pteridophytes and bryophytes, see appendix 1), and the spread of the plant threatens bog plants and woodland plants alike. Figure 4.5 shows the typical flora of the riparian habitats threatened by shading and litter production, including the saplings of *Alnus glutinosa*. In this habitat the reduction of ground cover was also seen to be resulting in soil erosion.

The plant also threatens the biodiversity of the ride habitats in exotic conifer plantations whose beneficial functions are discussed by Hill (1985). The future pattern in upland Britain could be one of blanket forestry and blanket *Rhododendron*.

Figure 4.5 Typical ground flora of the broadleaved dominated riparian corridor habitats. The species shown include *Luzula sylvatica*, *Viola riviniana*, *Anemone nemorosa*, a sapling of *Alnus glutinosa* and various moss species.

A species list of all plants growing in association with *Rhododendron* can be found in Appendix 1. No plant species were observed growing under the dense mature stands.

The future destruction of the native flora of the area, probably up to a certain altitude level, and the toxic nature of the foliage of *Rhododendron* (Cross,

1975) will combine with its exotic character and thus its depauperate insect community to reduce the grazing potential of the area and the feeding opportunities for birds and other animals. Thus, *Rhododendron* could have knock-on effects at the ecosystem level as shown with *Myrica faya* in Hawaii Vitousek (1990). The invasion could alter ecosystem properties such as productivity, nutrient cycling, and hydrology (Vitousek, 1990), thus threatening the animal species listed in appendix 2. Considering the high overall diversity of this area noted simply during the three week period of the field study, and the presence of rare species, destruction of this biota is unacceptable and control strategies must be implemented. Invasion on the scale predicted will destroy the aesthetic appeal of the area, and could also threaten nearby valleys, for although mature plants may be limited by altitude, the seeds are virtually immune to the effects of altitude and are only limited by dispersal distances.

If there is no concern for the sparse relict communities in the glen at present then in the light of current theories on climatic change and the proposed changes to be made in the designation of reserves, the Glen Etive site and many like it which are also threatened by *Rhododendron* invasion should still be protected. The area has a large vertical amplitude and a diverse range of physical habitats and climatic types and could thus accommodate range changes occurring in response to temperature changes and the formation of new biotic communities (Hunter, Jacobson and Webb, 1988).

Having considered the potentially harmful effects of *Rhododendron* it should be stated that some short-term beneficial effects were noted in the field. Firstly, although birds were rarely observed feeding amongst *Rhododendron* canopies, some species were found to nest in its dense cover (appendix 2). Compared to the northern end of the glen which is devoid of bushes and trees, the southern end (where the study site was) had a far larger amount of bird species. This was probably due to the number of habitat types present and the greater structural diversity available. It would be interesting to quantify the effect of *Rhododendron* on bird species diversity in terms of the structural layer it adds to the habitat and in terms of the horizontal mosaic it creates with other vegetation types. From the observations of the lack of a natural shrub layer in the field it is possible that a certain amount of *Rhododendron* is of benefit to the diversity of the area although this situation will only exist whilst it is part of a patchy mosaic with other habitat types which offer opportunities for feeding.

Another effect of the encroachment of the *Rhododendron* is its ability to act as a toxic nurse plant for other woody species. This effect was alluded to in section 3.2.6 where it was shown that there was a statistically significant association of taller tree saplings with the front of invasion. More specifically observation showed that there was a gradient in the heights of the saplings from tallest to shortest. The tallest saplings were associated to areas initially invaded and the shorter trees were found up to the edge of the *Rhododendron* encroachment. Beyond the invasion front were numerous "bonsai" tree specimens and although this suggests the presence of invasion, it again points to the intensity of the grazing regime as being of paramount importance. The hillside of Creag Dhubh is very inaccessible and so grazers are probably infrequent in this area, being frequent enough to keep tree species cropped and yet allow *Rhododendron* invasion to occur. The typical stem morphology of saplings growing within the protection of the *Rhododendron* canopy is shown in figure 3.2.6a). Observations suggest that there is probably a window within which tree sapling establishment can occur. This period is between being grazed out of a sward and the establishment of a *Rhododendron* bush canopy. This offers protection to the sapling which then grows up and outwards to avoid shading. Eventually the sapling grows through the canopy and is high enough to avoid grazing pressures. It does not appear to be the result of trees seeding in after the establishment of *Rhododendron* as no dicotyledon stage seedlings were found under mature canopies. A similar effect is seen with *Pteridium aquilinum* (bracken)although in this case the saplings top the canopy and are still within reach of grazers and are thus cropped. Bracken also offers protection to the relict woodland flora of *Hyacinthoides non-scripta* (bluebells), *Primula vulgaris* (primroses) and *Anemone nemorosa* (wood anemones). The deciduous character of bracken allowed these herbaceous species to flower in the spring. Such an event would be precluded by a toxic canopy of an evergreen character. The proposed nurse plant effect of *Rhododendron* is in need of further detailed quantification, and its implications in terms of the long-term survival of the local tree species also needs to be assessed. It is probable that this effect only represents a reprieve for the native species, as establishment of tree saplings was only observed in association with *establishing Rhododendron* bushes (and other protected environments such as rides, fence lines, rock faces, etc.) and no regeneration was seen within mature stands directly beneath potential seed sources.

Considering the threat to the native flora and fauna this particular woody taxon poses it would seem advisable to ban the planting of this species in landscaping schemes as was observed along a motorway embankment and to devise control strategies. The applied nature of the current project in the scale at which it works means that this is potentially possible and some early attempts are discussed below.

4.6 Use of the model in designing control strategies.

The broad types of control strategy simulated in figures 3.4.5a) and b) suggest that the culling of peripheral populations is desirable based on the likely patterns of spread predicted. The graphic output of the model and its ability to depict small-scale migrations in specific areas could provide a powerful tool for conservationists because diagrams are more universal in their ability to convey messages than words. This aspect again highlights the applied aspect of the model compared to those developed by others.

Control strategies will not simply be designed according to patterns of predicted spread, but will have to take into account other factors. For example, the accessibility of the population to control and disposal of cut material will also be important. Peripheral population control would be desirable in this respect with large areas of contiguous cover hampering control. Support for peripheral culls mainly represented by ride and mature conifer stand habitats comes from research into the control of other invasive shrubs. Luken and Mattimiro (1991) suggest that control of *Lonicera mackii* should concentrate on forest-growing rather than open-growing populations because these are least resilient to clipping. It is proposed that these plants have lesser reserves available for regrowth because of the shaded nature of the habitat in which they grow. Therefore the model and other considerations provide support for Usher's suggestion that containment rather than eradication should be attempted with invaders. If resources were available though, eradication of the total population would be desirable from the point of view of its likely long-term impact on the glen.

The integration of a GIS with the model means that actual numbers of plants and thus amounts of materials needed, such as "round-up", could be calculated from gridded outputs of distribution in which abundance is given in terms of actual numbers of plants per cell. The GIS would also provide a database for planning the overall strategy and a map on which cleared areas could be located. Attribute data of cleared areas would also be useful for the assignment of later monitoring schemes.

Shaw (1984) suggested that it may be possible to identify parts of a given population as being more active in causing further spread and to give these priority in control programs. This was achieved using the model. The control techniques used are often quoted in the literature as creating disturbance features of benefit to the seeds of *Rhododendron*. A fine balance is therefore required between the degree and the type of disturbance required to a maintain a high value for native species richness, and that which may result in successful invasion by introduced species (Fox and Fox, 1986). Disturbance, such as noise, caused by clearance must also take account of the species present, especially in reserve areas (Usher, 1986).

4.7 Other observations made on the ecology of *Rhododendron*.

The value of disturbance to invasive species is reported for *Rhododendron* by Cross (1981) but this suggests that high grazing intensities should thus be of benefit to its spread. This was not observed in the habitats studied in the current project and I would in fact advocate the use of intensive grazing as a potential form of control in open habitats. The trouble with the use of the term disturbance is that it is taken to represent a wide range of environmental changes, and as such there has been little study as to the direct nature and effects of disturbance. The discrepancies in the literature cited in the introduction, and compared to the findings of this project suggest a need for stricter definitions of disturbance regimes.

This project has emphasised to me the need to look not only at possible reasons for the invasion of certain areas but also to look at why invasion has *not* occurred in others.

The need for detailed study on the effects of grazing on the spread of *Rhododendron* is also suggested by this project. Shaw (1984) cites the increase in stocking rates and the less intensive management of rough grazing as being of importance to the spread of *Rhododendron*. The findings of the current project suggest that areas of intensive grazing are immune to invasion. Although the observations made during the fieldwork phase of this project suggested a negative effect on the rate of spread of increased grazing intensity, it is not clear what is meant by the word increased. There could have been increase from low to moderate or from moderate to high stocking densities. These changes could have very different effects on the dynamics of an ecosystem. There is probably a threshold level, as with many system processes, which once passed "flips" the system dynamics to another steady-state of lower productivity and diversity as is seen with pollution events. Thus the apparent paradox in the literature between the findings of Cross (1981) and Shaw (1984), and Thomson *et al.* (1993) could perhaps be resolved by experimental quantification of grazing regimes as suggested above. It could be that *Rhododendron* performs differently in different habitats due to the ease of detection of seedlings against a herb layer background or due to the differences in grazing or trampling probabilities characteristic of different ruminants and stocking densities.

4.8 The use of GIS to applied research.

Without reviewing the numerous ways in which GIS is being integrated into ecological research and other areas it should be realised that many aspects of this project depended on spatial data capture.

The distribution and abundance data is at a 10m resolution for the real world and predicted maps and thus this project is examining spread at a fine spatial scale which includes much detail. This was only possible through the use of a GIS which allows for accurate data capture and manipulation from different scale maps because they can be georeferenced to the same real world co-ordinates without large distortions.

CONCLUSIONS.

The present study shows the applied value modelling can have, although detailed parameterisation of variables is needed. This will require further field studies, and considering the likely future importance of the migration response to climate change this is highly recommended. The specific nature of the interactions between *Rhododendron* and other members of biological communities are also in need of study and further spread and planting of this invasive shrub should be prevented as much as possible. This project outlined how the integration of a simple deterministic model with a GIS could be of use to the prediction of the migration response in general, and at a fine scale, how control strategies for problem species could be implemented.

APPENDIX 1: Tree species and ground flora present at the study site.

Native tree species †.

Acer pseudoplatanus L.	Sycamore*
Alnus glutinosa (L.) Gaertner	Common alder
Betula pendula Roth.	Silver birch
Betula pubescens Ehrh.	Downy birch
Corylus avellana L.	Common hazel
Fagus sylvatica L.	Beech*
Fraxinus excelsior L.	Ash
Ilex aquifolium L.	Holly
Juniperus communis L.	Juniper
Pinus sylvestris L.	Scots pine
Populus tremula L.	Aspen
Quercus petraea (Mattuschka) Liebl.	Sessile oak
Salix cinerea L.	Common sallow
Sorbus aucuparia L.	Rowan

Introduced tree species †.

Abies procera Rehd.	Noble fir
Aesculus hippocastanum L.	Horse chestnut
Fagus sylvatica 'purpurea' L.	Copper beech
Larix × *eurolepis* Henry	Hybrid larch
Larix decidua Miller	European larch
Larix kaempferi (Lamb.) Carrière	Japanese larch
Picea abies (L.) Karsten	Norway spruce
Picea sitchensis (Bong.) Carrière	Sitka spruce
Pinus contorta Dougl. var *latifolia* Wats.	Lodgepole pine
Tsuga heterophylla (Rafin) Sargent	Western hemlock

* Although not native to the Glen they are considered as naturalised.

Angiospermae

Dicotyledones †:

Ajuga reptans L.	Bugle
Anemone nemorosa L.	Wood Anemone
Armeria maritima (Miller) Willd.	Thrift
Calluna vulgaris(L.) Hull	Heather
Cytisus scoparius (L.) Link	Broom
Dactylorhiza fuchsii (Druce) Soó	Common Spotted Orchid
Digitalis purpurea L.	Foxglove
Drosera rotundifolia L.	Round-leaved Sundew
Erica tetralix L.	Cross leaved Heath
Galium saxatile L.	Heath Bedstraw
Hyacinthoides non-scripta (L). Chouard ex Rothm.	Bluebell
Hypericum tetrapterum Fries	Square-stalked St. John's Wort
Melampyrum pratense L.	Common Cow-wheat
Myrica gale L.	Bog Myrtle
Oxalis acetosella L.	Wood-sorrel
Pedicularis sylvatica L.	Lousewort
Pinguicula vulgaris L.	Common Butterwort
Polygala vulgaris L.	Common Milkwort
Potentilla erecta (L.) Räuschel	Common Tormentil
Primula vulgaris Hudson	Primrose
Ulex europaeus L.	Common Gorse
Vaccinium myrtillus L.	Bilberry
Vaccinium vitis-idaea L.	Cowberry
Viola palustris L.	Marsh Violet
Viola riviniana Reichenb.	Common Dog-violet

Monocotyledones †:

Carex nigra (L.) Reich.	Common sedge
Deschampsia flexuosa (L.) Trin.	Wavy Hair-grass
Eriophorum angustifolium Honckeny	Common Cotton-grass
Eriophorum vaginatum L.	Cotton-grass

Juncus effusus L.	Soft Rush
Luzula sylvatica (Heids.) Gaud.	Greater wood rush
Molinia caerulea (L.) Moench	Purple Moor-grass

Pteridophyta ††.

Blechnum spicant (L.) Roth	Hard fern
Dryopteris diatata (Hoffm.) A. Gray	Broad buckler fern
Hymenophyllum wilsonii Hook.	Wilson's filmy fern
Thelypteris limbosperma (All.) H. P. Fuchs	Lemon scented fern

Bryophyta ††.

Dicranum majus Sm.
Diphasiastrum alpinum (L.) Holub.
Hylocomium splendens (Hedw.) Br. Eur.
Hyocomium armoricum (Brid.) Wijk & Marg.
Hypnum cupressiforme (Hedw.)
Isothecium myosuroides Brid.
Lepidozia reptans (L.) Dum.
Mnium hornum Hedw.
Plagiothecium denticulatum (Hedw.) Br. Eur.
Pohlia nutans (Hedw.) Lindb.
Polytrichum commune Hedw.
Pleurozium schreberi (Brid.) Mitt.
Sphagnum capillifolium (Ehrh.) Hedw.
Sphagnum palustre L. †††
Sphagnum papillosum Lindb. †††
Thuidium tamariscinum (Hedw.) Br. Eur.

† All scientific names and authorities from Clapham, Tutin and Warburg (1989).

†† All scientific names and authorities from Phillips (ed.) (1980).

††† All scientific names and authorities from Daniels and Eddy (1985).

APPENDIX 2: The animal species associated with broad habitat types.

Birds.

i) Sea loch/river mouth and marsh habitat:

Actitus hypoleucos *	Common Sandpiper
Ardea cinerea	Heron
Charadrius hiaticula	Ringed Plover
Haematopus ostralegus	Oystercatcher
Larus canus *	Common Gull
Mergus merganser	Goosander
Numenius arquata	Curlew
Riparia riparia *	Sand Martin

ii) Rough grazing with boulders and scree:

Anthus pratensis *	Meadow Pipit
Corvus corone cornix	Hooded Crow
Oenanthe oenanthe *	Wheatear

iii) Rough grazing/moorland with scattered birch, alder and oak:

Anthus trivialis *	Tree Pipit
Carduelis flavirostris	Twite
Corvus corone cornix *	Hooded Crow
Cuculus canorus *	Cuckoo
Falco tinnunculus	Kestrel
Motacilla alba	Pied Wagtail
Phylloscopus trochilus *	Willow Warbler
Saxicola rubetra *	Whinchat
Saxicola torquata *	Stonechat
Turdus viscivorus	Mistle Thrush

iv) River corridor habitat:

Cinclus cinclus *	Dipper
Corvus corone cornix *	Hooded Crow

Motacilla cinerea *	Grey Wagtail
Troglodytes troglodytes *	Wren

v) Coniferous and broadleaved woodland with shrubs:

Buteo buteo *	Buzzard
Carduelis spinus	Siskin
Columba palumbus *	Wood Pigeon
Corvus corone cornix *	Hooded Crow
Erithacus rubecula *	Robin
Fringilla coelebs *	Chaffinch
Garrulus glandarius	Jay
Parus ater	Coal Tit
Parus caeruleus	Blue Tit
Phylloscopus collybita	Chiffchaff
Phylloscopus trochilus *	Willow Warbler
Pyrrhula pyrrhula	Bullfinch
Regulus regulus *	Goldcrest
Scolopax rusticola *	Woodcock
Strix aluco *	Tawny Owl
Sylvia atricapilla *	Blackcap
Troglodytes troglodytes *	Wren
Turdus merula *	Blackbird
Turdus philomelos *	Song Thrush

vi) Aerial feeders (seen foraging for insects above all habitat types), and raptors:

Apus apus	Swift
Aquila chrysaetos	Golden Eagle
Buteo buteo	Buzzard
Delichon urbica	House Martin
Hirundo rustica	Swallow
Riparia riparia	Sand Martin

* evidence for the species using this habitat type for reproduction, ie. when the nest, eggs or young of the species were found, or the adults were displaying or carrying food. Other entries are only for birds seen feeding within these habitats.

Mammals †.

Capreolus capreolus	Roe deer
Cervus elaphus	Red deer
Martes martes	Pine marten
Microtis agrestis	Wood mouse
Mustela erminea	Stoat
Sorex araneus	Common shrew
Vulpes vulpes	Red fox

Amphibians and reptiles.

Anguis fragilis	Slow worm
Lacerta vivipara	Viviparous lizard
Rana temporaria	Common frog

† All scientific names as Corbett and Harris (1991).

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