

**Modelling population dynamics
of *Leysera gnaphalodes* in
Namaqualand, South Africa**

by

Jessica Kate Conradie

Submitted in partial fulfillment of the requirements for the degree

Magister Scientiae

in the Faculty of Natural & Agricultural Science

University of Pretoria

Pretoria

Supervisor: M.W. van Rooyen

October 2003

Contents

Chapter 1: Introduction	1
REFERENCES	4
Chapter 2 : Modelling and its application in Ecology	6
INTRODUCTION	6
THE USE OF MODELS IN ECOLOGY	10
THE PROCESS OF MODELLING	12
TYPES OF MODELS, THEIR ADVANTAGES, DISADVANTAGES AND USES	16
Non-quantitative models	20
<i>Physical models</i>	20
<i>Verbal models</i>	20
<i>Conceptual models</i>	21
Quantitative models	21
<i>Statistical models</i>	22
<i>Mathematical models</i>	24
<i>Deterministic models</i>	26
<i>Stochastic models</i>	26
<i>Chaotic models</i>	27
<i>Computer simulation models</i>	28
THE LOGISTIC MODEL	29
<i>Alternative forms and extensions</i>	31
<i>Applications of the logistic model in ecology</i>	32
CONCLUSION	33
RERERENCES	

Chapter 3: Population dynamics of Leysera gnaphalodes: A mathematical modelling approach	37
ABSTRACT	37
INTRODUCTION	38
MATERIALS AND METHODS	40
RESULTS	44
DISCUSSION AND CONCLUSIONS	52
RERERENCES	66
Chapter 4: Population dynamics of Leysera gnaphalodes: A statistical modelling approach	69
ABSTRACT	69
INTRODUCTION	70
MATERIALS AND METHODS	72
RESULTS	75
DISCUSSION AND CONCLUSIONS	79
RERERENCES	85
Chapter 5 Conclusion	87
RERERENCES	90
Summary	91
Acknowledgements	93
References	95

Chapter 1: Introduction

Namaqualand is world-renowned, and unique amongst the world's deserts, for its spectacularly colourful and diverse spring floral display (le Roux & van Rooyen 1999, van Rooyen 1999). Namaqualand has a higher species richness of plants than any other desert in the world (van Rooyen *et al.* 1996) and of the 3 500 species occurring in the area, 22% are endemic (le Roux & van Rooyen 1999). Despite its great conservation and ecotourism value, only 3.5% (Succulent Karoo Ecosystem Planning - Ecosystem Profile {http://www.dlist.org/util/resource_detail.cfm?FCID=210}, 12 February 2003) of the Succulent Karoo Biome (of which Namaqualand is a part) has been set aside for conservation. The conservation areas that do exist are thus of cardinal importance. One of these areas is Namaqua National Park where the focus of this study will lie.

This study focuses specifically on the portion of the park formerly known as Skilpad Wildflower Reserve. This area lies on the edge of the escarpment near Kamieskroon, in an area that receives orographic rainfall. It is situated in the “Klipkoppe” or “Hardeveld” vegetation type, which is regarded by locals as the true Namaqualand. The reserve, which was 1000 hectares in size, was established in 1988 to promote the conservation of Namaqualand's wildflower resources (van Rooyen *et al.* 1996). It has recently been combined with surrounding farmland to form the 73 619 hectare Namaqua National Park.

The floral display is created by various ephemeral species, and is especially prominent where they grow at high densities on abandoned fields, heavily grazed pastures and other disturbed areas (Rösch *et al.* 1997, van Rooyen 1999). Although wildflowers occur naturally in the vegetation of Namaqualand, in undisturbed veld they are interspersed with larger perennial plants and do not produce such a vivid splash of colour (Milton & Dean 1991).

Even in natural veld, the wildflowers select microhabitats characterised by disturbance. While human disturbances include tilling and grazing, natural disturbances come in the form of burrowing/digging/trampling by animals and drought. Small-scale natural disturbances tend to create small patches of soft, bare soil, often rich in nutrients due to defecation by animals. These patches provide the ideal habitat for colonisation by annuals (Dean & Milton 1991a, 1991b, Milton & Dean 1991, van Rooyen 1999)

Tilling, a form of anthropogenic disturbance, also promotes annual plant abundance. Annuals dominate recently cultivated lands, and it may take many decades for perennial plant assemblages to re-establish in these areas (Dean & Milton 1995). Total plant diversity increases steadily with time since cultivation, although annual plant diversity is not affected. Species richness is still highest in undisturbed vegetation (van Rooyen 1999).

It is not only plant diversity that is decreased by tilling, but invertebrate diversity too. Recently cultivated lands have an insect assemblage dominated by a single species of ant (*Anoplolepis steingroeveri*). Insect diversity is positively correlated with perennial plant diversity, and negatively with annual plant diversity (Dean & Milton 1995). This implies that insect diversity will also steadily increase with time since cultivation.

From the above discussion it becomes clear that the mass displays, or carpets of flowers for which Namaqualand has become famous are “unnatural” in that they are a result of agricultural disturbance (Milton & Dean 1991). The tourism brought into the Northern Cape region by the Namaqualand wildflowers is invaluable to the economy (le Roux & van Rooyen 1999), and preserving this floral spectacle is thus of great importance. However, from an ecological perspective, the areas that render these carpets of colour lack diversity. If they were to be managed to maximise the conservation of biodiversity (the normal strategy followed in such a species-rich area), more perennial-rich states in which total plant diversity and invertebrate diversity are higher would be favoured. Thus the demands of tourism and conservation appear to be

contradictory (van Rooyen 1999). It is this apparent contradiction which will be addressed in this study.

One of the reasons why tilling is presently applied in the Namaqua National Park is to control a species known as *Leysera gnaphalodes* (L.) L. (Asteraceae, Gnaphalieae). *Leysera gnaphalodes* encroaches into the wildflower displays of Namaqualand and “dampens” the colour (le Roux & van Rooyen 1999).

Leysera gnaphalodes is a perennial dwarf shrub growing 200 to 500 mm in height (Anderberg & Bremer 1991). It has wiry grey to green leaves and entirely yellow flower-heads up to 20 mm in diameter, which are present from September to December (van Rooyen *et al.* 1999). The plant occurs on sandy flats and slopes, in the Western, Eastern and Northern Cape Provinces of South Africa as well as in Namibia (van Rooyen *et al.* 1999).

To fully understand the effects of anthropogenic (or any other) disturbances on *L. gnaphalodes* and the floral display, it is necessary to understand their effects over an extended period of time and under varying climatic conditions. To do this experimentally is impractical, because by the time it has been established what the long-term effects of the different management strategies are, it is probably too late to apply any of them effectively. In addition, one cannot choose the weather conditions, so only the effects under the weather conditions which prevail will be known. For this reason the effects on the vegetation of various factors were studied using models (Wiegand & Kellner 2000).

Models are also advantageous in that they offer more flexibility than examining ecosystems experimentally. One can change things more quickly and easily, and understand the properties of the complex system more fully. If a system can be successfully modelled it gives one the assurance that the most important driving forces in the system are understood (Cross & Moscardini 1985, Wiegand & Kellner 2000).

The second chapter of this dissertation is a review of modelling and its application in ecology. Different types of models are defined and their

applications, advantages and disadvantages discussed. Special reference is made to the logistic growth model as it is applied later in this work.

Chapters three and four deal with the actual models of the population dynamics of *L. gnaphalodes*. Chapter three is a mathematical model and chapter four is a statistical model. These chapters are written in the form of independent articles and so the formats differ in some respects from the rest of the thesis. There may also be some repetition due to this.

The final chapter is a conclusion, which pulls together the results of the two different models and discusses the relative advantages and disadvantages of mathematical and statistical modelling techniques.

REFERENCES

- ANDERBERG, A.A. & BREMER, K. 1991. Parsimony analysis and cladistic reclassification of the *Rephalis* generic group Asteraceae, Gnaphalieae. *Annals of the Missouri Botanical Gardens* **78**:1061-1072.
- CROSS, M. & MOSCARDINI, A.O. 1985. *Learning the art of mathematical modelling*. Ellis Horwood Ltd., Chichester.
- DEAN, W.R.J. & MILTON, S.J. 1991a. Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: Mammal diggings as germination sites. *African Journal of Ecology* **29**:11-16.
- DEAN, W.R.J. & MILTON, S.J. 1991b. Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* **20**, 231-237.
- DEAN, W.R.J. & MILTON, S.J. 1995. Plant and insect assemblages on old fields in the arid southern Karoo, South Africa. *African Journal of Ecology* **33**:1-13.
- LE ROUX, A. & VAN ROOYEN, G. 1999. Succulent Karoo. *The Magnificent Natural Heritage of South Africa* (ed.) J. Knobel, pp. 94-107. Sun Bird Publishing, Cape Town.
- MILTON, S. & DEAN, R. 1991. Disturbances in dune grassland: Colourful consequences of clearing. *African Wildlife* **45**:199-203.
- RÖSCH, H., VAN ROOYEN, M.W. & THERON, G.K. 1997. Community-level competition between five Namaqualand pioneer plant species. *South African Journal of Botany* **63**:1-3.
- VAN ROOYEN, G., STEYN, H. & DE VILLIERS, R. 1999. *Cederberg, Clanwilliam & Biedouw Valley: South African Wild Flower Guide 10*. Botanical Society of South Africa, Kirstenbosch.

- VAN ROOYEN, M.W. 1999. Functional aspects of short-lived plants. In: W.R.J. Dean & S.J. Milton (eds.) *The Karoo – ecological patterns and processes* pp. 107-122. Cambridge University Press, Cambridge.
- VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1996. Skilpad Wildflower Reserve – A flower-lover's paradise. *Veld & Flora* 82:40-42.
- WIEGAND, T. & KELLNER, K. 2000. *Workshop at the 26th annual congress of the South African Association of Botanists: The role of models in long-term ecological research*, Unpublished report of abstract, January 2000, Potchefstroom University for Christian Higher Education, Potchefstroom.

Chapter 2:

Modelling and its application in ecology

INTRODUCTION

Modelling is the construction of models, and models are simplified pictures of reality that contain not all features, but all essential features of the system relevant to the problem being examined (Jorgenson 1994). These simplifications of the real world are thus not exact replicas, but contain all the essential components of reality (Cross & Moscardini 1985). Models are used to organise, condense and arrange data in order that we may understand, interpret and use them (Wiegand & Kellner 2000).

An example of a model is a small object with the outer shape of a ship, but with no inner detail. This could be used to measure resistance as a ship passes through water, and how this resistance might change as the shape of the ship changes. Although the model does not contain all the details, for example inner corridors and rooms, of the system (ship), it nevertheless contains enough of them to allow the necessary conclusions to be drawn. A model the size of a ship need not be built to examine how different shapes affect water resistance and thus use may be made of a cheaper and more manageable microcosm (Jorgenson 1994).

Maps are another example of models: Maps demonstrate how the characteristics included in a model depend on its purpose – the information depicted on a map depends on the purpose of the map. A street guide would include details of the road network that are simply irrelevant on a vegetation map. Conversely, it is unnecessary to include detailed information on the vegetation of an area in a street guide (Jorgenson 1994).

Modelling in general, and ecological modelling in particular, is a new field of science that has advanced rapidly in about the last three decades. This rapid

advance has occurred primarily for two reasons: Firstly, modelling has become more feasible, and secondly, the demand for the output of models has increased (Jorgensen, 1994).

Advances in computer technology (Jorgensen 1994) and improvements in computational methodologies (Rodin *et al.* 1990) have made it possible to deal with complex mathematics on large data sets – which makes modelling practically possible. Moreover, a better understanding of environmental and ecological systems and their quantification has allowed models of these systems to be built more successfully (Jorgensen 1994).

Advances in nuclear physics and ecology have required that analytical data be synthesised to give a holistic picture. This is due to the systems approach to problem solving adopted in recent times (Rodin *et al.* 1990). This approach is based on the recognition that systems possess properties greater than those of the sum of their parts. Absolute accuracy is no longer possible in modern science, and especially not in ecology. Reducing systems to their finest components and attempting to measure these accurately is simply useless, with few exceptions (Jorgensen, 1994). Models are the ideal tools for examining system behaviour as they allow interactions to be deciphered and understood. As modern society faces the challenges of dealing with climate change and successfully conserving our natural resources in the face of economic development, it is essential that we understand the ecosystems we work with as best as possible. This will enable decision-makers to choose their actions with at least partial wisdom.

A demand for pollution management, rather than simply banning of pollutants has resulted from the realisation that some pollution is unavoidable in modern society. Pollution management requires a thorough understanding of how pollutants enter, disperse through and react in the environment. This information is obtained from models and thus the demand for models has increased (Rodin *et al.* 1990)

Modelling requires three types of expertise in order to interpret natural systems in terms of logical language:

1. Knowledge of the real-world area in which the problem is to be understood (in this case ecology).
2. Knowledge of the abstract world of logic, mathematics, statistics and computer science.
3. The ability to relate these two fields to each other.

Points one and two require intellectual knowledge and abilities and represent the scientific side of modelling, whereas point three requires intuition, creativity and foresight which represents the artistic side of modelling. This point highlights that modelling requires a “feel” for what you are doing and a good intuition about what works, far more than simply the ability to solve complex sets of equations. This combination of science and art makes modelling a challenging and demanding field in which to work (Cross & Moscardini 1985, Rodin *et al.* 1990).

There are two possible ways of meeting the requirements of modelling for diverse expertise. Either specialists in one discipline can learn about the other(s), or a collaborative effort between different specialists can be made. From a mathematician’s perspective: “becoming an expert in a certain biological discipline...is probably the best way to ensure that any modelling efforts undertaken are firmly rooted in observations”. Further, “when one immerses oneself in a field...the biological intuition developed aids the rather interactive process of model construction” (Hallam & Levin 1986). Although it may be ideal that one person should be an expert in all spheres it is practically impossible. A combination of these two strategies is usually best – specialists from the different disciplines collaborate, providing expert knowledge, but each with sufficient knowledge of the other disciplines that they may communicate efficiently with each other (Hallam & Levin 1986).

Such collaborative efforts as described above often result in a discord of views or priorities between the different disciplines. For example, mathematicians may be more interested in the theoretical significance of the mathematics than in the practical applicability of the results. Conversely, ecologists tend to be far more interested in the practical conclusions that can be drawn. It is necessary that mathematicians see ecological modelling as a means to a biological, not a

mathematical end (Hallam & Levin 1986). However, developing and exploring complex mathematics is vital to mathematical research and should not be neglected. When mathematical ends are desired, either pure mathematical research should be performed or ecologists should return the favour by giving expertise during the model design on the understanding that it holds no immediate benefit to ecology. To describe these different approaches, the following terminology is used:

- **Biomathematics:** is modelling in which the emphasis is on mathematics, and the goal is to explore interesting mathematical expressions potentially arising in biological systems/phenomena.
- **Mathematical biology:** is modelling where the emphasis is on the biological problem and the model is built around it. Here the aim is to achieve biologically testable conclusions and practical solutions, not elegant mathematics, although if the mathematics can be elegant as well it should be considered a bonus.

These apparently conflicting approaches can be reconciled once it is realised that a proper mathematical analysis of a model can point out contradictory assumptions or show that the model contains no logical contradictions. Although a great number of biomathematical models are irrelevant to biological problems or outside the realm of biological testability, this is quite acceptable as long as it is recognised as such by the modellers. These models may also contribute to future research, which may indeed hold biological relevance. Mathematical biology can also produce elegant mathematical models, although it is not the primary aim and it should be remembered that “good applied mathematics is also good science” (Hallam & Levin 1986).

The potential of modelling for expanding knowledge and understanding in many areas of science, including ecology, has not yet been fully exploited (Grimm 1994). Collaborative modelling efforts can hold great benefit both for scientific research and society at large. Hopefully this discussion will lead to a fuller utilisation of a truly valuable tool.

THE USE OF MODELS IN ECOLOGY

Ecology is a science ideally suited to the application of modelling. In ecology the primary concern is with ecosystems and their structure and function. By their very nature, ecosystems are complex and interrelated. The traditional approach to studying complex systems involved reducing these systems to their component, manageable parts and studying these individually. The system is then viewed as the sum of these parts. In recent times the need to adopt a holistic approach to systems analysis has become increasingly clear. Holism is the theory that states that a system possesses additional characteristics not present in its components, due to its structure (Jorgenson 1994). Thus systems must be examined as wholes, not sums of parts.

The human mind can only handle three to four arguments at a time and as such our reasoning is insufficient to handle complex systems (Wiegand & Kellner 2000). In order for humans to understand complex, interrelated systems it is necessary to simplify them by means of abstractions (Grimm 1994). Here models assist as they allow us to make and test simplifications as well as keep track of multiple concurrent streams of reasoning, and allow us to determine their collective effect. Models also reveal the existence of and interaction between different processes, which helps us to get the whole picture. This can also reveal the driving mechanisms in the system and the dynamics of the system on large temporal and spatial scales (Wiegand & Kellner 2000).

In modelling for ecology there is often a trade-off between generality and the testability of results. Although other sciences such as physics and chemistry use abstractions to obtain general results, the level of abstraction necessary to achieve generality in ecology is several orders of magnitude greater. This greater level of abstraction means that models become further removed from reality, and thus it becomes difficult to relate their results back to real data (Grimm 1994). For this reason ecological models tend to be more specific to the particular situation being examined.

Models serve two primary purposes in ecology: Firstly, they are used as a management tool, especially in conservation and pollution management; and secondly they are used as a tool in scientific research (Jorgenson 1994).

A very important component of ecology is the development, implementation and monitoring of management plans for ecosystems. The widely used intuitive approach to management uses experience, concepts and generalisations to understand how the system operates and thus how it should be managed. This approach only works on a time scale of about twenty years, as the experience of managers is temporally limited and records from previous managers are often sparse, if present at all. Models are used to explore dynamics on larger, often more relevant, temporal scales and under conditions for which there is no prior experience (Wiegand & Kellner 2000).

Additional uses of models in management are the analysis of newly proposed designs or management strategies to assess possible effects before implementation; the optimisation of systems or processes; and the control of systems by seeing their response to certain actions in the model (Cross & Moscardini 1985)

Models serve various purposes in scientific research: Firstly, they are tools in the survey of complex systems. By revealing system properties models allow data to be organised and interpreted to the point where conclusions can be drawn in terms of general principles. Secondly, models reveal gaps in present knowledge and hence help to set research priorities. If attempts to make model behaviour mimic system behaviour fail, it indicates a lack of knowledge/understanding on some aspect of the system. As models are built it may be found that some data, which are not presently available, are required for the model. Lastly, models are used to test hypotheses, for example, ecosystem responses are simulated and compared to observations of actual response (Jorgenson 1994).

The certainty of hypothesis testing using models is not as high as that of standard hypothesis tests because there are four cases instead of the usual two (hypothesis true and hypothesis false). These four cases are:

1. The model is correct, and the hypothesis is true.
2. The model is incorrect but the hypothesis is true.
3. The model is correct but the hypothesis is false.
4. The model is incorrect and the hypothesis is false.

This situation arises because the model is a hypothesis in its own right (Jorgenson 1994). The model is the hypothesis that the system can be simplified, as done in the model, and retain all its characteristics relevant to the problem.

Whether the purpose is environmental management or scientific research, or indeed a combination of the two, models can do various things in ecology, namely to:

1. *Describe*: available information is displayed in an easy-to-read format, with no explanations given.
2. *Explain*: Simplifying assumptions are made about the real system and the logical implications thereof are found in order to explain phenomena.
3. *Predict*: The response of the system in conditions where this response has not been measured can be predicted using models.

Points one to three are not necessarily independent (Hallam & Levin 1986), and the same model may perform more than one of these functions.

THE PROCESS OF MODELLING

When a model is to be developed, there are two possible approaches – either use or adapt an existing model or develop a totally new one. The same model formulation can sometimes be used in different practical situations where the symbols in the model represent different things in the different situations (Rodin *et al.* 1990). An existing model may be adapted by, for example, adding time dependence and/or stochastic variation. A danger is that such adaptations may be driven by the desire to develop elegant mathematics, and be dictated by the researcher's field of expertise, rather than the requirements of the practical problem. Researchers using existing models must be willing to discard models, even well established ones, when they no longer adequately explain observed

phenomena. For example the medieval model which placed the earth at the centre of the universe was not discarded quickly enough when it ceased to explain observations because it suited the cause of the Church (Cross & Moscardini 1985). When developing a totally new model, it tends to be suited to the specific biological problem. In this respect developing new models for each problem is preferable. However, developing a brand-new model is very resource intensive and using elements from existing models is advisable, provided it is done with discretion (Hallam & Levin 1986).

Whether a new model is being developed, or an existing one is being adapted, it must be recognised that modelling is an iterative process, not a case of running once through it and it is over (Jorgenson 1994). One seldom obtains an adequate model on the first attempt and refinement is required. Once a model has been developed it is constantly tested, updated and improved upon as knowledge and understanding grows. It is in this process of recursive modification that the artistic side of modelling comes to the fore. For this reason the process of model construction is viewed as a cycle (as illustrated in Figure 1), through which modellers can pass multiple times (Rodin *et al.* 1990).

The first step in the modelling process is problem definition. Theoretically, this step is performed only once, before we enter the cycle for the first time. However, in reality, the recursion will sometimes also include a modified view of what the problem really is. The problem to be modelled must be fully described, including the spatial and temporal scales and the complexity to be considered.

The next step in the modelling process is the construction of a conceptual diagram. This is a diagrammatic representation of all the variables, interactions and processes to be involved in the model.

At this point it is necessary to make some simplifying assumptions. The real world is almost infinitely complex and to make it logically digestible it must be simplified. Great care must be taken when making these assumptions to ensure that variation, critical to the problem being addressed, is not lost (Grimm 1994). Assumptions that work in models in other areas of science can give fallacious

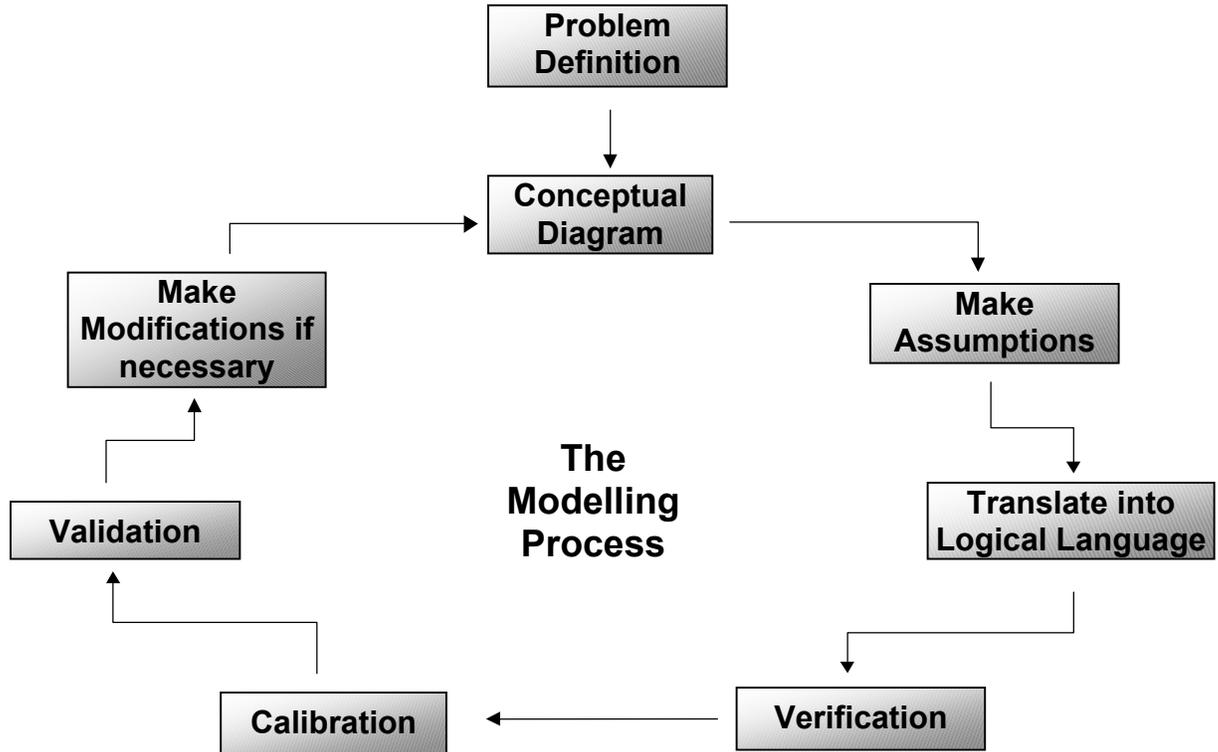


FIGURE 1: Schematic representation of the steps involved in the process of model construction.

results if simply applied in ecology (Ekschmitt & Breckling 1994). For this reason any assumptions made must be scrutinised closely.

The next step is to translate the assumptions and observations made into logical language and thus construct a logical system in the language of mathematics and computers (Grimm 1994; Wiegand & Kellner 2000). Such a logical system is desirable because it allows us to analyse our knowledge using logical tools and its construction is the most important step of the modelling process. The mathematical solution is obtained by solving the equations and the quality of the solution depends on the quality of the translation (Rodin *et al.* 1990).

A process known as **verification** is now performed, this is when all of our logic and assumptions are double-checked for consistency with each other and reality. The consequences of the logic and assumptions should also be examined in this way. Very few models can stand up to vigorous scrutiny of their assumptions, but when they can it often implies good, testable results (Hallam & Levin 1986). The main aim here is to check one has not “said” something that is either obviously false or contradictory.

The model is then calibrated, this is when any empirical constants specific to the case under study are measured and/or incorporated into the model. One of the causes of inaccuracies in model results is incorrect estimation of parameters and hence great care must be taken to perform calibration as accurately as possible (Chuine *et. al.* 1999).

Validation is now performed, in other words, solving the equations or running the simulations to obtain results, which are interpreted back into the real situation (Grimm 1994). These results are then examined in the context of the real situation. A good way to test a model is to “predict” some already known data not used in the construction of the model and see how closely the predicted values correlate with the actual values.

If models yield incorrect or incomprehensible results, the assumptions need to be changed and/or observations checked, which may lead to changed equations. All assumptions should be independently tested and new models should be constructed based only on the good/corrected assumptions. Hence, the cycle is re-commenced (Grimm 1994, Chuine *et al.* 1999).

Merely because one has been through this cycle a few times does not necessarily mean one is closer to understanding the actual ecological system or process (Grimm 1994).

The steps involved in constructing a model were summarised by Rodin *et al.* (1990) as follows:

1. Problem formulation in the language of the real-world situation.
2. Mathematical description of the problem.
3. Mathematical analysis of the mathematical description.

4. Interpretation of the mathematical analysis in terms of the real situation.

TYPES OF MODELS, THEIR ADVANTAGES, DISADVANTAGES AND USES

Models can be classified into different types in a wide variety of different ways and on several different levels. These different types of models exhibit different advantages and disadvantages for various applications.

One way in which models can be classified is according to whether or not they give understanding. In the case of **causal** (Jorgenson 1994), **explanatory** (Hallam & Levin 1986), **conceptual** (Grimm 1994) or **mechanistic models** (Cross & Moscardini 1985, Grimm 1994) formulations are constructed which explain the actual biological mechanisms leading to the cause and effect relationships associated with the phenomenon being examined. In order for an intellectual tool (model) to help its users gain understanding, it must be understandable itself. Hence another important characteristic of these models is that they are understandable (Grimm 1994). These kinds of models are advantageous in that they are often applicable outside the specific system in which they were developed (Jorgenson 1994). They are disadvantageous in that they are more difficult to develop than models that offer no explanations. **Black-box** (Jorgenson 1994) or **descriptive models** (Hallam & Levin 1986) are models in which statistical analysis or other methods are used simply to obtain the relationships between parameters. These types of models are much easier to construct, but cannot be utilised in systems other than the one for which they were developed (Jorgenson 1994).

A model of any type is also known as a **predictive model** if it can be used to make predictions about future events. Sometimes black-box/descriptive models can be more accurate in making predictions than mechanistic/causal models. For example in predicting crop yields, regression analyses were more accurate than physiology based mechanistic crop growth models (Hallam & Levin 1986).

Models that provide no understanding can sometimes be used to organise and interpret data in such a way as to promote understanding and/or be used to make predictions. They are often used in modelling entire systems that are too complex to understand fully. An example is the use of Geographic Information Systems (GIS) to organise and manipulate spatially referenced data (Wiegand & Kellner 2000).

Models aimed specifically at gaining understanding are used to test if knowledge and hypotheses are consistent and are usually case studies of specific situations. These models make use of abstraction and generalisations to simplify the system and usually only include the most fundamental components and processes. Examples of such models are differential equations, rule-based computer simulations and grid-based spatially explicit/cellular automata models (Wiegand & Kellner 2000).

Another way in which models can be classified is according to their purpose: **Research models** are used as a tool in scientific research and **management models** are used as a tool in ecosystem management (Jorgenson 1994). In this case there are no clear differences in the actual model, it is merely an indication of what purpose must be fulfilled, thus there are also no clear advantages or disadvantages of the different types. These two purposes can also be fulfilled concurrently by the same model.

Models can also be classified according to the approach adopted: **Holistic models** use general principles whilst **reductionistic models** incorporate as much detail as possible (Jorgenson 1994).

Models can be classified according to the area of ecology in which they are used. **Biodemographic** models are those used in population and community dynamics. **Bioenergetic** models are those used to look at productivity and energy flow in ecosystems and **biogeochemical** models are those used to examine the movement of chemical substances/nutrients in the ecosystem. Biogeochemical models find special application in pollution management (Jorgenson 1994). Again, here it is merely a case of the role to be fulfilled by the model and there are no clear advantages or disadvantages to a particular type.

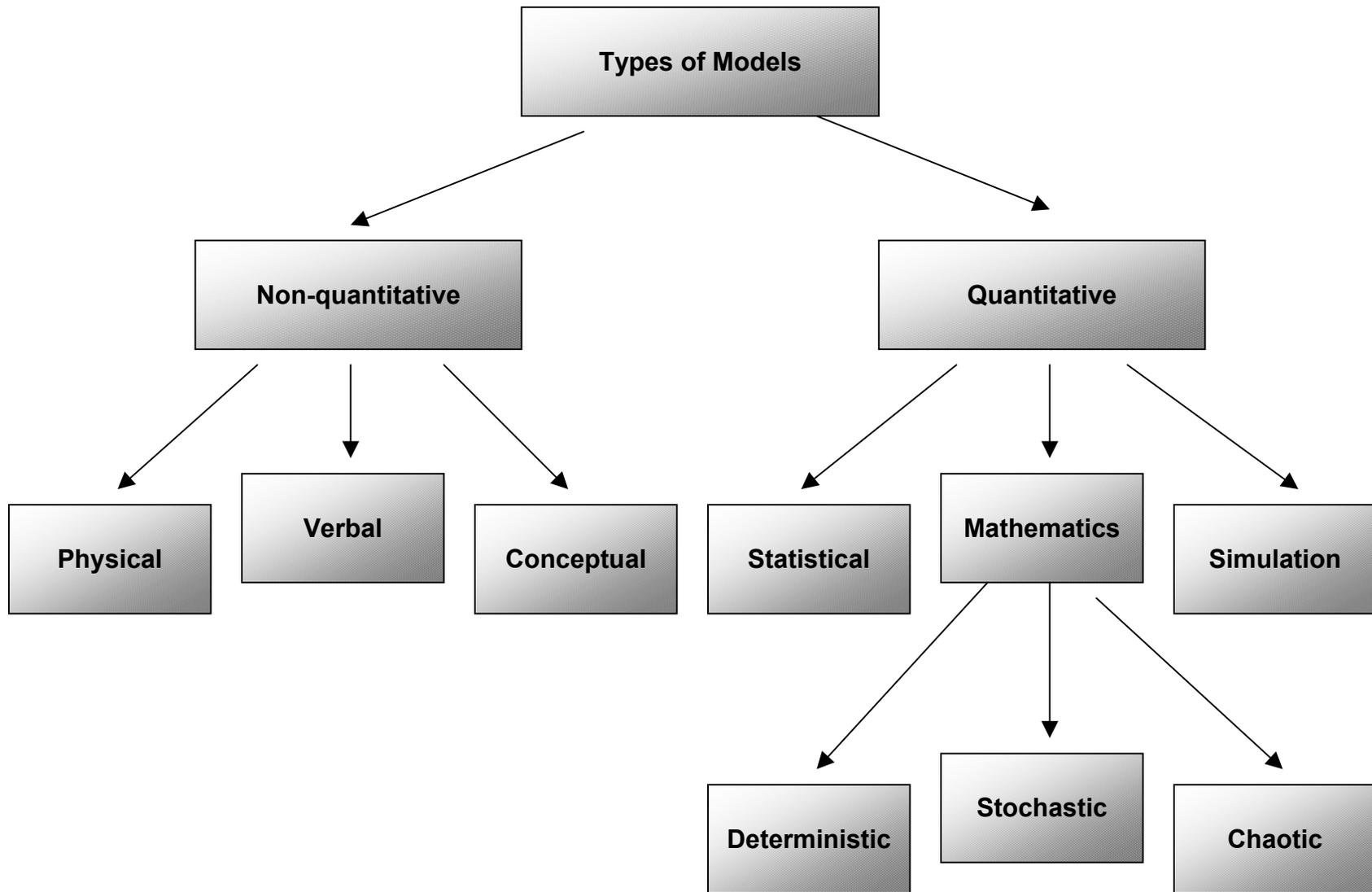


FIGURE 2: Schematic representation of the classification of models according to the type of logical language/constructs they use.

Tactical/strategic/phenomenological models are models that are tailored to a specific experimental situation, or designed to address a particular problem (Grimm 1994).

Free-style models are models with a high level of generality whose results come to fruition in a realm detached from reality. In these models the point of departure is a search for general principles. Free-style modelling in ecology should rely more on the power of thinking of the modeller than on mathematical formulations, unless the goal of the model is mathematical research (Grimm 1994). These models can be seen as a type of brain storming tool.

Pattern-oriented models are models with an intermediate level of generality with the express purpose of producing testable results. In these models the point of departure is a pattern that can be observed in an actual ecosystem. Sadly, there are very few generally observable patterns in ecology and most patterns are specific to case studies. If models are pattern-oriented it seems to deter theoreticians from becoming theoretical to the extent that the practical testability of the model is lost. Pattern-oriented models are one of the types of models that can lead to understanding of ecological systems and processes (Grimm 1994).

If patterns already existing in ecological systems are used as a starting point for models, rather than questions of a general nature, all the advantages of conceptual models (see the following section) are derived without relinquishing testability of the hypothesis proposed. Using a pattern as a starting point is disadvantageous in that it limits general applicability of the model, but it can increase predictive power. Simply because a pattern is used as a starting point, does not mean that the sole aim of the model is to understand that pattern in the ecosystem under consideration. If the driving mechanisms that create the pattern are found in one ecosystem, extrapolations can often be made to other systems, since the same mechanisms may cause the same/similar pattern elsewhere (Grimm 1994).

Models can also be divided according to the types of logical language/constructs used in their construction. These classifications are depicted in Figure 2 and discussed in the following sections.

Non-quantitative models

Non-quantitative models are models that do not have any numerical input or output. There are three types of non-quantitative models, namely physical, verbal and conceptual models.

Physical models

A **physical model** is a, possibly simplified, microcosm of reality. For example the ship-shaped model with no inner detail that was described earlier for examining resistance as a ship passes through water (Jorgenson 1994). An ecological example would be cultivating plants in pots in sterile sand enriched only with known nutrients selected by the researcher. This would enable researchers to remove almost every possible causal factor of a phenomenon other than those being studied.

Physical models do not give any causal explanations: For example when testing cars in wind tunnels, no explanations of the causes of drag are given. Mathematical or other explanatory models can overcome this difficulty (Cross & Moscardini 1985). Physical models offer the advantage of being relatively simple and easy, though sometimes expensive to construct. Modifications to models already constructed can also be difficult to make.

Verbal models

Words may sometimes be used to describe something to someone else, where the words are not an exact replica of what is being described, but come close enough to communicate the necessary information. For example it may be said

"karee trees look similar to bush willows", although karee trees do not look exactly like bush willows, this may help someone identify them. These are known as **verbal models**.

Conceptual models

Conceptual models are diagrams, schematic representations or ways of thinking about things that assist their users in understanding and communicating concepts. They also help users to see the general theory and draw analogies.

Conceptual models that use graphical representations to display or organise data are also known as **graphical models**. Examples include maps, graphs, schematic representations and flow charts.

Conceptual models are advantageous in that they are easy to construct, but disadvantageous in that they do not offer any analytical ability.

An example of a conceptual model in ecology is the state-and-transition model of community succession. In this model an ecosystem is seen to have certain states in which it can "settle", with given transitions that can occur between states (Westoby *et al.* 1989). Thus succession is viewed as a set of transitions and relatively stable states that need not necessarily occur in a specific chronological order.

Quantitative models

Quantitative models are models whose input and/or output is at least partly numerical. Only quantitative models can make quantitative predictions and this is the capability and the limit of quantitative models (Grimm 1994).

Advantages of quantitative models over physical models are that they are cheap – not requiring physical construction; safe - because they do not make possibly detrimental alterations to the physical world; and that they can be used where physical models are either unsuitable or impractical (Rodin *et al.* 1990). They are superior over all forms of non-quantitative models for their ability to

quantify their results and/or predictions. However, some level of expertise and skill is required to construct, apply and interpret them.

Quantitative models can be classified according to whether or not they include time as a parameter. **Static** (Jorgenson 1994) or **steady-state models** (Cross & Moscardini 1985) are models in which the variables defining the system are not time-dependent. In **dynamic models** at least some of the variables are functions of time (Jorgenson 1994). Static models are usually easier to build because they include less detail. In systems with essential spatial complexity static models are often developed first and dynamics are introduced later, if necessary. However, in some systems their dynamic nature is essential and dynamic models must be used from the outset (Cross & Moscardini 1985).

Dynamic quantitative models can then be classified according to the type of time dependence that they incorporate. **Discrete models** deal only with a finite number of fixed points in time while **continuous models** deal with all, infinitely many, points in time falling within a certain interval (Cross & Moscardini 1985).

Models that cater for variation in space and time are known as **distributed** models while in **lumped models** some/all of the parameters are only considered within certain spatial and temporal locations, and hence are constants (Jorgenson 1994).

Statistical models

Statistical models are models in which the predicted values are extrapolations made on simple regression analyses. If measured outputs are related to input parameters using statistical equations, these relationships are empirical in nature (Grimm 1994). Statistical models offer the advantage of being relatively simple to use; not requiring highly specialised expertise. There is also a vast array of computer software available to aid in their construction. They are especially useful to discover trends, patterns and correlations but tend to offer no or few explanations as to why things happen the way they do.

Simple statistical relationships between measured outputs and input parameters are often used in two stages of the modelling process. Firstly, in the beginning to establish relationships between the different parameters and later, toward the end of the process to condense information for efficiency and control (Cross & Moscardini 1985).

Casebolt (1986) used statistical models in the form of logistic regression and log-linear models to analyse non-human primate population data. Logistic regression was less successful when used by Sealbloom *et al.* (2001) who built a series of successively more complex simulation models to examine how the community composition in a wetland was affected by a fluctuating water depth gradient. The simplest model, which was not very successful, was based on logistic regressions. The more complex, and more successful, models were spatially explicit grid-based models.

McAllister & Kirkwood (1998) analysed stocks in fisheries and the uncertainty associated with taking certain actions by means of Bayesian statistics, which assumes parameters in the model to be random variables. They believe this method is well suited to such applications in fisheries.

Statistical models were successfully used to examine the effects on intra- and interspecific competition on vole population dynamics as well as the causes of cycles in vole populations (Hansen *et al.* 1999).

Artificial Neural Network (ANN) models, a class of statistical models, were successfully used to predict Collembolan diversity and abundance by Lekang *et al.* (1999).

Using statistical techniques to analyse presence/absence matrices in which rows represent species and columns represent sites is a common practise in community ecology. Patterns are identified and it is determined whether these patterns are a result of random noise in the data or ecological processes. Gotelli (2000) conducted a study which examined different indices for analysing these matrices for their susceptibility to type I and type II error.

Mathematical models

A **mathematical model** is an abstract description of a situation using mathematical formulations. Once constructed, this abstract model is divorced from the real world and can only be handled mathematically (Rodin *et al.* 1990). The strength of mathematical models is that they often offer good mechanistic explanations for the phenomena they describe. However, their construction, application and interpretation requires substantial expertise and skill.

Mathematical models can be classified according to how the predicted values are calculated: in **deterministic models**, the predicted values are calculated exactly whilst in **stochastic models** they are dependent on probability distributions (Jorgenson 1994). **Chaotic models** use equations with chaotic behaviour to calculate the predicted values. Chaotic behaviour is when the value at time $t+1$ can be exactly calculated (using a deterministic equation) but it cannot directly be inferred from the value at time t . In other words, the values jump around in a very disorderly manner, not following a clear trend(s).

Deterministic models

Deterministic models can be classified according to the mathematical formulations they use. In **compartmental models** the variables defining the system are quantified by means of time-dependent differential equations, whilst **matrix models** use matrices as a mathematical tool. Compartmental models can be further classified according to the type of differential equations used: In **autonomous models** the derivatives are not explicitly dependent on the independent variable, whilst in **non-autonomous models** they are (Jorgenson 1994).

Deterministic models can also be classified according to the types of equations used: **Linear models** use only first-degree equations, whilst in **non-linear models** at least one of the equations is not first degree (Jorgenson 1994).

The term **conceptual mathematical model** is sometimes used for a deterministic mathematical model, which is understandable, manageable, and

capable of being completely explored (Grimm 1994). Examples of conceptual mathematical models would include the logistic growth, Lotka-Volterra, Nicholson-Bailey and reaction-diffusion equations.

Deterministic models find many applications in ecology, for example partial differential equations were used by Lefever *et al.* (1998) to model the dynamics of the spatial distribution of plants in a community that exhibits periodicity.

Haydon (2000) used theoretical mathematical models to examine the relationships between stability and complexity in ecosystems. They found that the most mathematically stable system is that system where there is a high level of connectedness, especially between components that are highly self-regulated and those that are not. The implications of these results for ecological theory were also discussed.

Another type of deterministic models widely used in ecology are matrix models. Hobbs & Legg (1983) used Markov-chain matrix models to examine the post-fire succession in some Scottish heathlands with special reference to the influence of initial floristic composition on later vegetation states. These authors concluded that simple Markov-chain models can successfully be used to study successional processes if used comparatively.

Size-structured matrix models were constructed on the perennial grasses of two African savannahs by O'Connor (1993) to examine the effects of rainfall and grazing on the demographics of the grasses. The model was used to explore experimental results and thus was not tested against other real data.

Gino & Seno (1997) used transition matrix models to examine the population dynamics of plant species that depend on ecological disturbance for their persistence.

Markov-chain models were also used by Balzter (2000) to predict grassland community data from four different data sources. Data was considered on both a macro and micro scale. He concluded that the performance of the model varied with the data set used but that macro data could generally be predicted more accurately.

Stochastic models

Stochastic models, because they incorporate probabilities, are very useful in helping their users to predict what may happen in uncertain/unpredictable environments.

A stochastic model based on game theory was constructed to examine the invasion of plant communities by new species. This model was very successful because it is both realistic and easily calibrated (Vonhulst 1987).

A stochastic model that examined the effects of colonisation, relative abundance and seed size on population recruitment in three grassland plant species was constructed by Erikson (1997) based on experimental data. The model could successfully predict relative abundance of the species at a large scale but was less successful at a smaller scale.

In a more theoretical study a spatial stochastic model based on moment equations was used by Bolker & Pacala (1998) to theoretically explore the various strategies of exploitation and competition available to plants.

Chaotic models

Chaotic models have become increasingly popular in recent times. Their unpredictable, yet not random, behaviour makes them incredibly useful when dealing with unpredictable systems and they accurately describe many naturally occurring patterns.

Chaotic models do not necessarily use special mathematical formulations. Many commonly used mathematical equations, including the discrete logistic growth curve, exhibit chaotic behaviour under certain circumstances.

Inghe (1990) used difference equations to model resource levels in ramets, which show chaotic fluctuations. Irregular flowering of perennial herbs was successfully explained by the chaos arising from these equations.

Huisman & Weissing (2001) studied the conditions under which competition between populations for abiotic resources will result in stable coexistence, competitive exclusion, oscillations and chaos. The authors give a discussion of how realistic this model is in relation to the dynamics of

phytoplankton communities but more data is required before it can be determined whether or not the model is indeed realistic.

Computer simulation models

Simulation models are computer programs composed of a sequence of logical operations that attempt to mimic the natural interactions and processes present in an ecosystem. Complex (simulation) models of ecological systems are lacking in that their long-term behaviour cannot be fully explored and hence it is not always possible to ascertain which factors are causing the results achieved (Grimm 1994). Each possible set of inputs must be simulated separately, and no general conclusions can be drawn. A strong advantage offered by these models is that they can deal with much more complex sets of interacting processes than can ordinary mathematical equations.

Simulation models find widespread application in ecology: Bugmann (1996) showed how existing models of species composition in forests along climatic gradients could be simplified without reducing the realism of model behaviour.

Spatial simulation models were used to examine the factors and processes involved in grass and tree coexistence in savannahs. The same model was also used to explore the long-term effects of different levels of fire, rainfall and grazing on the ecology of the area (Jeltsch *et al.* 1996). Spatially explicit grid-based simulation models (cellular automata) were also used by Jeltsch *et al.* (1997a & b) to examine pattern formation and long-term scenarios of bush encroachment around artificial waterholes in the semiarid Kalahari, southern Africa.

Balster *et al.* (1998) used a type of cellular automata model called a Spatio-Temporal Markov Chain (STMC) to model population dynamics of three plant species in a lawn. The model was successful in simulating one of the three species. Another case in which spatially explicit simulation models were used

explored the connection between landscape structure and the dynamics of source-sink and metapopulations (Wiegand *et al.* 1999).

Pausas (1999a) used two different simulation modelling approaches to examine the effects of changes in the fire regime on different plant functional types in the Mediterranean basin. Both models' predictions concurred well with each other as well as field observations. Pausas (1999b) also used mechanistic simulation models to explore gap and vegetation dynamics in Mediterranean vegetation.

THE LOGISTIC MODEL

The logistic model of population growth is a very well known deterministic mathematical model that is applied later in this dissertation. For this reason the logistic model and its use in ecology is reviewed here.

The logistic curve is both one of the most fruitful and unsatisfactory models of population growth ever developed. It is very simple, sometimes to the point of being inadequate, despite the fact that many more complex versions of the model have been developed. However, it describes a widely observed pattern in biological population dynamics and for this reason remains a very successful model (Kingsland 1982).

The logistic model was independently described both in 1845 by Verhulst and in 1920 by Pear and Read (Kingsland 1982). Verhulst first proposed the model as a law of growth and it was vigorously criticised as such, but emerged as a central model of population biology in the late 1930s and 1940s. It is thought the model probably got the name logistic model because it calculates or keeps stock of the population. More detail on the development of the model can be found in Kingsland (1982).

The logistic curve describes the growth of a population over time by means of the following equation:

$$P(k) = \frac{C}{1 + Ae^{-rk}}$$

Where $P(k)$ is the population size at time k , C is the upper asymptote or ecological capacity, r is the maximum rate of increase in an unrestricted population and A is a constant of integration that is related to the initial population size and indicates how close the population is to ecological capacity when you start (Kingsland 1982, Hughes-Hallett *et al.* 1997). This model makes three key assumptions: Firstly, that r and C are constant; Secondly, that there are no time-lags in the response of the actual growth rate to changes in the population size; and thirdly that all individuals are equal in their effect on the actual growth rate (Kingsland 1982).

The mathematical conditions under which generalised Verhulst logistic growth can occur in a population were discussed by Rosen (1984). This paper also gives examples of where the model may be applied in biology.

Alternative forms and extensions

Many alternative forms of and extensions to the logistic model exist that have not been applied to real ecological problems. These theoretical models are important because they may be useful in future ecological research.

Mickens (1988) constructed a quasi-linear first-order differential equation, which models the growth of a single population growing logistically with linear advection. Prajneshu (1980) constructed and analysed a logistic model where the environmental parameter (ecological capacity) varied with time. Marcati (1982) on the other hand analysed an age-dependent extension of the logistic model with a non-linear death rate.

In 1979 Poulsen constructed a difference equation model to describe how frequency- and density-dependent selection occurs in a population with discrete generations and differing genotypes. In the case where there was no difference between the genotypes the model gives logistic population regulation.

The logistic model has been used in the analysis of harvesting strategies. For example Gopalsamy (1980) examined the effect of a variable rate of

harvesting on a single-species logistic population. He uses optimal stabilisation theory to attempt to keep the harvested population approximately at an asymptote (i.e. stable). An algorithm to solve a set of differential equations describing the dynamics of interacting populations that are being harvested was constructed by De Gee & Grasman (1998). The goal of this algorithm was to find the optimal harvesting levels. This algorithm was also applied to the time-dependent logistic equation, where the growth rate and ecological capacity fluctuate seasonally.

A stochastic analogue of the logistic model of population growth was discussed by Norden (1982). In his paper the distribution of the time to extinction is analysed and the author is of the opinion that the results obtained are applicable to real populations. Tognetti & Winley (1980) examined a stochastically growing population where the mean population is described by the logistic growth curve.

The logistic model is problematic as a model of declining populations. Fulda (1981) discussed some shortcomings of the discrete logistic model as a model of population decline, and suggested ways to improve the model in this regard. Three models were constructed by Hanson & Tuckwell (1997) that combined the logistic growth and exponential decay curves with various stochastic functions. The aim of the models was to examine the effect of random jumps (sudden increases or decreases in population size) on the expected time to extinction of logistically growing populations)

The logistic equation has also been extended to deal with spatially structured populations. Tuckwell & Koziol (1987) constructed an extension of the logistic equation where a term was added that described random dispersal of individuals in the population between different available sites. Cantrell & Coster (1989) studied a class of diffusive logistic equations where a random walk process is added to describe how individuals disperse through the environment . They suggest these as models of population growth in spatially heterogeneous environments. Cui & Chen (1998) constructed models of source-sink populations

with diffusion between patches at varying rates based on the logistic growth model.

Applications of the logistic model in ecology

The logistic model has also been applied to practical ecological problems. For example Brewer *et al.* (1985) predicted top height of loblolly pines (*Pinus taeda*) at age 25 from data up to age 20 using five different models. The first-degree logistic model was a poor predictor compared with some of the other models tested. The logistic model was also found to be problematic as a model of plant growth by Caloin & Yu (1982). They examined the effect of irradiance on plant growth and specifically the relative dry masses of the root and shoot portions of the plants. They found the logistic model's predictions of the upper asymptote to be inaccurate at high levels of irradiance. They used an extension of the logistic model proposed by Lotka in 1925 which makes the growth rate proportional to fractional powers of the plant's mass.

Basson *et al.* (1991) constructed a model aimed at determining the general long-term sustainable yield of ivory from African elephants. They used a logistic model of population growth with additional functions to describe the relationship between the number of individuals and the mass of ivory harvested as well as the collection of ivory from animals dying of natural causes. They did not calibrate the model to any actual data but discussed the ranges within which the coefficients should fall according to current knowledge.

Jolicoeur & Pontier (1989) developed a four-parameter generalisation of the logistic curve specifically to apply to populations that rise up to a certain maximum and then decline back to zero. The model fitted well both to populations of male flies of the species *Meromyza variegata* and for *Paramecium caudatum* that was outcompeted by *Paramecium aurelia*.

Van der Bosch & Gabriel (1997) explored the effects of cannibalism by the predators on the dynamics of predator-prey interactions. They used a Lotka-Volterra predator-prey model with logistic population growth and hyperbolic type

II functional response. Simulation models of actual ecosystems in the North Sea were constructed during previous research with these types of models and they appeared to be successful.

CONCLUSION

The one thing this literature review highlights is that modelling is a very diverse discipline, with many approaches, types of models and a vast body of terminology. Each researcher has his/her own unique way of approaching problem solving. This is a direct consequence of the somewhat artistic nature of modelling: There is not at present, and probably will never be, one method or approach that works in every case to solve any problem. At the end of the day if one can develop a model that works, it is irrelevant how you got there, provided it was scientifically sound.

It is said by some experienced modellers that often in developing the best models there is no better explanation for how they came to the formulations than intuition or gut feeling. This is an exciting aspect of modelling in that it means that the quality of thinking of the modeller is paramount – more than textbook knowledge, skill or experience is required – almost a different kind of mental functioning.

Almost as a result of its difficulty, modelling is a truly valuable discipline. It enables its users to understand and analyse complex systems, such as those encountered in ecology, in a way that would not be possible simply with human mental faculties. Modelling can provide much-needed direction in attempts to deal with environmental management challenges. It offers an invaluable opportunity to derive general principles and test out management strategies before implementation. Modelling is under-utilised for this purpose and should be considered as a tool by all working in this area.

REFERENCES

- BALZTER, H. 2000. Markov chain models for vegetation dynamics. *Ecological Modelling* **126**:139-154..
- BALZTER, H., BRAUN, P.W. & KOHLER, W. 1998. Cellular automata models for vegetation dynamics. *Ecological Modelling* **107**:113-125.
- BASSON, M., REDDINGTON, J. R. & MAY, R. 1991. An assessment of the maximum sustainable yield of ivory from African elephant populations. *Mathematical Biosciences* **104**:73-95.
- BOLKER, B.M. & PACALA, S.W. 1998. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. *The American Naturalist* **153**:575-602.
- BREWER, J.A., BURNS, P. & CATO, Q.V. 1985. Short-term projection accuracy of five asymptotic height-age curves for Loblolly Pine. *Forest Science* **31**:414-418.
- BUGMANN, H.K.M. 1996. A simplified forest model to study species composition along climate gradients. *Ecology* **77**:2055-2074.
- CALOIN, M. & YU, O. 1982. An extension of the logistic model of plant growth. *Annals of Botany* **49**:599-607.
- CANTRELL, R.S. & COSTER, C. 1989. Diffusive logistic equations with indefinite weight: population models in disrupted environments. *Proceedings of the Royal Society of Edinburgh, Section A: Mathematics* **112**:293-318.
- CASEBOLT, D. 1986. Analysis of primate population data using logistic regression and loglinear models. *American Journal of Primatology* **10**:383.
- CHUINE, I., COUR, P. & ROUSSEAU, D. D, 1999. Selecting models to predict the timing of flowering of temperate trees: Implications for tree phenology modelling. *Plant, Cell & Environment* **22**:1-13.
- CROSS, M. & MOSCARDINI, A.O. 1985. *Learning the art of mathematical modelling*. Ellis Horwood Ltd., Chichester.
- CUI, J. & CHEN, L. 1998. The effect of diffusion on the time varying logistic population growth. *Computational Mathematics and Applications* **36**:1-9.
- DE GEE, M. & GRASMAN, J. 1998. Sustainable yields from seasonally fluctuating biological populations. *Ecological Modelling* **109**:203-212.
- EKSCHMITT, K. & BRECKLING, B. 1994. Competition and coexistence, the contribution of modelling to the formation of ecological concepts. *Ecological Modelling* **75/76**:71-82.
- ERIKSON, O. 1997. Colonization dynamics and relative abundance of three plant species (*Antennaria dioica*, *Hieracium pilosela* and *Hypochoeris maculata*) in dry semi-natural grasslands. *Ecography* **20**:559-568.

- FULDA, J.G. 1981. The logistic equation and population decline. *Journal of Theoretical Biology* **91**:255-259.
- GINO, H. & SENO, H. 1997. Transition matrix modelling on disturbance-controlled persistence of plant population. *Ecological Modelling* **94**:207-219.
- GOPALSAMY, K. 1980. Optimal stabilisation and harvesting in logistic population models. *Ecological Modelling* **11**:67-69.
- GOTELLI, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.
- GRIMM, V. 1994. Mathematical modelling and understanding in ecology. *Ecological Modelling* **15**:641-651.
- HALLAM, T.G., & LEVIN, S.A. (eds.). 1986. *Biomathematics volume 1: Mathematical Ecology*. Springer-Verlag, Berlin, Heidelberg.
- HANSEN, T.F., STENSETT, N.C., HUNTONEN, H. & TAST, J. 1999. Interspecific and intraspecific competition as causes of direct and delayed density-dependence in a fluctuating vole population. *Proceedings of the National Academy of Science of the United States of America* **96**:986-991.
- HANSON, F.B. & TUCKWELL, H.C. 1997. Population growth with randomly distributed jumps. *Journal of Mathematical Biology* **26**:169-187.
- HAYDON, D.T. 2000. Maximally stable model ecosystems can be highly connected. *Ecology* **81**:2631-2636.
- HOBBS, R.J. & LEGG, C.J. 1983. Markov models and initial floristic composition in heathland vegetation dynamics. *Vegetatio* **56**:31-43.
- HUGHES-HALLETT, D., GLEASON, A.M., LOCK, P.F., FLATH, D., GORDON, S.P., LOMEN, D.O. & LOVELOCK, D. 1997. *Brief calculus for business, social sciences and life sciences* (preliminary edition) pp. 234-248. John Wiley & sons Ltd., Brisbane.
- HUISMAN, J. & WEISSING, F.J. 2001. Biological conditions for oscillations and chaos generated by multi-species competition. *Ecology* **28**:2682-2695.
- INGHE, O. 1990. Computer simulations of flowering rhythms in perennials – is there a new area to explore in the quest for chaos? *Journal of Theoretical Biology* **147**:449-469.
- JELTSCH, F., MILTON, S. J., DEAN, W. R. J. & VAN ROOYEN, N. 1996. Tree spacing and coexistence in semi-arid savannahs. *Journal of Ecology* **84**:583-595.
- JELTSCH, F., MILTON, S.J., DEAN, W.R.J. & VAN ROOYEN, N. 1997a. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* **8**:177-188.
- JELTSCH, F., MILTON, S.J., DEAN, W.R.J. & VAN ROOYEN, N. 1997b. Analysing shrub encroachment in the southern Kalahari: a grid-based approach. *Journal of Applied Ecology* **34**:1497-1508.

- JOLICOEUR, P. & PONTIER, J. 1989. Population growth and decline: a four-parameter generalization of the logistic curve. *Journal of Theoretical Biology* **141**:563-571.
- JORGENSON, S.E. 1994. *Developments in environmental modelling 19 – Fundamentals of ecological modelling*. Elsevier, Amsterdam.
- KINGSLAND, S. 1982. The refractory model: The logistic curve and the history of population ecology. *Quarterly Review of Biology* **57**:29-51.
- LEFEVER, R., LEJEUNE, O. & COUTERON, F. 1998. Generic modelling of vegetation patterns: A case study of *Tiger Bush* in sub-saharian Sahel. *Proceedings of the workshop on pattern formation and morphogenesis: Model systems*. University of Minnesota, Minneapolis.
- LEKANG, S., DEHARVENG, L. & LEK, S. 1999. Predictive models of the Collembolan diversity and abundance in a riparian habitat. *Ecological Modelling* **120**:247-260.
- MARCATI, P. 1982. On the global stability of the logistic age-dependent population growth. *Journal of Mathematical Biology* **15**:215-226..
- MCALLISTER, M.K & KIRKWOOD, G.P. 1998. Bayesian stock assessment – a review and example application using the logistic model. *ICES Journal of Marine Science* **55**:1031-1060.
- MICKENS, R.E. 1988. Exact solutions to a population model: The logistic equation with advection. *SIAM Review* **30**:629-633.
- NORDEN, R.H. 1982. On the distribution of the time to extinction in the stochastic logistic population model. *Advances in Applied Probability* **14**:687-708.
- O'CONNOR, T.G. 1993. The influence of rainfall and grazing on the demography of some African savannah grasses: A matrix modelling approach. *Journal of Applied Ecology* **30**:119-132.
- PAUSAS, J. G. 1999b. Mediterranean vegetation dynamics: Modelling problems and functional types. *Plant Ecology* **140**:27-39.
- PAUSAS, J.G. 1999a. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems – A simulation approach. *Journal of Vegetation Science* **10**:717-722.
- POULSEN, E.T. 1979. A model for population regulation with density- and frequency-dependent selection. *Journal of Mathematical Biology* **8**:325-343.
- PRAJNESHU 1980. Time-dependent solution of the logistic model for population growth in random environments. *Journal of Applied Probability* **17**:1083-1086.
- RODIN, E.Y., MURTHY, D.N.F. & PAGE, N.N. 1990. *Mathematical modelling*. Pergamon Press, New York.
- ROSEN, G. 1984. Characterising conditions for generalised Verhulst logistic growth of a biological population. *Bulletin of Mathematical Biology* **64**:963-965.
- SEALBLOOM, E.W., MOLONEY, K.A. & VAN DER VALK, A.G. 2001. Constraints on the establishment of plants along a fluctuating water depth gradient. *Ecology* **82**:2216-2232.

- TOGNETTI, K. & WINLEY, G. 1980. Stochastic growth models with logistic mean population. *Journal of Theoretical Biology* **82**:167-169.
- TUCKWELL, H.C. & KOZIOL, J.A. 1987. Logistic population growth under random dispersal. *Bulletin of Mathematical Biology* **49**:495-506.
- VAN DER BOSCH, F. & GABRIEL, W. 1997. Cannibalism in an age-structured predator-prey system. *Bulletin of Mathematical Biology* **59**:551-567.
- VONHULST, R. 1987. Invasion models of vegetation dynamics. *Vegetatio* **69**:123-131.
- WESTOBY, M., WALKER, B.H. & NOY-MEIR, I. 1989. Range management on the basis of a model which does not seek to establish equilibrium. *Journal of Arid Environments* **17**:235-239.
- WIEGAND, T. & KELLNER, K. 2000. *Workshop at the 26th annual congress of the South African Association of Botanists: The role of models in long-term ecological research*, Unpublished report of abstract, Potchefstroom University for Christian Higher Education, Potchefstroom
- WIEGAND, T., MOLONEY, K.A., NAVES, J. & KHAUER, F. 1999. Finding the missing link between landscape structure and population dynamics: A spatially explicit perspective. *The American Naturalist* **154**:605-627.

Chapter 3:

Population dynamics of *Leysera gnaphalodes*: A mathematical modelling approach

KEYWORDS: Ecological modelling, Logistic growth, Namaqualand, Perennial shrub

ABSTRACT

Leysera gnaphalodes is a short-lived perennial shrub occurring in the Namaqualand region of South Africa. *Leysera gnaphalodes* encroaches into the spring mass flower displays in this region. The population dynamics of *L. gnaphalodes* were investigated in order to find possible management solutions to this encroachment. A rule-based mechanistic mathematical model based on the logistic growth curve was constructed to describe the population dynamics of this species. Data from an eight-year ecological study were used in the model construction. The model-fit was evaluated using correlation coefficients and graphs, and proved to be a good model. Simulations based on the model were run to test three different management strategies under stochastic rainfall conditions. The management strategy, which most effectively controlled the population was to till the lands whenever the population of *L. gnaphalodes* reaches or exceeds a relative frequency of 45%.

INTRODUCTION

Namaqualand is famous throughout the world for the display of wildflowers occurring there in early spring (le Roux & van Rooyen 1999; van Rooyen 1999). This region has a higher species richness of plants than any other desert in the world (Lovegrove 1993, van Rooyen, Theron & van Rooyen 1996, Milton *et al.* 1997) and of the 3 500 species occurring in the area, 22% are endemic (le Roux & van Rooyen 1999). The Succulent Karoo Biome is the only arid region to qualify as a hotspot of global significance.

The floral display is created by various annual species, and is especially prominent where they grow at high densities on abandoned fields, heavily grazed pastures and other disturbed areas (Rösch, van Rooyen & Theron 1997; van Rooyen 1999). It is these mass displays of wildflowers which many tourists come to see, bringing much-needed income to this otherwise fairly barren region (le Roux & van Rooyen 1999) Although wildflowers occur naturally in the vegetation of Namaqualand, in undisturbed vegetation they are limited to small patches characterised by high levels of natural disturbance. This results in them being interspersed with larger perennial plants and not producing such vivid carpets of colour (Dean & Milton 1991a, b, Milton & Dean 1991, van Rooyen 1999).

Namaqualand is found in the northwestern corner of the Northern Cape Province of South Africa and forms part of the Succulent Karoo Biome. It is a desert-like area with low winter rainfall, extreme summer aridity and lime-rich, poorly developed soils (Milton *et al.* 1997, le Roux & van Rooyen 1999)

Leysera gnaphalodes (L.) L. (Asteraceae, Gnaphalieae) encroaches into the wildflower displays of Namaqualand (van Rooyen, Steyn & de Villiers 1999; le Roux & van Rooyen 1999). *Leysera gnaphalodes* is a perennial dwarf shrub growing 200 to 500 mm in height (Anderberg & Bremer 1991). It has wiry grey to green leaves and entirely yellow flower heads up to 20 mm in diameter, which are present from September to December (van Rooyen, Steyn & de Villiers 1999). The plant occurs on sandy flats and slopes, in the Western, Eastern and

Northern Cape Provinces of South Africa as well as in Namibia (van Rooyen, Steyn & de Villiers 1999).

Recently cultivated lands producing mass floral displays are dominated by annuals and characterised by a loss of plant diversity. After cultivation is stopped it may take many decades for perennial plant assemblages to re-establish in these areas (Dean & Milton 1995). Not only plant diversity is decreased by tilling/cultivation, but invertebrate diversity too. Recently cultivated lands in this area have an insect assemblage dominated by a single species of ant (*Anoplolepis steingroeveri*). Furthermore, insect diversity is positively correlated with perennial plant diversity, and negatively with annual plant diversity (Dean & Milton 1995). This implies that, as for perennial plant diversity, insect diversity will also steadily increase with time since cultivation.

If this area were to be managed purely for maximum biodiversity cultivation would be minimised, to maximise all forms of plant and invertebrate diversity. However, taking the economy of the region into account it is essential that some areas of mass flower displays are maintained. The question is: how can this be done such that it has the least possible negative effect on biodiversity?

The focus of this study lies in the portion of Namaqua National Park that was formerly Skilpad Wildflower Reserve. The reserve lies on the edge of the escarpment near the small town of Kamieskroon, and was established with the express purpose of promoting the conservation of Namaqualand wildflower resources (van Rooyen, Theron & van Rooyen 1996).

Tilling is presently applied in Namaqua National Park, as a means to manage the flower display. If tilling does not take place *L. gnaphalodes* returns into the predominantly annual pioneer community quite quickly. It does not bear its flowers until after the annual wildflowers and its flowerless greyish-green appearance dulls the wildflower display. Though regular tilling can alleviate this problem, such high levels of disturbance are undesirable within a National Park where biodiversity conservation is a priority. By studying the population dynamics of this species and especially how it is affected by different management

practises (including tilling) and environmental conditions it was hoped that some compromises could be found between conservation and socio-economics.

Mechanistic mathematical modelling was used on collected field data to approach this problem because if a system can be successfully modelled it gives us the assurance that we understand the most important driving forces in the system (Cross & Moscardini 1985; Wiegand & Kellner 2000). This understanding gives managers the ability to, at least qualitatively, project the system's response to different management strategies and thus plan management accordingly.

It was hypothesised that *L. gnaphalodes*' populations would be reduced by tilling, grazing or by a "dry spell" of several dry years in a row. Thus dry weather, when it occurs or grazing may be possible substitutes for the more disruptive practise of tilling. A model was constructed to test the validity of these hypotheses.

MATERIALS AND METHODS

The data utilised in the construction of the model were collected on experimental plots in Namaqua National Park. The nine experimental treatments were laid out in the same old field, such that environmental variation between treatments is minimal. The treatments differ on the basis of the frequency of tilling (soil disturbance) and the presence/absence of grazing animals (Table 1). All treatments were tilled the year before the study commenced. Annual surveys were conducted in each treatment during late August or early September, where the frequencies of the various plant species were determined using the step-point method with 200 points per treatment. At each point the nearest annual as well as the nearest perennial species were recorded. Thus the measurements of population size used for this model are the frequency (%) of *L. gnaphalodes* relative to the rest of the perennial community. The precipitation data collected by the staff in the Park were used in constructing the model.

TABLE 1: The nine different treatments in the experimental data used for the model

Treatment no.	Description
1	Grazed only (no soil disturbance)
2	Common agricultural practise: crop cultivation alternated with grazing
3	Tilled every fourth year & grazed
4	Tilled every second year & grazed
5	Tilled only once at the beginning of the study & grazed
6	Tilled every fourth year (not grazed)
7	Tilled every second year (not grazed)
8	Tilled only once at the beginning of the study (not grazed)
9	Undisturbed control treatment (no tilling, no grazing)

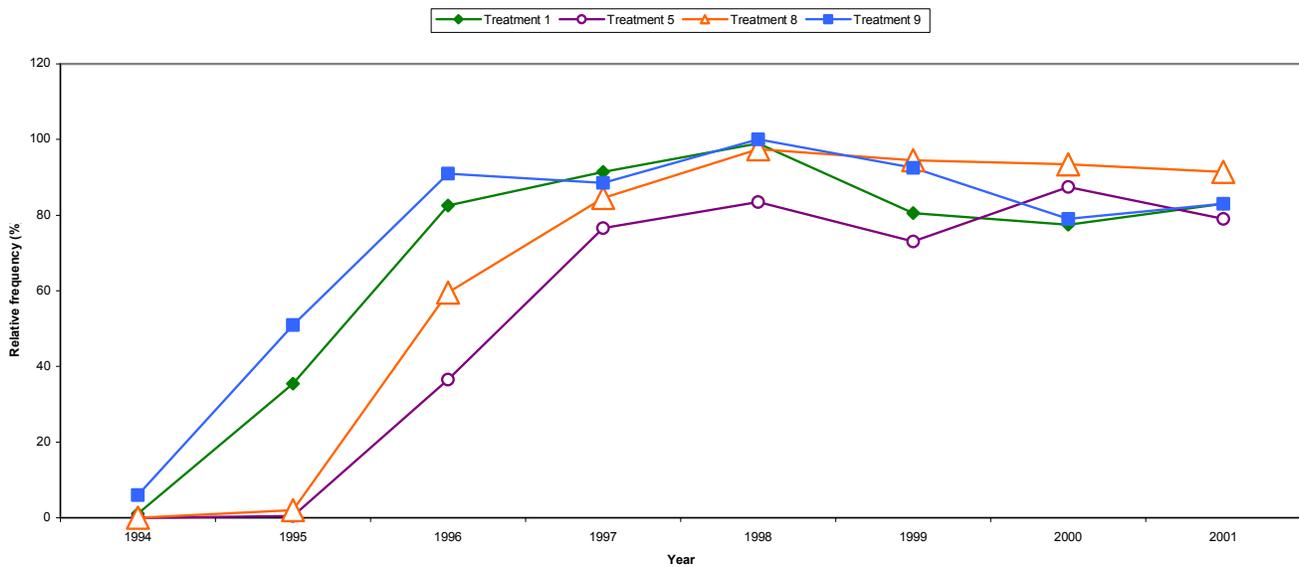


FIGURE 1: Graph of population size of *Laysera gnaphalodes* (as relative frequency) plotted against time for treatments 1, 5, 8 and 9 (which did not experience regular tilling during the experiment). These graphs illustrate that the populations of *L. gnaphalodes* in these treatments exhibited a clear sigmoidal trend.

The model was constructed in a step-wise fashion. First the simplest scenario was modelled and then progressively more and more of the complexities were considered.

The simplest case is that of treatment 9 where there was no tilling or grazing. Thus, in this treatment it can be seen how the population would behave under relatively undisturbed circumstances. Treatment 8 where tilling occurred only once at the beginning of the study and grazing animals were absent should show the same behaviour but with a delay of one year. Treatments 1 and 5 which had the same tilling regime as 9 and 8 respectively, but where grazing animals were present, should also show qualitatively similar behaviour but the populations are expected to be slightly smaller due to grazing. Graphs of relative frequency against time were plotted for these four treatments (Figure 1). These treatments showed a very clear logistic trend.

The following standard continuous form of the logistic growth curve was fitted to the data with no applied disturbance, namely treatment 9:

$$P(k) = \frac{C}{1 + Ae^{-rk}}$$

Where P is the population frequency at step k ($k = 0, 1, 2, \dots$), C is the ecological capacity, r is the maximum annual growth rate in an unrestricted population and $P(0) = C/(1 + A)$ thus $A = (C/P(0)) - 1$ thus A is a constant determined by initial population size (Kingsland 1982, Hughes-Hallett *et al.* 1997).

The curve was fitted using non-linear regression (Gauss-Newton method) in SAS (Statistical Analysis Systems version 6.12, SAS Institute). This method requires initial approximations for the constants it estimates. Initial estimates for the ecological capacity (C) were obtained by averaging all the points that visually appeared to be at ecological capacity in treatments 8 and 9 (i.e. those treatments not tilled regularly or grazed). Initial approximations for the other parameters (r and A) were obtained by linearising the equation (including the approximation for ecological capacity already obtained) and using ordinary least squares linear

regression (Hughes-Hallett *et al.* 1997) in Microsoft Excel (Microsoft Excel 97, Microsoft Corporation).

The Gauss-Newton method converges to the correct values only if initial approximations are sufficiently close to these correct values (Burden & Faires 2001). For this reason the sensitivity of the results to changes in the initial estimates was analysed. Sensitivity was evaluated by running the non-linear regression with the lowest and highest biologically meaningful values for each parameter. It was found that within biologically meaningful ranges the results were unchanged.

Once the basic model was obtained for the simplest case, the effects of different disturbances were considered. Graphs of relative frequency against time, rainfall, seedbank size and tilling were plotted and examined visually to help in this process. It was observed, for example, that once the population reached a certain level, then it decreased after tilling before increasing again, along what appeared to be the same logistic growth curve. Rules were developed to describe the effects of the different disturbances. These rules were formulated into logical language and incorporated into the model.

The model-fit was evaluated using Pearson's correlation coefficients (Gujurati 1995) and graphs showing model predictions and observed values. The various rules were added and removed so that their effect on the model-fit could be evaluated. Several different rules were tested for the effects of each factor (tilling, grazing and rainfall) and the rule describing the effect of each factor best was then chosen. All the factors were included in the final model except grazing. The best rule for grazing stated that grazing reduces the population by a percentage that is dependent on rainfall. When the rule was included, the model's correlation with observations decreased. Thus, the final model excluded grazing as a factor that determines population size.

It should be noted that only the data for treatment 9 was used in the non-linear regression so the data for the other treatments, especially 1, 5 and 8 where the rules play little or no part, can be considered as out of sample. As such the model was tested on data not used in its construction.

A simulation model was constructed based on this mathematical model. In this simulation rainfall was generated stochastically such that the same proportion of years will be above/below average as in the observed rainfall data. When the model is run an initial population size (low, medium or high) can be set and one of three possible basic management strategies chosen (Table 2). The parameter values in the management strategy must also be specified. The projected effects of the management strategy under stochastic rainfall can then be seen over the desired number of years. Several simulations were run to test the various management strategies.

RESULTS

The treatments that did not experience regular tilling during the duration of the experiment exhibited a strong sigmoidal trend (Figure 1). The treatments that were grazed (treatments 1 and 5) lie slightly below those that were not grazed (treatments 8 and 9) and the treatments that were tilled at the beginning of the experiment (treatments 5 and 8) lag slightly behind those that were not (treatments 1 and 9). This agrees with theoretical predictions and implies that grazing reduces population size and that tilling effectively sets the population back along its growth curve.

The following model was obtained to describe the population dynamics of *L. gnaphalodes*:

$$P(k_t) = \frac{89.30}{1 + 656.78e^{-3.40k_t}}$$

Where P is relative frequency in the perennial community and t is time in years, with $t \in \mathbb{N}$ and $t = 0$ in the year 1994. Then k_t is defined by:

$$k_0 = 0$$

if the lands were tilled between the 1993 and 1994 flower seasons; and

$$k_0 = 1$$

TABLE 2: The three basic management strategies that can be selected in the simulation model. Where applicable, tilling interval and/or critical population size can be specified. The initial population size and number of years for which the simulation must be run can also be specified.

	Management approach
1	Till at regular intervals
2	Till when the population reaches a critical size
3	Till at regular intervals and intervene with extra tilling if the population is above a certain level.

if the lands were not tilled in this period (all treatments were tilled the previous year between the 1992 and 1993 seasons.

THEN IF

1. The lands have been tilled at two-year intervals for at least the previous three years, such that they have been tilled at least twice **or** the population has been below 20% for at least the previous three years;

and

2. The previous three years' rainfall has been below average;

and

3. The lands have been tilled between the previous and present flower seasons and $P(t-1)$ is greater than or equal to 45%

$k_t = k_{t-1} - 2$; if $k_{t-1} \leq 3$; and

$k_t = 1$; if $k_{t-1} > 3$

ELSE IF

1. The lands have been tilled at two-year intervals for at least the previous three years, such that they have been tilled at least twice **or** the population has been below 20% for at least the previous three years;

and

2. The previous three years' rainfall has been below average;

and

3. The lands have not been tilled between the previous and present flower seasons **or** the lands have been tilled but $P(t-1)$ is less than 45%

$k_t = k_{t-1} - 1$; if $k_{t-1} \leq 3$; and

$k_t = 2$; if $k_{t-1} > 3$

ELSE IF

1. The lands have not been tilled at two-year intervals for at least the previous three years, such that they have been tilled at least twice **and** the population has not been below 20% for at least the previous three years;

or

2. The previous three years' rainfall has not been below average;

and

3. The lands have been tilled between the previous and present flower seasons and $P(t-1)$ is greater than or equal to 45%

$$k_t = k_{t-1} - 1; \text{ if } k_{t-1} \leq 3; \text{ and}$$

$$k_t = 2; \text{ if } k_{t-1} > 3$$

OTHERWISE

$$k_t = k_{t-1} + 1$$

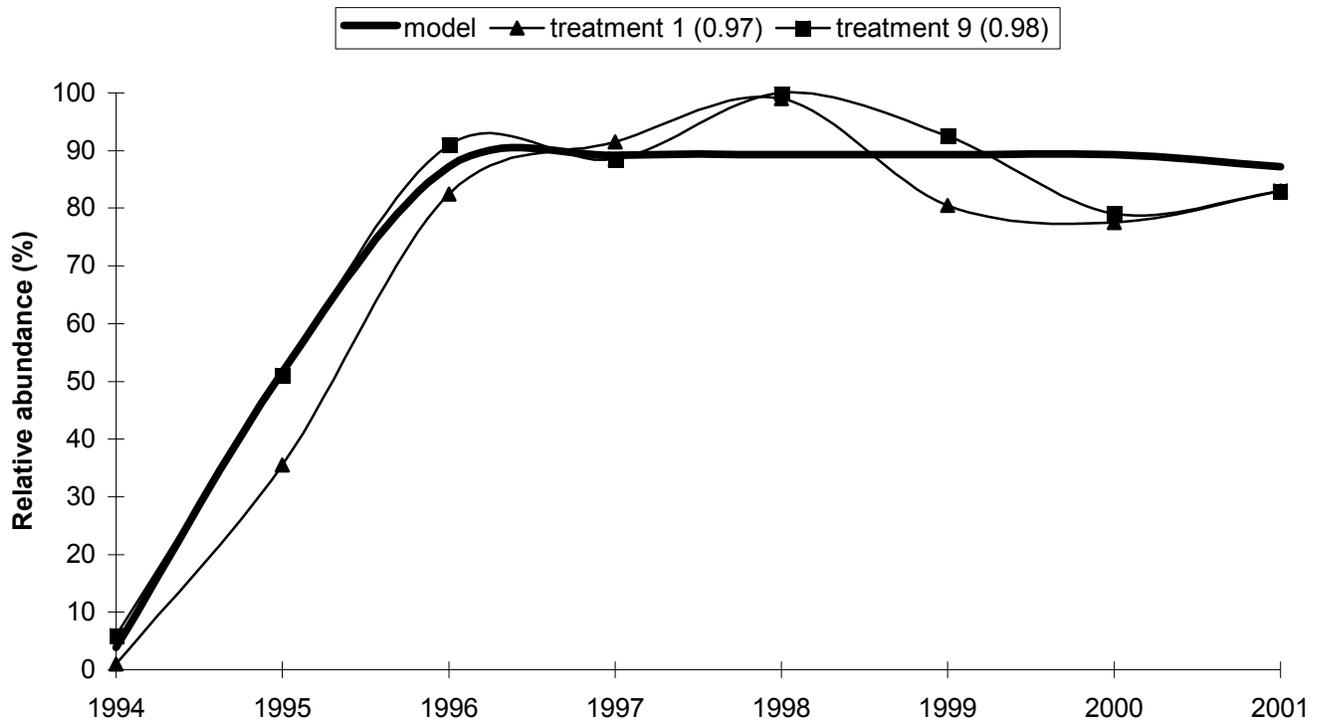
The population size of *L. gnaphalodes* under each of the nine experimental treatments, for the period of the experiment, was predicted using the model. The predicted and observed values are plotted together in Figure 2. The Pearson's correlation between the predicted and observed values is given in the legend of the graph in brackets after the treatment number. The fit of the model to the data can be seen in these graphs. It should be noted that the grazed and ungrazed treatments with the same tilling regime have the same predicted values. This is because grazing is not a variable in the model. Further, it should be noted that the model does not predict the population sizes under treatment 2 accurately. This is because treatment 2 was tilled and sown with crops every second year, a treatment not covered by the model.

Populations of *L. gnaphalodes* appear to be decreased ("set back") along the logistic curve by tilling only if the population prior to tilling is sufficiently large (greater than or equal to 45%). This can be seen in Figure 2 (d) where tilling in 1998 but not in 1996 reduces the population. The pictures of tractors pulling ploughs indicate that the lands were tilled prior to that year's flower season.

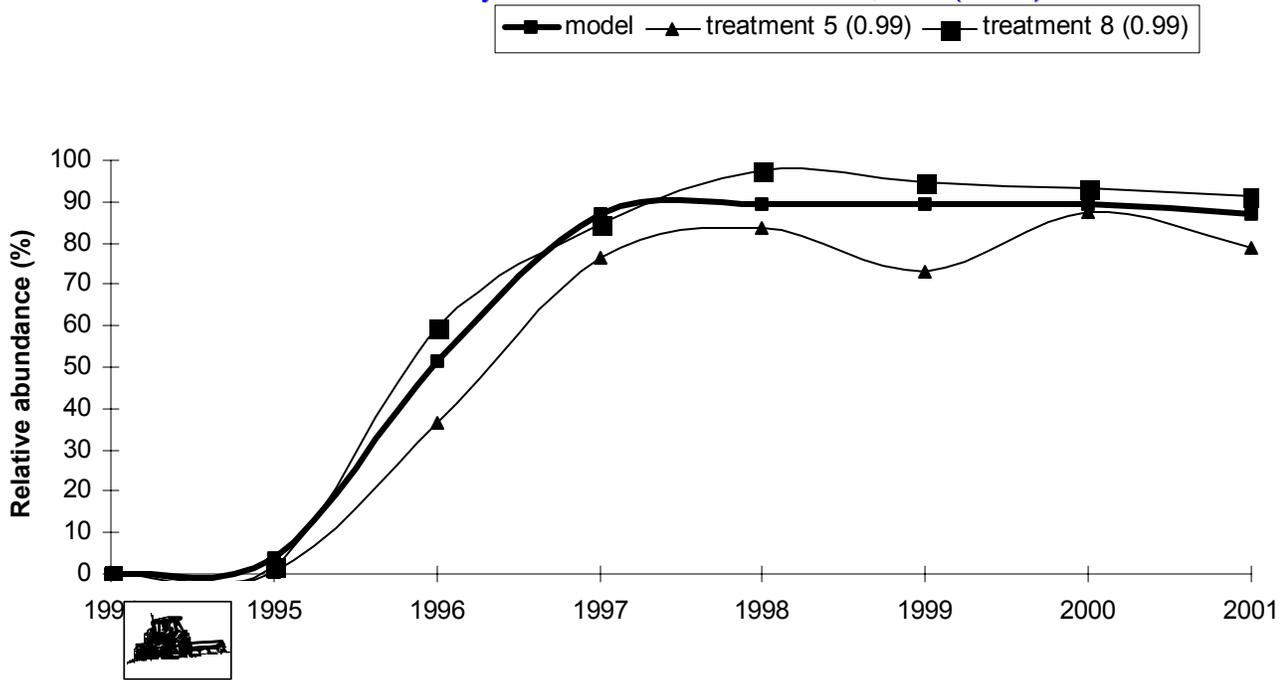
Figure 2 (d) indicates that the populations in the treatments that were tilled every second year decreased in 2001 even though tilling was not applied in any of the treatments that year. This is attributed to the fact that the three previous year's (1998, 1999 and 2000) rainfall was below average (Figure 3). Seedbank size was also measured during the experiment and was small in 2001 in all of the treatments and overall smaller in those tilled every second year (treatments 4

(a) Treatment 1 and 9 : No soil disturbance

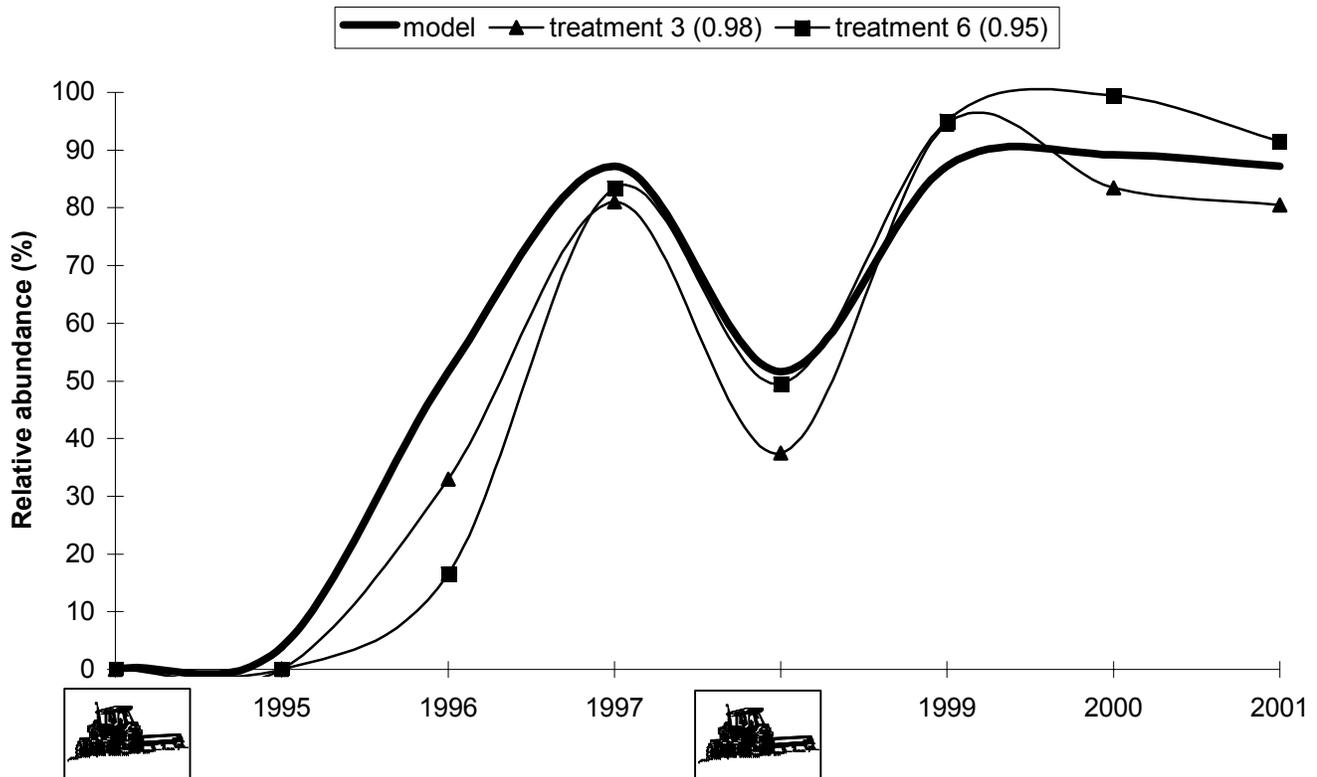
FIGURE 2: Observed and predicted population size (in relative frequency) plotted against time for the various treatments in the experiment. A picture of a tractor pulling a plough indicates that the lands were tilled prior to the flower season that year. Pearson's correlation coefficients between the predicted and observed values are given in the legend in brackets after the treatment number.



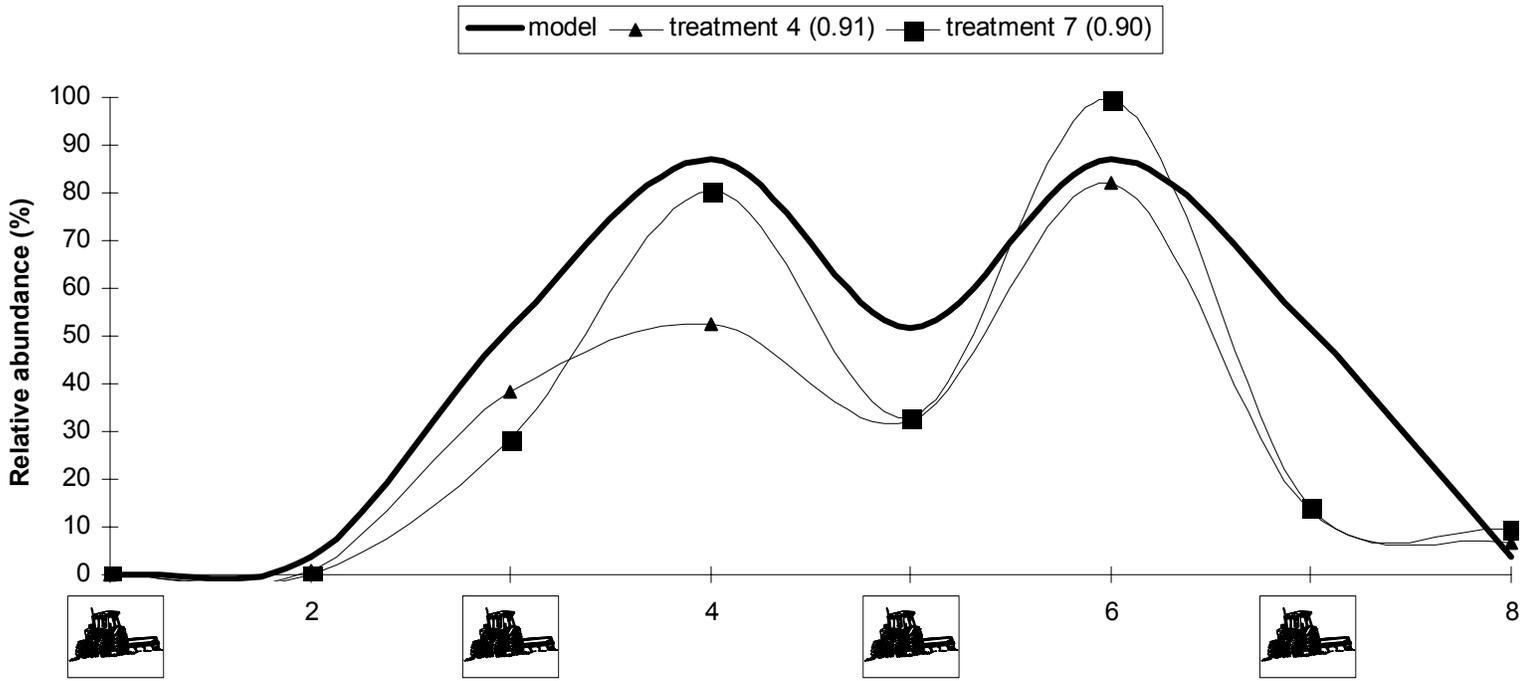
In each case treatments that have been grazed are indicated by triangles and treatments that are ungrazed are indicated by a squares.



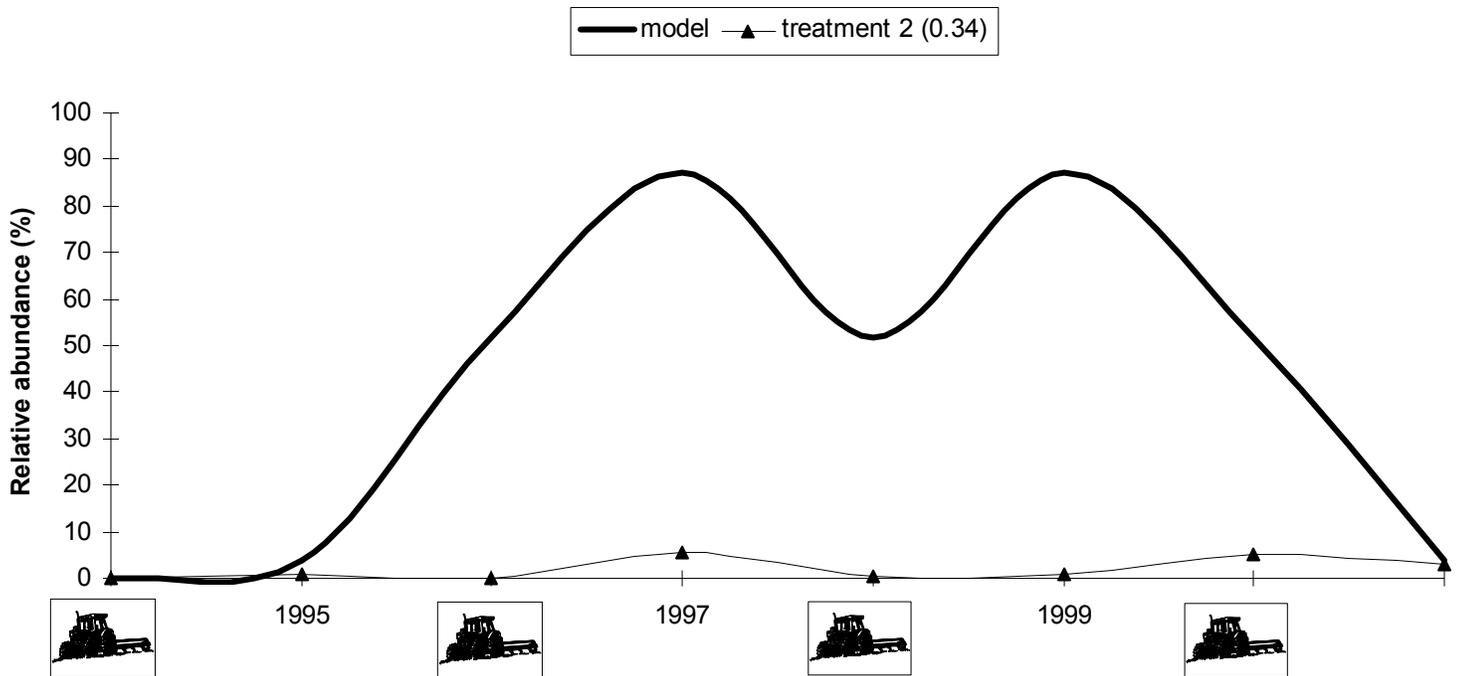
(b) Treatments 5 and 8 : Tilled only once at the beginning of the study



(c) Treatments 3 and 6 : Tilled every four years



(d) Treatments 4 and 7 : Tilled every two years



(e) Treatment 2 : Common agricultural practice – tilled and sown every second year

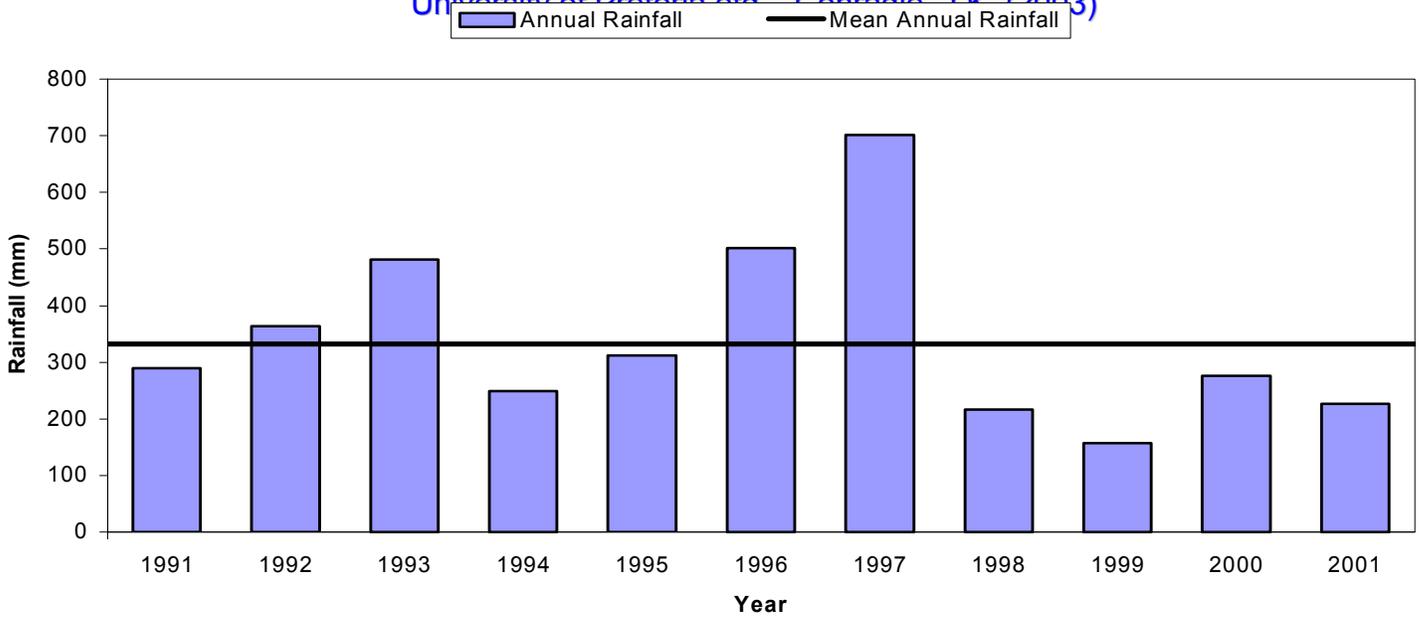


FIGURE 3: Rainfall at the study site from 1991 to 2001. The horizontal line indicates the mean annual rainfall at the site.

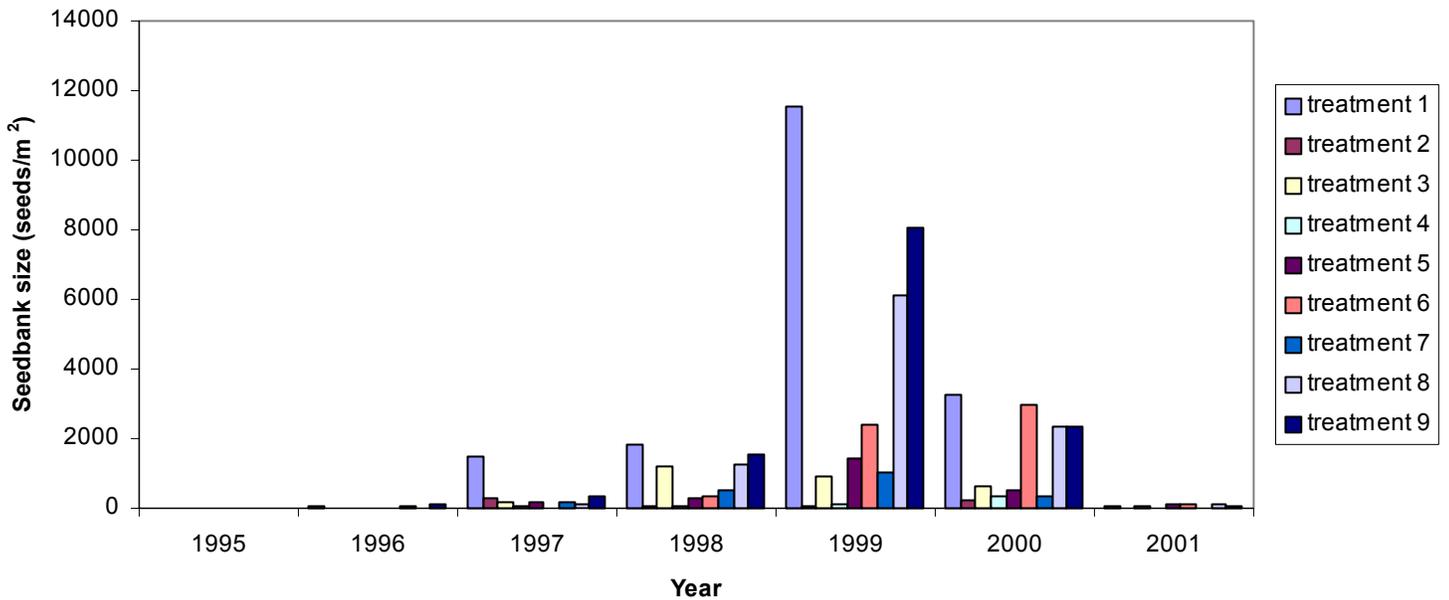


FIGURE 4: Seedbank size (in seeds/m²) of *Leysera gnaphalodes* in each of the nine treatments over a seven-year period.

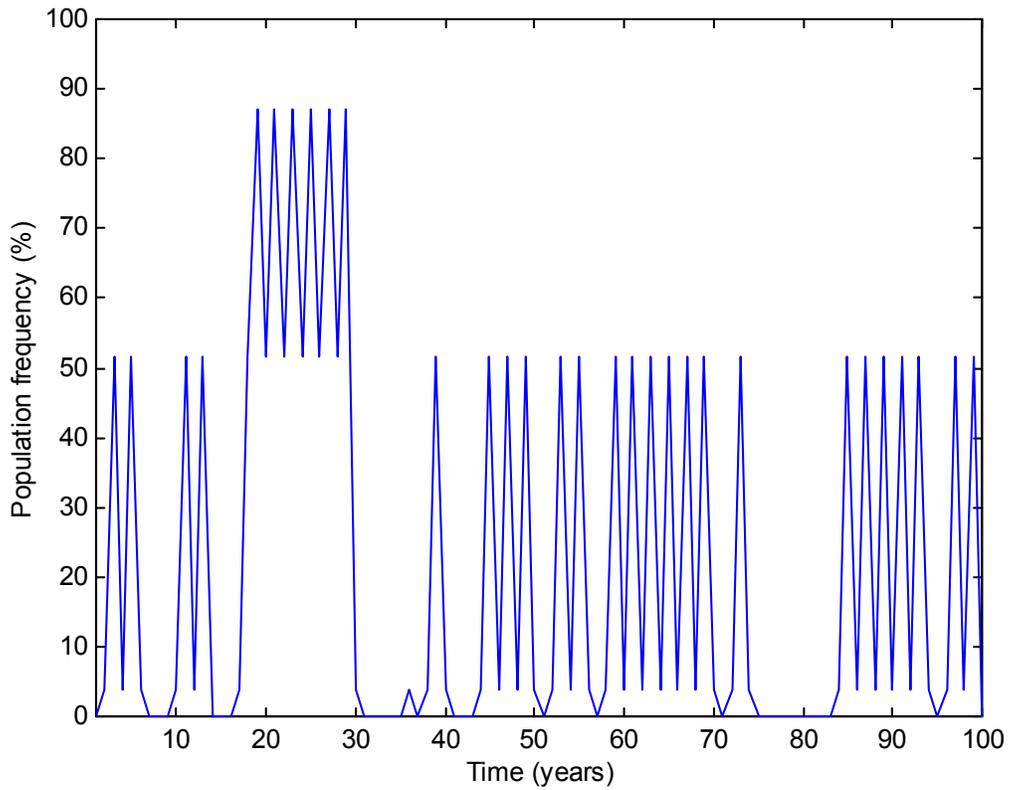
and 7) (see Figure 4). It should be noted that more complex rules for the effect of low rainfall were tested but proved less successful than the one ultimately used.

Simulations were performed over 100 years for each of the possible management strategies in the simulation model. Strategy 1 was simulated with tilling intervals of both two and four years and low and high starting populations/ Strategy 2 was simulated with a critical level of 45% and 60% with medium starting populations. Strategy 3 was simulated with a critical level of 45%, tilling intervals of two and four years and a medium starting population. The resulting populations are plotted in Figure 5.

DISCUSSION AND CONCLUSIONS

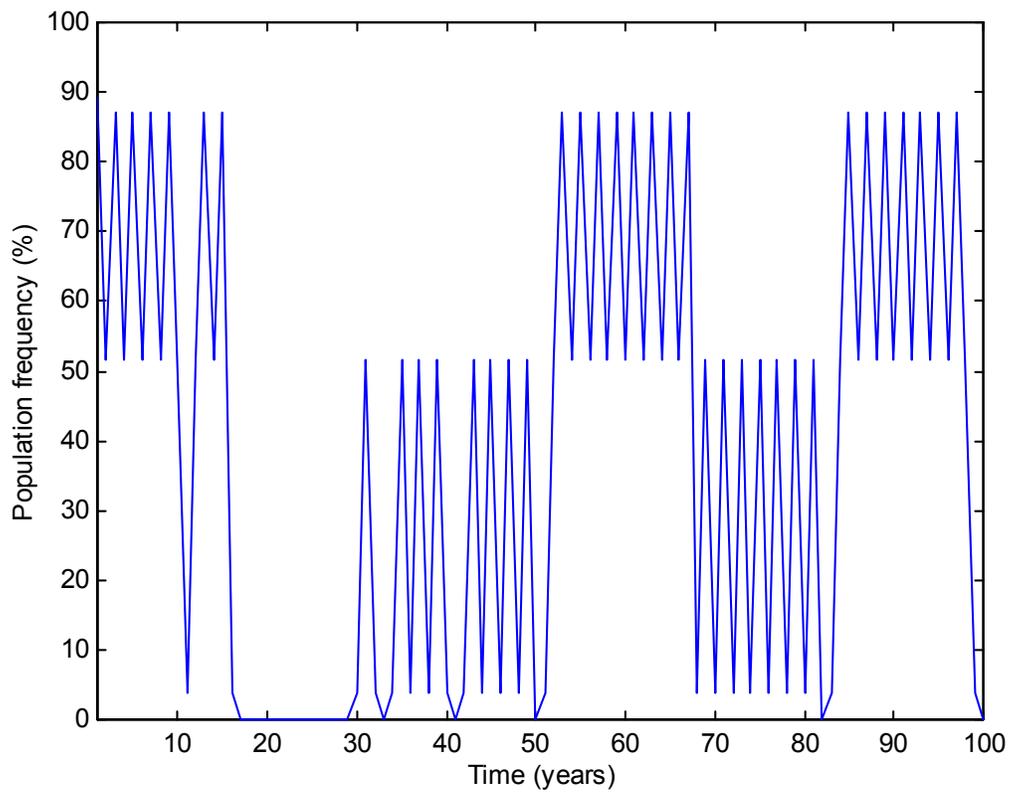
First-degree logistic growth curves have been used in forestry for the modelling of height-age relationships in trees. Brewer, Burns & Cato (1985) examined the accuracy of five-year projections of top height of loblolly pines (*Pinus taeda*) at an age of 25 years from data up to age 20 using five different curves. The first-degree logistic and Gompertz curves produced relatively large errors using both fixed and estimated upper asymptotes, rendering the other curves tested more suitable. The curves were fitted to the data using the Gauss-Newton method for nonlinear regression in SAS, the same technique used in the current study.

Caloin & Yu (1982) examined the effect of irradiance on plant growth and specifically the relative dry masses of the root and shoot portions of the plants. They tested the logistic model as a model of plant growth but found that its predictions of the upper asymptote were inaccurate at high levels of irradiance. Thus they used an extension of the logistic model proposed by Lotka in 1925 which made the growth rate proportional to fractional powers of the plant's mass. There are however, also applications where the logistic curve has been successful: Van der Bosch and Gabriel (1997) explored the effects of cannibalism by the predators on the dynamics of certain types of predator-prey populations. They constructed a Lotka-Volterra predator-prey model with logistic

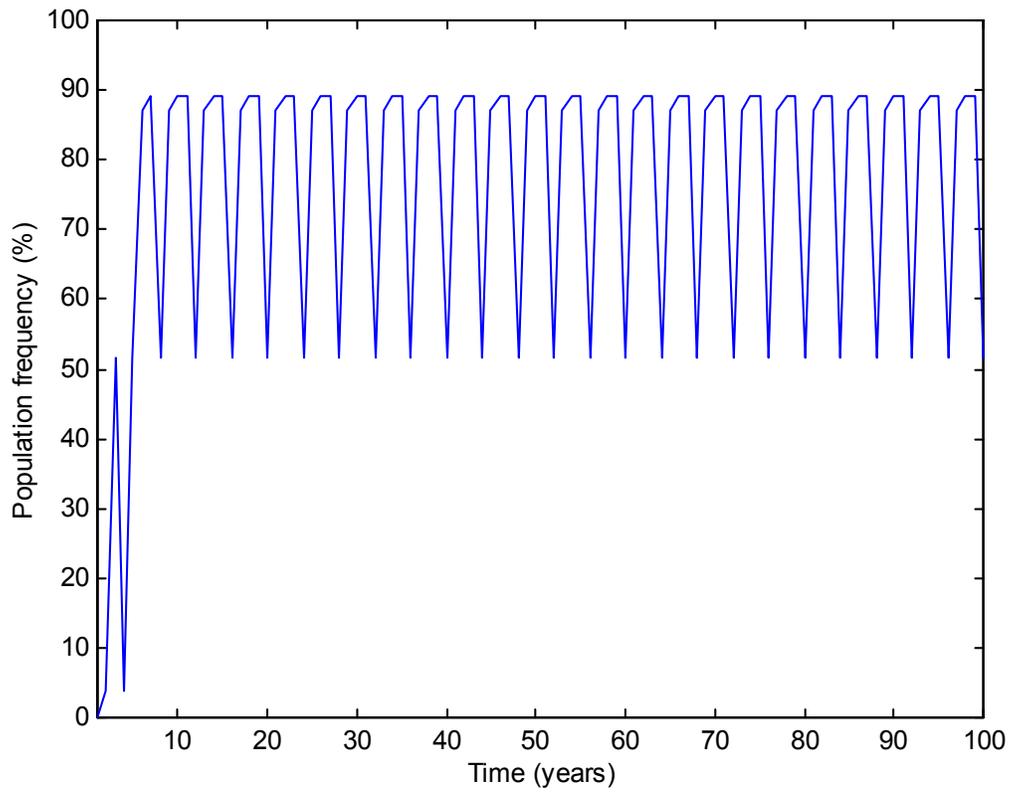


(a) Strategy 1.1: Till at two-year intervals with low initial population

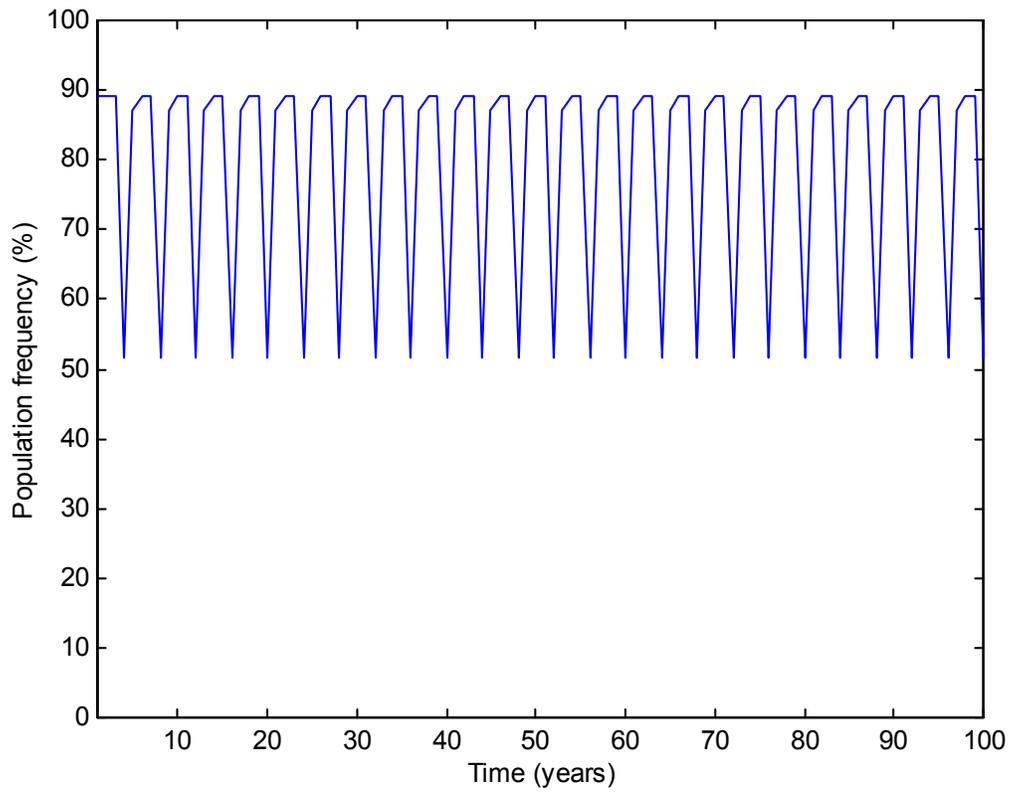
FIGURE 5: Simulated population size of *Leysera gnaphalodes* over a period of 100 years, as predicted by the model under stochastic rainfall conditions. The simulations are run under various possible management strategies and with different initial population sizes.



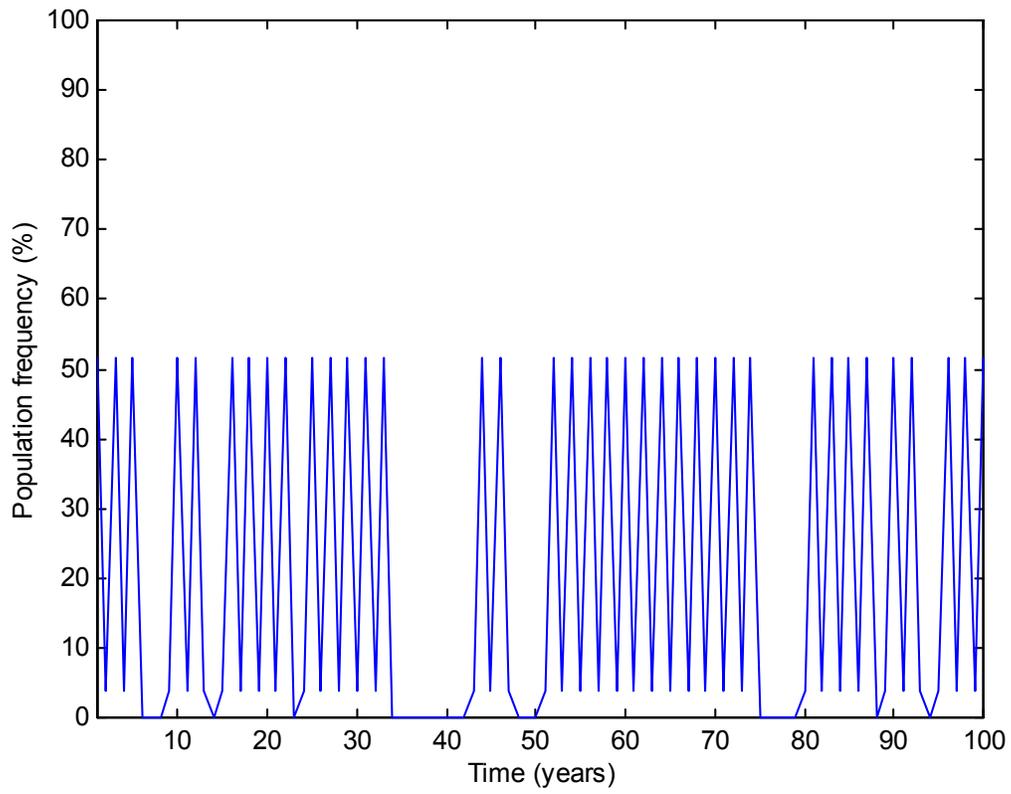
(b) Strategy 1.2: Till at two-year intervals with high initial population



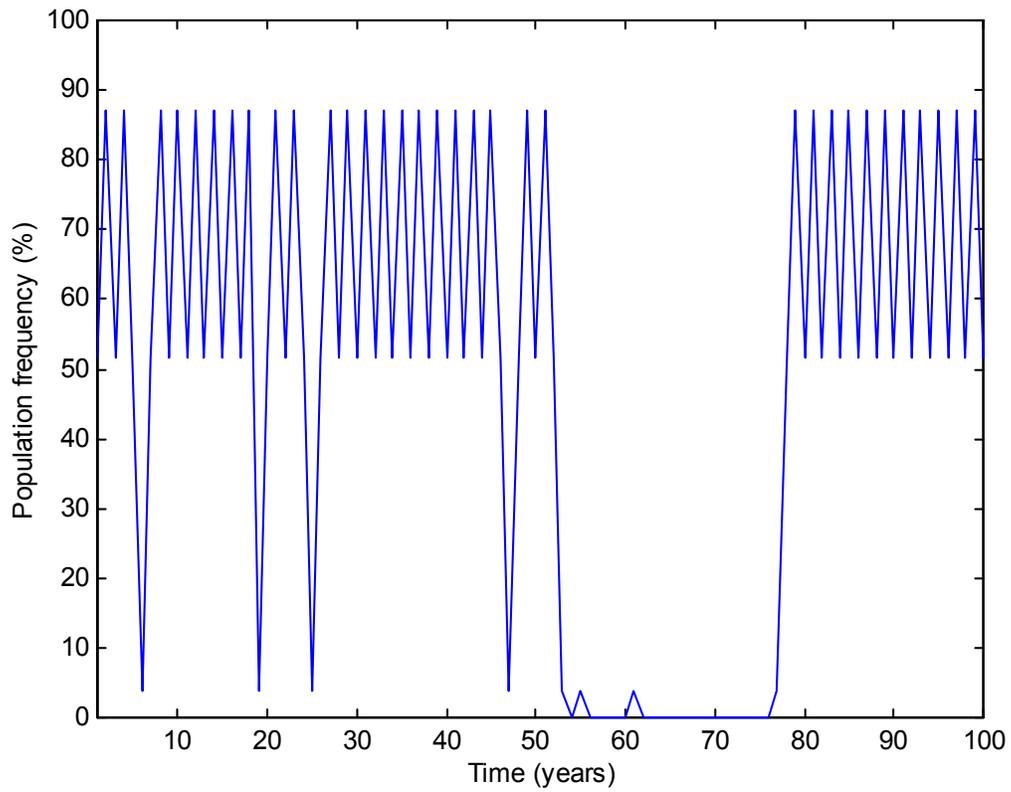
(c) Strategy 1.3: Till at four-year intervals with low initial population



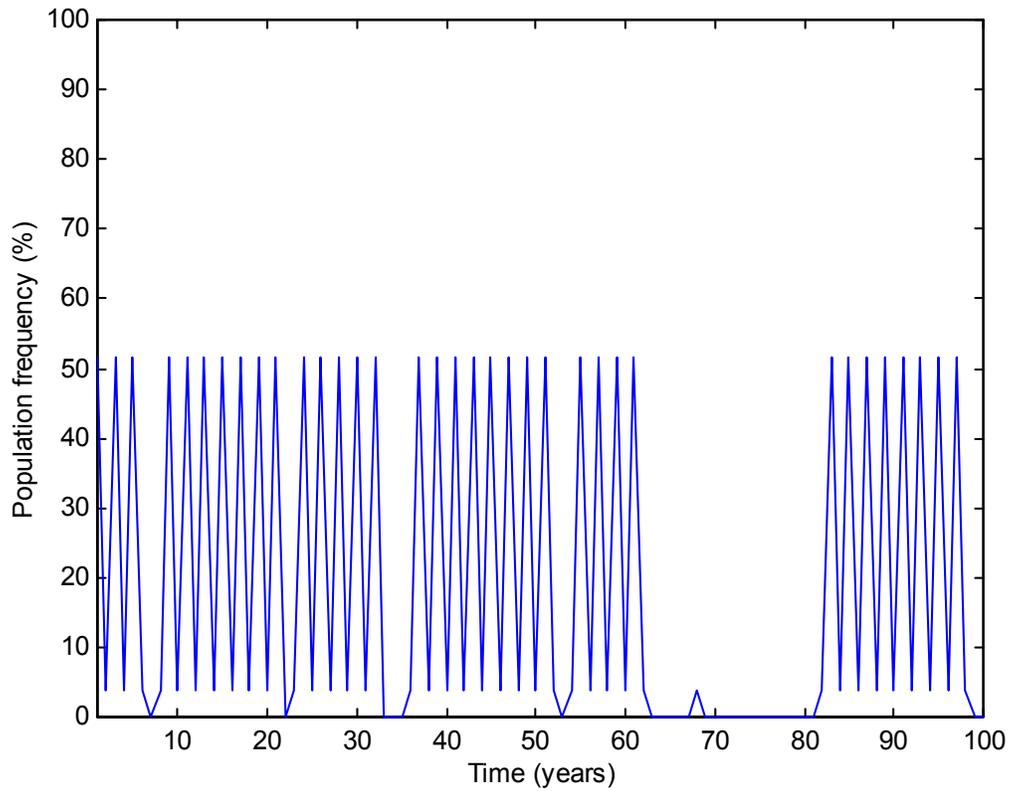
(d) Strategy 1.4: Till at four-year intervals with high initial population



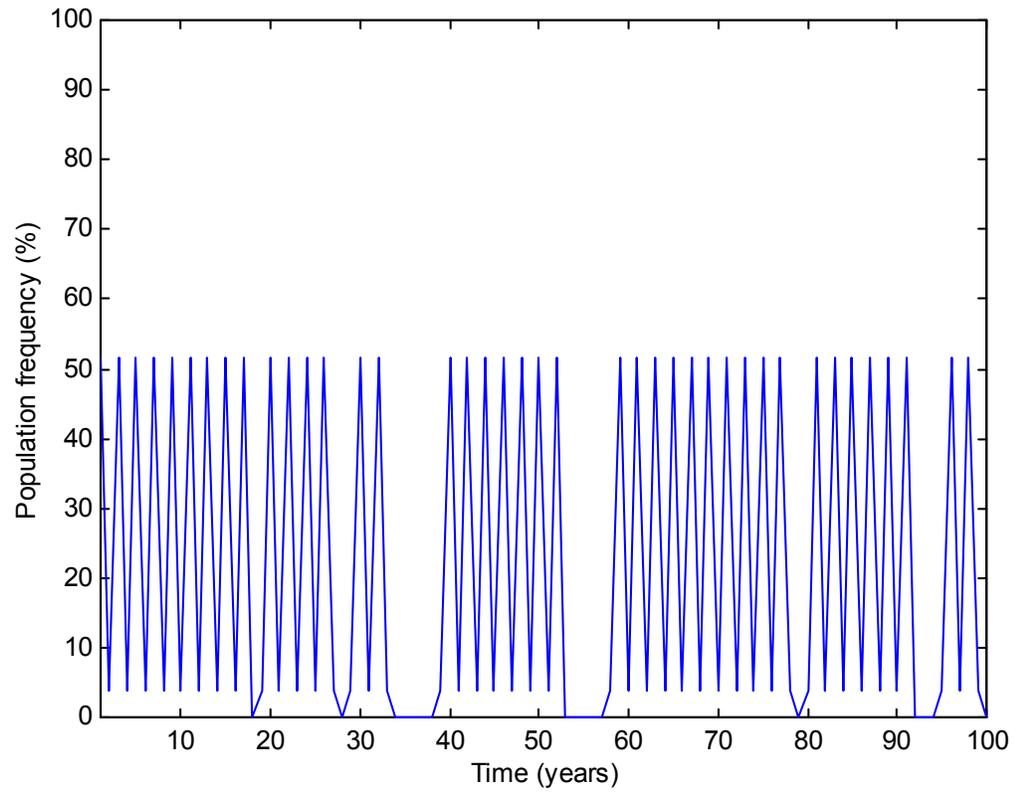
(e) Strategy 2.1: Till when the population is or exceeds 45%



(f) Strategy 2.2: Till when the population is or exceeds 60%



(g) Strategy 3.1: Till at two-year intervals and in between if the population is or exceeds 45%



(h) Strategy 3.2: Till at four-year intervals and in between if the population is or exceeds 45%

population growth and hyperbolic type II functional response. Simulation models of actual ecosystems in the North Sea were constructed during previous research using these types of models and they were successful. The authors then used their model to mathematically explore the effects of predator cannibalism on predator-prey systems and found that they generally stabilise the oscillations in the system.

A four-parameter generalisation of the logistic curve was developed specifically for application to populations that rise up to a certain maximum and then decline back to zero. This is the case, for example, in insect populations that show seasonal trends in certain stages of their life cycle. This model also applies to the growth and decline of cellular and molecular populations within an organism. The model fitted well to both data of male flies of the species *Meromyza variegata* and the protozoan *Paramecium caudatum* that was out-competed by *Paramecium aurelia* (Jolicoeur & Pontier 1989).

Sex and age-structured models of population growth and harvesting are often used to determine maximum sustainable yield of ivory from African elephant populations. Basson, Beddington & May (1991) constructed a more general model aimed at determining the general long-term sustainable yield of ivory. They used a logistic model of population growth with additional functions to describe the relationship between number of individuals and the mass of ivory harvested and the collection of ivory from animals dying of natural causes. They did not calibrate the model to any actual data but discussed the ranges within which the coefficients should fall according to current knowledge. They also examined the behaviour of the model under various harvesting strategies.

The logistic growth model, with added rules, also proved a success in the current study. With the exception of treatment 2, which was not included during the construction of the model, all the treatments show correlation coefficients of at least 0.90. The graphs in Figure 2 also show that the model follows the observed values very well.

The management goal of the particular portion of the park under consideration in this study is to maximise the mass effect of the flower display.

To achieve this it is essential to minimise the population size of *L. gnaphalodes*, due to this species' greyish appearance which dulls the colourful floral display.

The model implies that there are two situations in which the population will decline, namely:

- (i) If it is tilled, provided the population size was at least 45% in the season preceding tilling (see Figure 2(d) in 1994 and 1996).
- (ii) In the fourth year, after three years' rainfall has been below average, provided the area has been tilled at two year intervals for at least the previous three years, such that it has been tilled at least twice or the population has been below 20% for at least the previous three years (see Figure 2 (d) (e in the year 2001).

If these two factors occur in the same year their effect is cumulative. Thus having twice the reducing effect on the population that either of them would have on their own. To reduce the population by as much as possible our goal is to have both of these factors occurring concurrently.

Factor (i) will be referred to as "tilling" and factor (ii) as "low rainfall" for the purposes of the discussion that follows.

Tilling can be "applied" as and when managers see fit, but it only has an effect in reducing the population if the population is above a certain level (45%) when it is applied. Thus it is not effective under all circumstances.

Low rainfall is dependent on weather patterns over which managers have no control in their management strategy. Low rainfall cannot be "applied", but its occurrence can be used to our maximum benefit, when nature obliges. Low rainfall has the same effect on the population irrespective of population size, which is very useful as this is not the case for tilling.

Low rainfall is thought to have an effect on the population because it depletes the seedbank. Furthermore, treatments tilled at two-year intervals would have a smaller population of adults surviving into the next season and thus would be more affected by changes in the seedbank size. This is thought to be why areas tilled at two-year intervals or where the population is small are affected by low rainfall.

Three possible basic management strategies were proposed as listed in Table 2. Considering the model would suggest that the most effective management strategy should be as follows:

- Tilling should take place at least every second year, unless the population has been below 20% for three years, to enable low rainfall to have an effect when it does occur.
- If *L. gnaphalodes* comprises more than 45% of the perennial community, in a year when the lands would not ordinarily be tilled, the manager should “intervene” and the lands should be tilled anyway. This prevents the population from becoming too large.

The only way that the population of *L. gnaphalodes* can be eradicated completely or brought down very low is by low rainfall, and low rainfall is unpredictable and only effective if the lands have been tilled every second year or the population has been low. Low rainfall reduces the population along the logistic curve from where it is currently. The smaller the population is when low rainfall occurs, the smaller the resulting population will be. Therefore effective management should keep the population of *L. gnaphalodes* as small as possible at all times, so that when low rainfall does occur, it can have the maximum effect. The only other means to reduce the population is tilling, which only works when the population is sufficiently large. It thus follows that tilling should be applied whenever the population is sufficiently large for it to be effective. That way when low rainfall does occur managers derive maximum benefit. Therefore, based purely on the deterministic model management approach two or three with a critical level of 45% would be the most effective.

Grazing is not incorporated into the management strategy since grazing was shown to be ineffective in reducing populations of *L. gnaphalodes*. Grazing here refers to grazing by sheep in the summer months. It is therefore possible that grazing by different animals or at different times of year may in fact be an effective means of controlling *L. gnaphalodes* populations. This, however, falls out of the scope of the present study.

The discussion above refers to the optimal management approach as determined by the deterministic equation. However, in reality management takes place under stochastic environments. A simulation model was built with stochastic rainfall. Various forms of the three different management strategies were all applied over a period of 100 years and the resulting fluctuations in the population examined (Figure 5).

In management strategies 1.1. and 1.2., shown in Figure 5 (a) and (b), tilling was applied at two-year intervals with low and high initial population sizes respectively. This resulted in populations that oscillated around a certain level for a while before dropping or rising to another level and oscillating there. There were also longer dips in the population where low rainfall reduced it right below the level where tilling could make it oscillate. The initial population size only had an effect in the first few years; the long-term pattern remained the same in both strategies. These strategies are not very effective since at times during the simulation the population is at high levels for relatively extended periods of time. One needs to intervene as the population starts to become too large so that it never remains at such high levels.

In strategies 1.3. and 1.4., shown in Figure 5 (c) and (d), the lands are tilled at four-year intervals with low and high initial population sizes respectively.. The population drops to around 50% when it is tilled, before rising back up to around 90% until it is next tilled. There are no dips lower than 50%, or dips that persist for more than one year since low rainfall can never have an effect. This is because the population is never tilled at two-year intervals or less than 20%. These strategies are thus ineffective in keeping the population low. Again initial population size only makes a difference during the first few years of the simulation. This shows the importance of managing the population such that rainfall can have an effect on the population.

In strategies 2.1. and 2.2., shown in Figure 5 (e) and (f) the population is tilled whenever it reaches or exceeds a certain level, namely 45% and 60% respectively. This causes the population to oscillate below a maximum of around 50% and 90% respectively. Thus the level of 45% used in 2.1. is a better choice.

It should be noted that there are longer drops down out of the oscillations in these two strategies even though the lands are not explicitly tilled at two-year intervals. This is because in effect this management strategy causes the land to be tilled every second year unless the population is reduced by low rainfall.

It was noted that strategies 1.1. And 1.2. Need to be extended to include intervention that prevents the population from becoming too large. This is done in strategies 3.1 and 3.2. shown in Figure 5 (g) and (h). The intervention added is that the area is tilled if the population exceeds 45% and it would not otherwise have been tilled. We see that it has the desired effect of keeping the population permanently below about 50% and reducing it to very low levels when rainfall is low. The tilling interval specified in the strategy has little or no effect since, as in strategies 2.1. and 2.2. the lands are effectively tilled every second year for long periods.

From the graphs it can be seen that strategies 2.1., 3.1. and 3.2. are the most effective strategies, and are all equally effective. This agrees with the predictions made from the deterministic model that keeping the population as small as possible and tilling regularly would be the most effective management strategy.

It is therefore recommended that the area be tilled whenever the population reaches or exceeds 45%. The area can also be tilled at regular intervals in addition to whenever the population is or exceeds 45%. The choice between these two strategies is left to the manager, who may have other factors to take into consideration. Tilling as little as possible may be advantageous to biodiversity conservation, in which case the former strategy is slightly preferable.

The time of year at which tilling takes place may also have an influence on the effect of the tilling. Tilling in this experiment was done after *L. gnaphalodes* had already set seed. Figure 3 and 4 indicate that when the rainfall is consistently low and/or tilling takes place every second year, the seed bank is depleted. In Figure 2 we see that when the rainfall has been low in the treatments tilled every second year, and hence the seedbank is depleted, the population declines. Therefore, if the management strategy applied could deplete

the seedbank it may well be effective in reducing the population. For this reason tilling before *L. gnaphalodes* has set seed but after the main flower display is over (i.e. in October) may also be an effective solution. This may have to be repeated several years in a row in order to effectively deplete the seedbank, but thereafter the population should remain small until particularly favourable conditions prevail.

Consideration should also be given to the effects of the technique used to measure population size on the results. The measure of population size used (relative frequency) is, firstly, relative. If the other components of the community undergo some dramatic change in size, it could appear as if the population of *L. gnaphalodes* had increased/decreased when in reality it had not. An attempt was made to minimise this effect by taking population size relative to the **perennial** community as opposed to the **entire** community. The perennial community in this area is relatively stable, whereas the annual community undergoes large fluctuations.

Secondly, it should be noted that population size was measured, with no indication of individual size. In the conclusions regarding management strategies the aesthetic impact of *L. gnaphalodes* on the vegetation as a whole was considered, which is clearly dependent on individual plant size, as well as number. There may be effects not detected in this data brought on by variations in individual plant size. For example, an area tilled during the preceding summer may have exactly the same frequency of *L. gnaphalodes*, as an area not tilled; yet the individuals may be much smaller in the tilled area. These smaller individuals may have less of an aesthetic impact on the mass displays than the larger ones.

REFERENCES

- ANDERBERG, A.A. & BREMER, K. (1991) Parsimony analysis and cladistic reclassification of the Reophalis generic group *Asteraceae, Gnaphalieae(. *Annals of the Missouri Botanical Gardens* **78**,1061-1072.

- BASSON, M., BEDDINGTON, J.R. & MAY, R.M. (1991) An assessment of the maximum sustainable yield of ivory from African elephant populations. *Mathematical Biosciences* **104**,73-96
- BREWER, J.A., BURNS, P.& CATO, Q.V. (1985) Short-term projection accuracy of five asymptotic height-age curves for Loblolly Pine. *Forest Science* **31**,414-418.
- BURDEN, R.L. & FAIRES, J.D. (2001) *Numerical Analysis* (7th ed.), Brooks/Cole Publishing Company, Pacific Grove.
- CALOIN, M. & YU, O. (1982) An extension of the logistic model of populations growth. *Annals of Botany* **49**,599-607.
- CROSS, M. & MOSCARDINI, A.O. (1985) *Learning the art of mathematical modelling*. Ellis Horwood Ltd., Chichester.
- DEAN, W. R. J. & MILTON, S. J. (1991b) Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* **20**,231-237.
- DEAN, W. R. J. & MILTON, S.J. (1995) Plant and insect assemblages on old fields in the arid southern Karoo, South Africa. *African Journal of Ecology* **33**,1-13.
- DEAN, W.R.J. & MILTON, S.J. (1991a) Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: Mammal diggings as germination sites. *African Journal of Ecology* **29**,11-16.
- GUJURATI, D. N. (1995) *Basic Econometrics* (3rd ed.) pp. 77 & 767. McGraw-Hill Book Co., Singapore.
- HUGHES-HALLETT, D., GLEASON, A.M., LOCK, P.F., FLATH, D., GORDON, S.P., LOMEN, D.O. & LOVELOCK, D. (1997) *Brief calculus for business, social sciences and life sciences* (preliminary edition) pp. 234-248. John Wiley & sons Ltd., Brisbane.
- JOLICOEUR, P. & PONTIER, J. (1989) Population growth and decline: a four-parameter generalisation of the logistic curve. *Journal of Theoretical Biology* **141**,563-571.
- KINGSLAND, S. (1982) The refractory model: The logistic curve and the history of population ecology. *The Quarterly Review of biology* **57**,29-52.
- LE ROUX, A. & VAN ROOYEN, G. (1999) Succulent Karoo. In: J. Knobel (ed.) *The Magnificent Natural Heritage of South Africa*, pp. 94-107. Sun Bird Publishing, Cape Town.
- LOVEGROVE, B. (1993) *The living deserts of Southern Africa*. Longmans, London.
- MILTON, S. & DEAN, R. (1991) Disturbances in dune grassland: Colourful consequences of clearing. *African Wildlife* **45**,199-203.
- MILTON, S.J., YEATON, R.I., DEAN, W.R.J. & VLOK, J.H.J. (1997) *Succulent Karoo*. In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.) *Vegetation of Southern Africa*, pp. 131-166, Cambridge University Press, Cambridge

- RÖSCH, H., VAN ROOYEN, M.W. & THERON, G.K. (1997) Community-level competition between five Namaqualand pioneer plant species. *South African Journal of Botany* **63**,1-3.
- VAN DER BOSCH, F. & GABRIEL, W. (1997) Cannibalism in an age-structured predator-prey system. *Bulletin of Mathematical Biology* **59**,551-567.
- VAN ROOYEN, G., STEYN, H. & DE VILLIERS, R. (1999) *Cederberg, Clanwilliam & Biedouw Valley: South African Wild Flower Guide 10*. Botanical Society of South Africa, Kirstenbosch.
- VAN ROOYEN, M.W. (1999) Functional aspects of short-lived plants. In: W.R.J. Dean & S.J. Milton (eds.) *The Karoo – ecological patterns and processes pp. 107-122*. Cambridge University Press, Cambridge.
- VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. (1996) Skilpad Wildflower Reserve – A flower-lover's paradise. *Veld & Flora* **82**,40-42.
- WIEGAND, T. & KELLNER, K. (2000) *Workshop at the 26th annual congress of the South African Association of Botanists: The role of models in long-term ecological research*, Unpublished report of abstract, January 2000, Potchefstroom University for Christian Higher Education, Potchefstroom.

Chapter 4:

Population dynamics of *Leysera gnaphalodes*: A statistical modelling approach

KEYWORDS: Ecological modelling, Namaqualand, Perennial shrub, Stepwise regression

ABSTRACT

Namaqualand is world renowned for its mass displays of annual wildflowers occurring in highly disturbed areas. *Leysera gnaphalodes* is a short-lived perennial shrub that encroaches into this wildflower display, lessening the aesthetic appeal. For this reason populations of *L. gnaphalodes* need to be kept as small as possible. This is usually achieved by tilling the area regularly, but a less disruptive method would be preferable. Alternatives to this approach are explored. It was hypothesised that grazing and low rainfall could also control the population size. An eight-year study was conducted to determine the effects of tilling, grazing and environmental factors on the seedbank and population size of *L. gnaphalodes*. Multivariate statistical models were constructed to determine the effects of all of these factors on the population of *L. gnaphalodes*. Tilling was confirmed to be effective in reducing the population, but grazing was found to have no effect. Low rainfall was also effective in controlling the population but has the disadvantages of being out of management control and also affecting the desirable wildflowers.

INTRODUCTION

Namaqualand is famous throughout the world for the display of wildflowers occurring there in early spring (le Roux & van Rooyen 1999; van Rooyen 1999). This region has a higher species richness of plants than any other desert in the world (Lovegrove 1993, van Rooyen, Theron & van Rooyen 1996, Milton *et al.* 1997) and of the 3 500 species occurring in the area, 22% are endemic (le Roux & van Rooyen 1999). The Succulent Karoo Biome is the only arid region to qualify as a hotspot of global significance.

The floral display is created by various annual species, and is especially prominent where they grow at high densities on abandoned fields, heavily grazed pastures and other disturbed areas (Rösch, van Rooyen & Theron 1997; van Rooyen 1999). It is these mass displays of wildflowers which many tourists come to see, bringing much-needed income to this otherwise fairly barren region (le Roux & van Rooyen 1999) Although wildflowers occur naturally in the vegetation of Namaqualand, in undisturbed vegetation they are limited to small patches characterised by high levels of natural disturbance. This results in them being interspersed with larger perennial plants and not producing such vivid carpets of colour (Dean & Milton 1991a, b, Milton & Dean 1991, van Rooyen 1999).

Namaqualand is found in the northwestern corner of the Northern Cape Province of South Africa and forms part of the Succulent Karoo Biome. It is a desert-like area with low winter rainfall, extreme summer aridity and lime-rich, poorly developed soils (Milton *et al.* 1997, le Roux & van Rooyen 1999)

Leysera gnaphalodes (L.) L. (Asteraceae, Gnaphalieae) encroaches into the wildflower displays of Namaqualand (van Rooyen, Steyn & de Villiers 1999, le Roux & van Rooyen 1999). *Leysera gnaphalodes* is a perennial dwarf shrub growing 200 to 500 mm in height (Anderberg & Bremer 1991). It has wiry grey to green leaves and entirely yellow flower-heads up to 20 mm in diameter, which are present from September to December (van Rooyen, Steyn & de Villiers 1999). The plant occurs on sandy flats and slopes, in the Western, Eastern and

Northern Cape Provinces of South Africa as well as in Namibia (van Rooyen, Steyn & de Villiers 1999).

Recently cultivated lands producing mass floral displays are dominated by annuals and characterised by a loss of plant diversity. After cultivation is stopped it may take many decades for perennial plant assemblages to re-establish in these areas (Dean & Milton 1995). Not only plant diversity is decreased by tilling/cultivation, but invertebrate diversity too. Recently cultivated lands in this area have an insect assemblage dominated by a single species of ant (*Anoplolepis steingroeveri*). Furthermore, insect diversity is positively correlated with perennial plant diversity, and negatively with annual plant diversity (Dean & Milton 1995). This implies that, as for perennial plant diversity, insect diversity will also steadily increase with time since cultivation.

If this area were to be managed purely for maximum biodiversity cultivation would be minimised, to maximise all forms of plant and invertebrate diversity. However, taking the economy of the region into account it is essential that some areas of mass flower displays are maintained. The question is how can this be done such that it has the least possible negative effect on biodiversity?

The focus of this study lies in the portion of Namaqua National Park that was formerly Skilpad Wildflower Reserve. The reserve lies on the edge of the escarpment near the small town of Kamieskroon, and was established with the express purpose of promoting the conservation of Namaqualand wildflower resources (van Rooyen, Theron & van Rooyen 1996).

Tilling is presently applied in Namaqua National Park, as a means to manage the flower display. If tilling does not take place *L. gnaphalodes* returns into the predominantly annual pioneer community quite quickly. It does not bear its flowers until after the annual wildflowers and its flowerless greyish-green appearance dulls the wildflower display. Though regular tilling can alleviate this problem, such high levels of disturbance are undesirable within a National Park where biodiversity conservation is a priority. By studying the population dynamics of this species and especially how it is affected by different management

practises (including tilling) and environmental conditions it was hoped that some compromises could be found between conservation and socio-economics.

Multivariate statistical modelling was used on collected field data to approach this problem because if a system can be successfully modelled it gives us the assurance that we understand the most important driving forces in the system (Cross & Moscardini 1985; Wiegand & Kellner 2000). This understanding gives managers the ability to, at least qualitatively, predict the system's response to different management strategies and thus plan management accordingly.

It was hypothesised that *L. gnaphalodes*' populations would be reduced by tilling, grazing or by a "dry spell" of several dry years in a row. Thus dry weather, when it occurs or grazing may be possible substitutes for the more disruptive practise of tilling. A model was constructed to test the validity of these hypotheses.

MATERIALS AND METHODS

The data utilised in the construction of the models was collected on experimental plots in Namaqua National Park. The nine experimental treatments were laid out in the same old field, such that environmental variation between treatments is minimal. The treatments differ on the basis of the frequency of tilling (soil disturbance) and the presence/absence of grazing animals (Table 1). All treatments were tilled the year before the study commenced. Annual surveys were conducted in each treatment during late August or early September, where the frequencies of the various plant species were determined using the step-point method with 200 points per treatment. At each point the nearest annual as well as the nearest perennial species were recorded. Thus the measurements of population size used for this models are the frequency (%) of *L. gnaphalodes* relative to the rest of the perennial community. Treatment 2 was not considered in these models, as it is a treatment not relevant to conservation management. Monthly precipitation data used were collected by the staff at the park. Monthly temperature data was obtained from the South African Weather Bureau for the nearest weather station at the town of Springbok.

TABLE 1: The nine different treatments in the experimental data used for the model

Treatment no.	Description
1	Grazed only (no soil disturbance)
2	Common agricultural practise: crop cultivation alternated with grazing
3	Tilled every fourth year & grazed
4	Tilled every second year & grazed
5	Tilled only once at the beginning of the study & grazed
6	Tilled every fourth year (not grazed)
7	Tilled every second year (not grazed)
8	Tilled only once at the beginning of the study (not grazed)
9	Undisturbed control treatment (no tilling, no grazing)

It was felt that the environmental data needed to be reduced before the model was constructed, so an oblique principal component cluster analysis was performed in SAS (Statistical Analysis Systems version 6.12, SAS Institute). In this technique variables are clustered on the basis of their correlation matrix into hierarchical groups that are progressively more highly correlated with each other. The monthly rainfall data as well as average monthly temperatures were analysed.

The aim of the model was to describe how various factors affect the population size of *L. gnaphalodes* as well as make short-term projections about future population sizes under various conditions. Multivariate stepwise linear regression was performed in SAS ((Statistical Analysis Systems version 6.12, SAS Institute) to determine the relationship between population size and the other factors. This is a procedure where the software automatically selects the variables that are significant at the 0.15 level of significance from a list of possible variables.

The regression analyses were run with four different sets of possible variables. These sets were compiled based on the results of the hierarchical cluster analysis and the factors/combinations of factors that ecological theory predicts may be important. The models are all forced through the origin since this produced more effective models.

The models were constructed on the data set excluding the data for 2001, the last year of the study. The values in 2001 were then predicted using the models and compared to the actual data by means of the mean absolute deviation (MAD) or mean absolute error (Kennedy 1992). MAD is the absolute difference between observed and predicted values averaged over all the values that were predicted, i.e. in this case all the values in 2001. MAD is a means of evaluating the predictive power of the models relative to one another. It was decided not to select one model but rather to weigh up the relative strengths and weaknesses of the models. This is seen by some as a more statistically sound approach because it takes a holistic view rather than looking at a limited number

of test statistics/indices/ (Johnson 1999). A demonstration of how mean absolute error can be used to compare the projection accuracy of different models can be found in Brewer *et al.* (1985).

Graphs of all the predicted and observed values are also presented for each model. Again these graphs are used to evaluate visually the effectiveness of the model in predicting the actual values.

The implications of the results for possible management strategies and the behaviour of the model are also analysed.

RESULTS

The results of the principal component analysis are displayed in the tree diagram Figure 1. Examining Figure 1 we observe that for all of the months bar four (January, May, September and November) the temperature and rainfall variables for the month are in the same cluster at the lowest level of the tree diagram. In the case of January, the variables are in the same cluster at the second from lowest level, but in the cases of May, September and November, the temperature and rainfall variables are separated at the highest level in the cluster analysis. Furthermore it is observed that in the case of January, May and November the rainfall variable for these months form a distinct cluster all on their own. Thus, disregarding them would affect the explanatory power of the model. On the other hand the temperature variables for all four months where temperature and rainfall are separated are in clusters which have other months' rainfall variables in them. For this reason it was decided to discard all the temperature variables and retain all the rainfall variables as the environmental variables with which to construct the models.

The stepwise regressions were then run on four different sets of variables and produced four different models (models A, B, C and D). The four different sets of variables are laid out in Table 2. All four sets include the previous year's population size, tilling in the present and previous year and grazing in the present year as variables. The previous year's population size is in percentage frequency

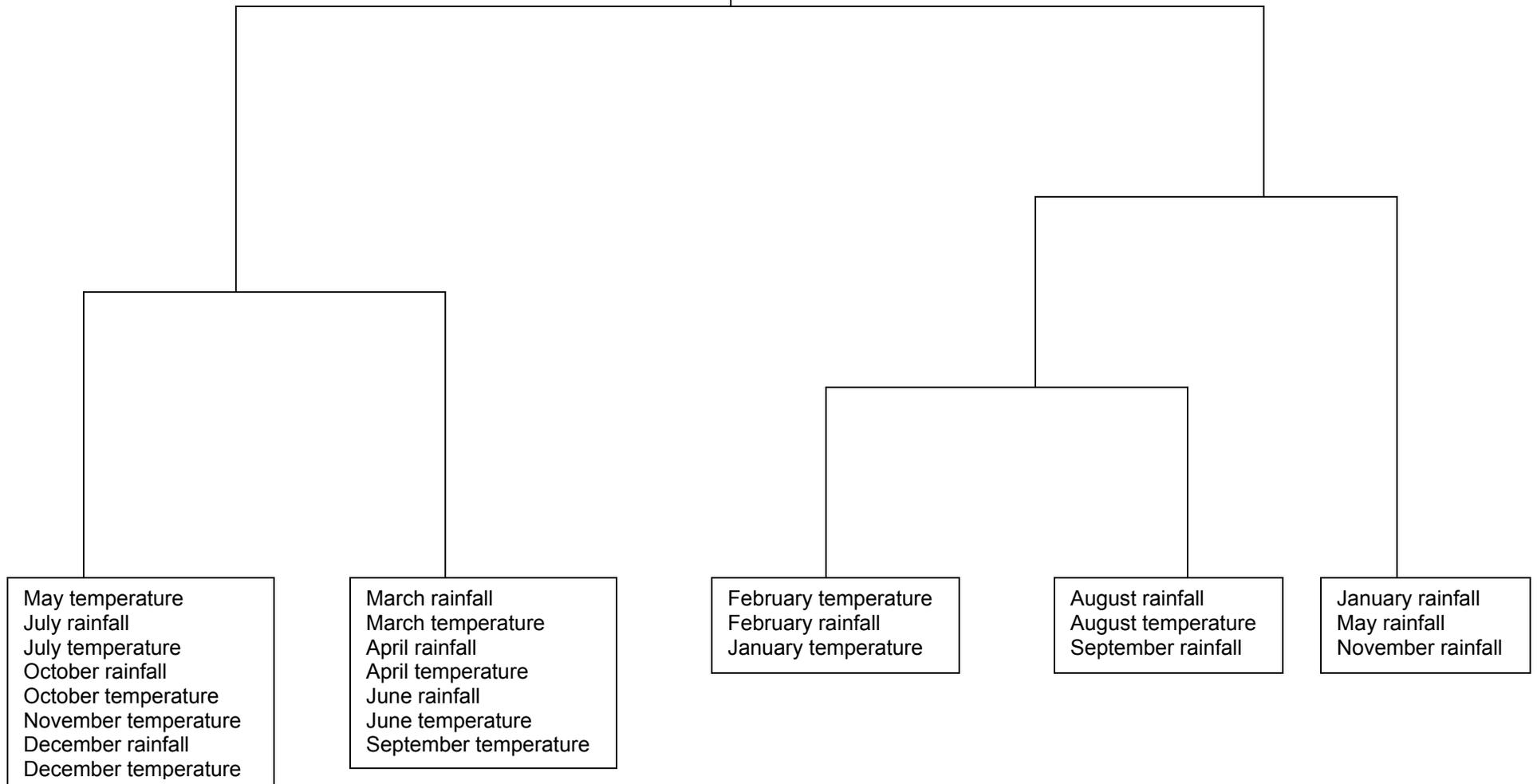


FIGURE 1: Tree diagram displaying the results of a oblique principal component cluster analysis performed on the environmental variables, namely monthly rainfall and average monthly temperature. The data is initially divided into three clusters, which explain 63% of the variance, then into four which explain 67% and five which explain 72%.

TABLE 2: The four different sets of variables used in the stepwise regressions to construct the models

Model	A	B	C	D
Variables	<ul style="list-style-type: none"> ◆ Previous year's population size ◆ Tilling in current year (t) ◆ Previous year's tilling (t-1) ◆ Grazing ◆ Total summer rainfall* ◆ Total winter rainfall** 	<ul style="list-style-type: none"> ◆ Previous year's population size ◆ Tilling in current year (t) ◆ Previous year's tilling (t-1) ◆ Grazing ◆ Seedbank size ◆ Total winter rainfall 	<ul style="list-style-type: none"> ◆ Previous year's population size ◆ Tilling in current year (t) ◆ Previous year's tilling (t-1) ◆ Grazing ◆ January rainfall ◆ February rainfall ◆ March rainfall ◆ April rainfall ◆ May rainfall ◆ June rainfall ◆ July rainfall ◆ August rainfall ◆ September rainfall ◆ October rainfall ◆ November rainfall ◆ December rainfall 	<ul style="list-style-type: none"> ◆ Previous year's population size ◆ Tilling in current year (t) ◆ Previous year's tilling (t-1) ◆ Grazing ◆ Seedbank size ◆ April rainfall ◆ May rainfall ◆ June rainfall ◆ July rainfall ◆ August rainfall ◆ September rainfall

*Summer is taken as October to March inclusive.

**Winter is taken as April to September inclusive.

and tilling and grazing are binary variables with a value of one if the area was tilled/grazed and a value of zero if it was not. Set A and C then include rainfall as additional variables, with set A using total seasonal rainfall for the winter and summer months and set C using each month's mean rainfall as a variable. Sets B and D replace the summer rainfall component(s) of set A and C with seedbank size and again B uses seasonal rainfall where D uses monthly rainfall. Rainfall is measured in millimetres (mm) and seedbank size in seeds per square metre (seeds/m²).

The regressions were then run both allowing the model to have an intercept and forcing them through the origin. The results where models were forced through the origin were far superior and the four models produced by these regressions are given here:

$$\mathbf{A: } P_{t,A} = 0.77P_{t-1} - 40.41tilling_t + 0.13summrain_t + 0.06wintrain_t \quad (R^2 = 0.91)$$

$$\mathbf{B: } P_{t,B} = 0.81P_{t-1} - 38.02tilling_t + 0.10wintrain_t \quad (R^2 = 0.90)$$

$$\mathbf{C: } P_{t,C} = 0.22P_{t-1} - 48.70tilling_t - 0.74octrain_t + 0.75novrain_t \\ + 1.30febrain_t + 0.34junrain_t + 0.37seprain_t \quad (R^2 = 0.95)$$

$$\mathbf{D: } P_{t,D} = 0.74P_{t-1} - 34.04tilling_t + 1.35aprrain_t + 0.27seprain_t \quad (R^2 = 0.92)$$

Where

- $P_{t,I}$ is the population frequency in the current year as predicted by model I; P_{t-1} is the size of the population (frequency as percentage) measured in the previous year;
- $tilling_t$ is a binary variable indicating whether or not the area was tilled during the summer since the population was last measured;
- $summrain_t$ is the total rainfall over the summer since the population was last measured;
- $wintrain_t$ is the total rainfall over the winter since the population was last measured; and
- $octrain_t$, $novrain_t$, $febrain_t$, $aprrain_t$, $junrain_t$, and $seprain_t$ are the monthly average rainfall for the months of October, November, February, April, June and September respectively,

All of these values are taken in the year since the population was last measured. The current year, denoted by t , is taken to have started in the October of the previous calendar year and run through to the September of the current calendar year. The frequency of *L. gnaphalodes* is measured every year in September.

When the four models given above were used to predict the population frequency in 2001 the MAD for each of the four models' predictions is shown in Table 3. The standard deviations on the absolute errors are also shown in Table 3.

Figure 2 (a) through (d) shows graphs of the actual population frequencies and the population frequencies predicted by models A through D respectively. It is observed that all of the models follow the actual population quite closely, but that at some points population frequencies above 100% or below 0% were predicted. It should be noted that for the purposes of management these values should be rounded off to 100% or 0% respectively.

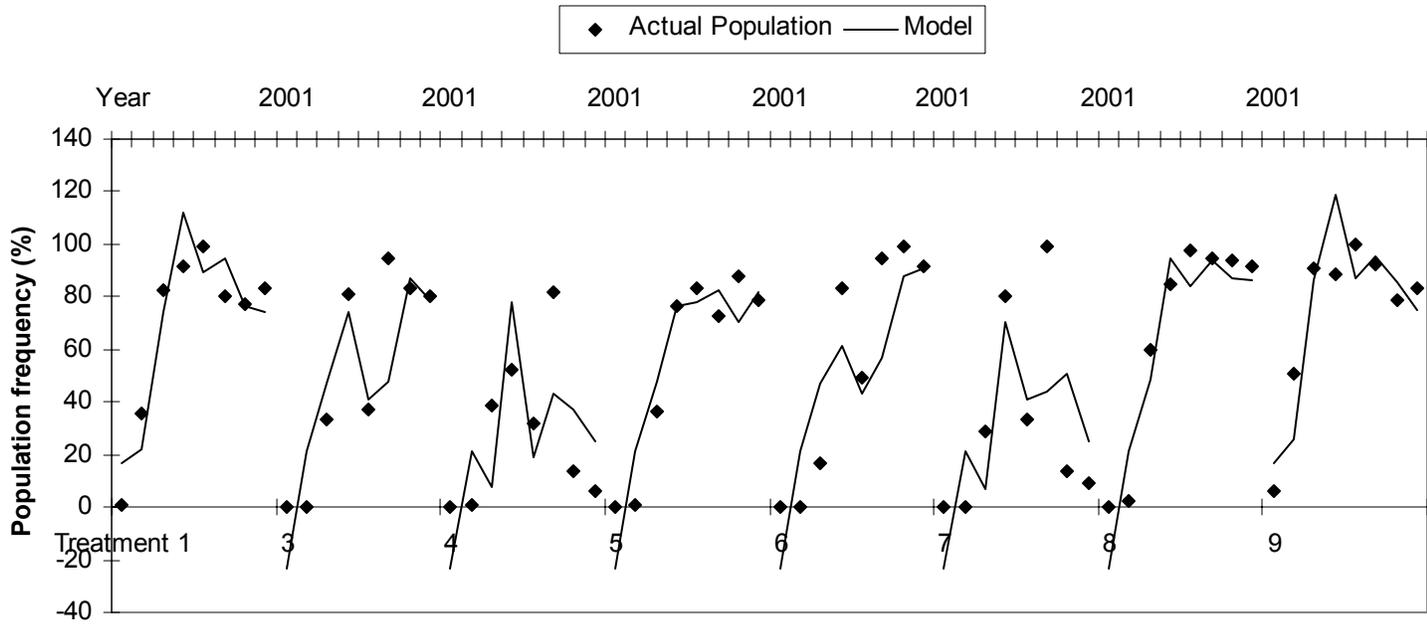
DISCUSSION AND CONCLUSIONS

As stated in the results, the tree diagram in Figure 1 shows that the rainfall and temperature variables for each month are generally highly correlated with one another. This makes ecological sense because of the climate of the region: In the winter months, the rainy season in Namaqualand, the rain is brought by cold fronts, so when it rains it gets cold, or when it gets cold it rains. In the summer months rainfall events are very rare, if they occur at all, but if they occur they will also cause a change in temperature because they are associated with cloud cover which cools the hot, arid, conditions. The moisture in the air may also regulate the daily temperature oscillations. For this reason the results were deemed realistic and it was decided that only rainfall variables would be used in the regression.

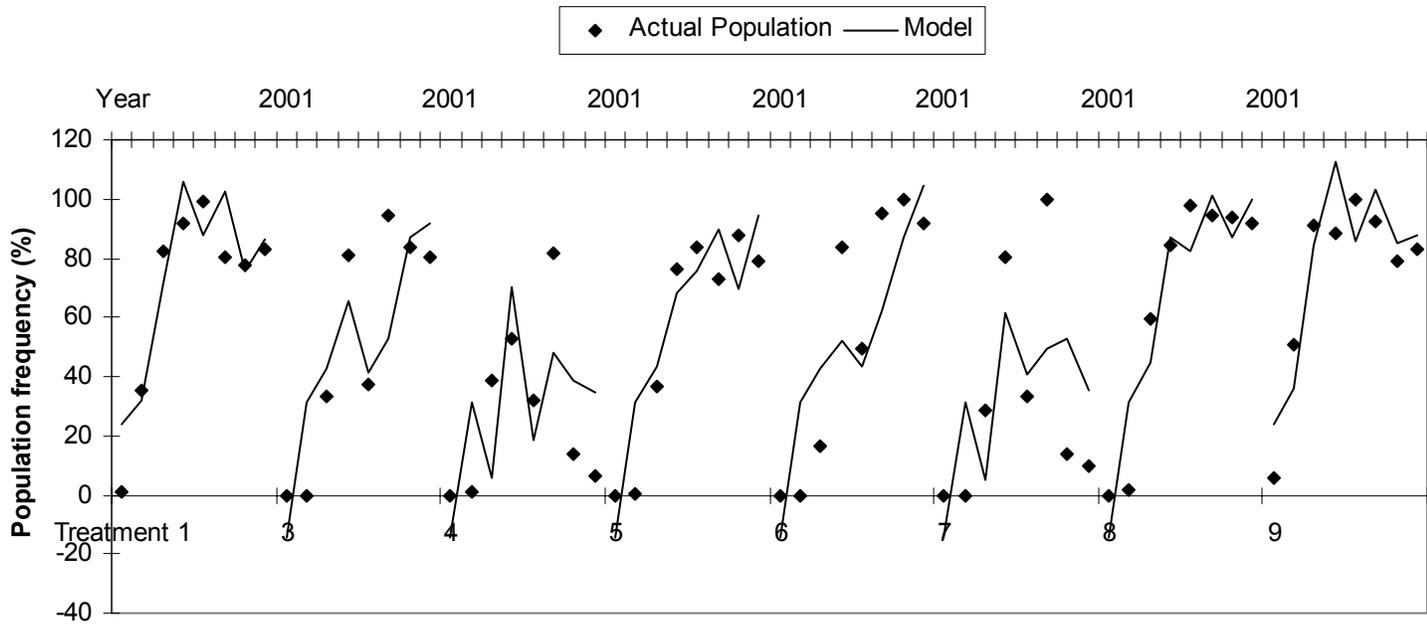
It was further decided that either summer rainfall or seedbank size should be included in a model because they are likely to be inter-related. Seeds are

TABLE 3: The mean absolute deviation (MAD) for the model predictions of models A, B, C and D in the year 2001. The data for the year 2001 was not included in the data set used to perform the regressions, so these predictions are extrapolations

Model	A	B	C	D
Mean absolute deviation (MAD)	7.63	13.77	46.16	10.88
Standard Deviation on Absolute Error	6.42	9.11	27.83	5.63

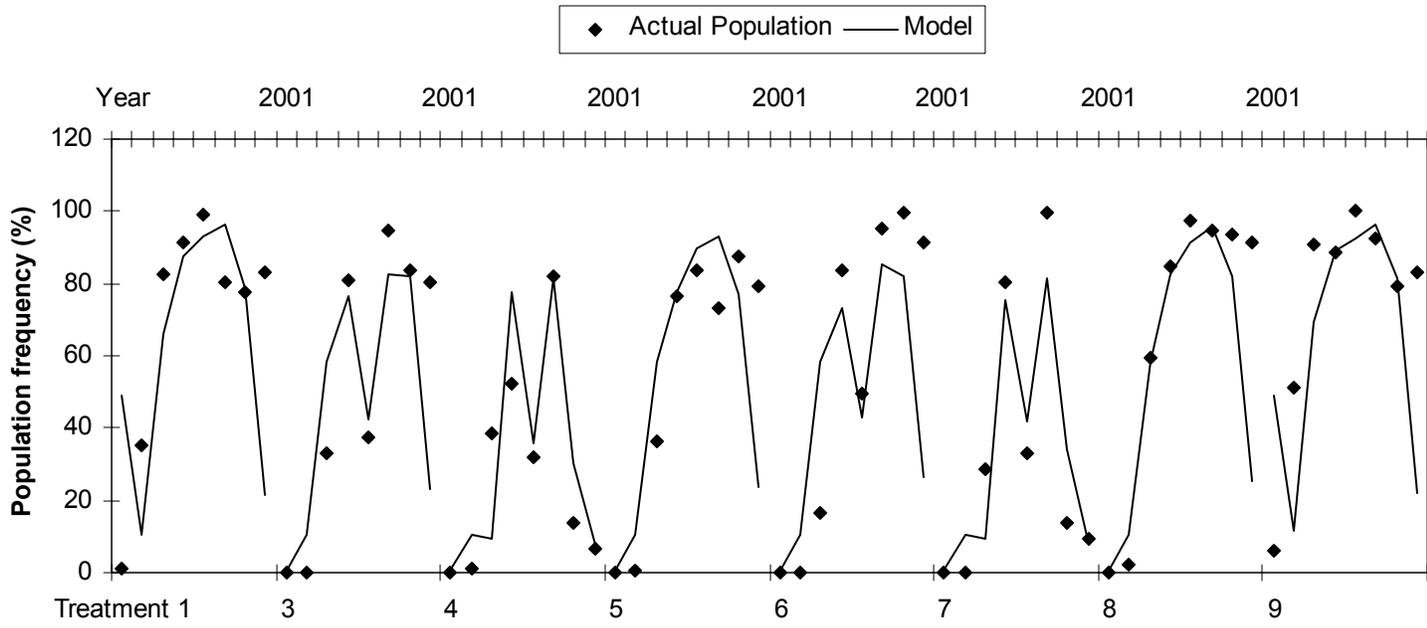


(a) Model A

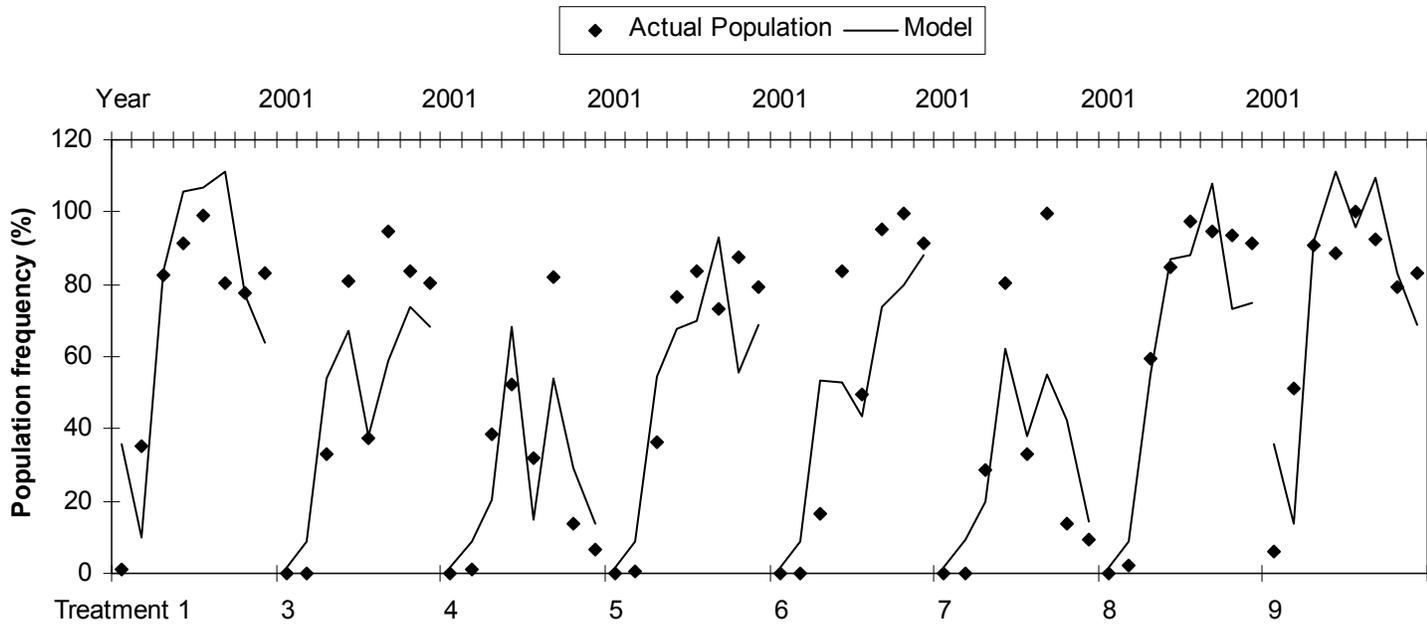


(b) Model B

FIGURE 2: Graphs of predicted and observed population frequency (%) against time over all eight treatments for each of the four different models.



(c) Model C



(d) Model D

formed during the early summer months (October to December) and thus the rainfall at this time is likely to have a large impact on seed production. If there is no rainfall the plants may die before even producing seeds. For this reason, seedbank size was included in the possible set of variables for models B and D and summer rainfall for models A and C. Winter rainfall was included in all the sets of variables as this is renowned as the main determinant of the vegetation cover in Namaqualand.

Looking at the four models one sees that the R^2 values for all four lie between 0.90 (model B) and 0.95 (model C). We could say, based on R^2 value, that model C is the best model, but actually all of these models have very high R^2 values and the differences between them are relatively negligible.

Looking at the model's predictive power tells a different story. Models A, B and D all make relatively good predictions whereas model C makes very poor predictions (Table 3). This appears to be a classic case of fitting the data too well within the sample and not being able to predict effectively out of the sample.

The graphs of the actual and predicted population frequencies in Figure 2 tell a very similar story. It should be noted that the predictions for the year 1994 are rather inaccurate for all of the models. This is most likely because in 1994 there was no data available on the previous year's population frequency, an important parameter in the model. The graph of model C (Figure 2 (c)) clearly shows that it generally underestimates the population in 2001, explaining its high MAD value. Other than this it is difficult to distinguish which model may be stronger or weaker from the graphs, they all appear fairly equal.

Looking at the equations for models A through D given above we see that all of them have a positive coefficient between 0 and 1 for the previous year's population. This can be interpreted as meaning that a certain proportion of the previous year's population survives to the current year. Since *L. gnaphalodes* is a perennial plant, this is entirely plausible. Furthermore, the models all have a negative coefficient between -34 and -49 for tilling, suggesting that tilling reduces the population by between 34 and 49 percentage points. It is noted that neither grazing, the previous year's tilling nor the seedbank size was included in any of

the final models. This indicates that they are not important in determining the population size of *L. gnaphalodes*.

The coefficients for the rainfall variables in the models are all positive except for the coefficient of October's rainfall in model C that is negative. Positive rainfall coefficients make ecological sense since the more rain there is the better one expects the plants to grow/reproduce and hence the larger the population. The negative coefficient for October's rainfall in model C cannot be explained in terms of the theory and this is taken as a further indication that this model is not as good as the others.

In selecting a model for use as a management tool we consider all of the above factors. Model C is definitely not a good choice because despite its high R^2 value its predictive power is very poor and it contains many variables making it cumbersome to use. Models A and D appear to be the best options, although B is not far behind, they are slightly superior in both R^2 and predictive power. An advantage of model B is that it only contains three variables, but its predictive power is a problem. Model D is superior to model A in that it uses data that can be collected at very specific times of year. Data need only be collected during April, September and the time of tilling. This makes it an ideal model for managers who are not permanently stationed in the area. Model A on the other hand requires that rainfall records be kept for the entire year. Model B is intermediate in this regard, requiring records for the entire winter but not the summer months.

The management implications of models A and D are qualitatively identical. The present year's population of *L. gnaphalodes* can be kept small by one of three things:

- (i) The previous year's population being small;
- (ii) Tilling the land; and
- (iii) Relatively low rainfall.

Number (iii) is, firstly, out of a manager's control and, secondly, undesirable because it will result in a poor flower display. Thus, only points (i) and (ii) are considered further. Point (i) is best achieved by a consistent management

approach that keeps the population of *L. gnaphalodes* at low levels. Point (ii) is thus the most effective tool to reduce the population.

Tilling is thus confirmed as the only practical management action that can be used to reduce the population of *L. gnaphalodes* in Namaqualand. Grazing, which was also hypothesised to have this effect was shown to be ineffective. A “dry spell” of several years of low rainfall would most probably also work but is not under a manager’s control.

REFERENCES

- ANDERBERG, A.A. & BREMER, K. 1991. Parsimony analysis and cladistic reclassification of the Reophalis generic group *Asteraceae, Gnaphalieae . *Annals of the Missouri Botanical Gardens* **78**:1061-1072.
- BREWER, J.A., BURNS, P.& CATO, Q.V. 1985. Short-term projection accuracy of five asymptotic height-age curves for Loblolly Pine. *Forest Science* **31**:414-418.
- CROSS, M. & MOSCARDINI, A.O. 1985. *Learning the art of mathematical modelling*. Ellis Horwood Ltd., Chichester.
- DEAN, W.R.J. & MILTON, S.J. 1991a. Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: Mammal diggings as germination sites. *African Journal of Ecology* **29**:11-16.
- DEAN, W.R.J. & MILTON, S.J. 1991b. Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* **20**: 231-237.
- DEAN, W.R.J. & MILTON, S.J. 1995. Plant and insect assemblages on old fields in the arid southern Karoo, South Africa. *African Journal of Ecology* **33**: 1-13.
- JOHNSON, D.H. 1999. The insignificance of statistical significance. *Journal of Wildlife Management* **63**:763-772.
- KENNEDY, P, 1992. *A Guide to Econometrics* (3rd edition) pp. 271. MIT Press, Cambridge.
- LE ROUX, A. & VAN ROOYEN, G. 1999. Succulent Karoo. In: J. Knobel (ed.) *The Magnificent Natural Heritage of South Africa*, pp. 94-107. Sun Bird Publishing, Cape Town.
- LOVEGROVE, B. 1993. *The living deserts of Southern Africa*, Longmans, London.
- MILTON, S. & DEAN, R. 1991. Disturbances in dune grassland: Colourful consequences of clearing. *African Wildlife* **45**:199-203.
- MILTON, S.J., YEATON, R.I., DEAN, W.R.J. & VLOK, J.H.J. 1997. *Succulent Karoo*. In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.) *Vegetation of Southern Africa*, pp. 131-166, Cambridge University Press, Cambridge

- RÖSCH, H., VAN ROOYEN, M.W. & THERON, G.K. 1997. Community-level competition between five Namaqualand pioneer plant species. *South African Journal of Botany* **63**:1-3.
- VAN ROOYEN, G., STEYN, H. & DE VILLIERS, R. 1999. *Cederberg, Clanwilliam & Biedouw Valley: South African Wild Flower Guide 10*. Botanical Society of South Africa, Kirstenbosch.
- VAN ROOYEN, M.W. 1999. Functional aspects of short-lived plants. In: W.R.J. Dean & S.J. Milton (eds.) *The Karoo – ecological patterns and processes* pp. 107-122. Cambridge University Press, Cambridge.
- VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N.. 1996. Skilpad Wildflower Reserve – A flower-lover's paradise. *Veld & Flora* **82**:40-42.
- WIEGAND, T. & KELLNER, K. 2000. *Workshop at the 26th annual congress of the South African Association of Botanists: The role of models in long-term ecological research*, Unpublished report of abstract, January 2000, Potchefstroom University for Christian Higher Education, Potchefstroom.

Chapter 5: **Conclusion**

In this dissertation two different modelling approaches were used to find the optimal management strategy for the control of encroachment by *Leysera gnaphalodes* in Namaqualand. This discussion focuses on the concurrence, or otherwise, between the results of the two models and the relative strengths and weaknesses offered by the two approaches.

In developing management strategies for *L. gnaphalodes* our goal is not only to reduce the encroachment by this species, but also to minimise disturbance of the landscape in the process. It was hypothesised that *L. gnaphalodes*' populations would be reduced by tilling, grazing or by a "dry spell" of several years in a row with relatively low rainfall. Thus dry weather, when it occurs or grazing may be possible substitutes for the more disruptive practise of tilling.

The mathematical model discussed in chapter three recommended that to minimise populations of *L. gnaphalodes* the area should be tilled whenever the population reaches or exceeds 45%. The area can also be tilled at regular intervals in addition to whenever the population is or exceeds 45%. This model gives us a clear understanding of exactly what factors reduce populations of *L. gnaphalodes*, and allows us to clearly see what the most effective yet least disturbance-intensive management strategy would be. The model describes *L. gnaphalodes* as growing along a logistic curve, and thus the present year's population can be kept low by keeping the previous year's population low. Thus, it is generally recommended to keep the population levels as low as possible at all times. The model further shows that tilling only has an effect if the population exceeds 45%, and thus it is clear that tilling more frequently is not necessarily beneficial. Further, the model tells us that low rainfall can reduce the population, but only if the lands have been tilled at two-year intervals during the preceding

years or the population has been consistently low. Thus these two factors are combined and full use is made of all the means at our disposal.

The statistical models in chapter four indicate that the present year's population of *L. gnaphalodes* can be kept small by one of three things:

- (i) The previous year's population being small;
- (ii) Tilling the land; and
- (iii) Relatively low rainfall.

Point (i) is best achieved by a consistent management approach that keeps the population of *L. gnaphalodes* at low levels. Tilling (point (ii)) is thus the most effective tool to reduce the population. Low rainfall, as mentioned in point (iii) can also be used, but is not under the control of the manager.

At this point it is pertinent to note that both of the models highlight basically the same factors as being effective in controlling populations of *L. gnaphalodes* – consistent good management, tilling and low rainfall. Grazing, which was originally hypothesised to also have an effect in controlling these populations, was shown to be ineffective by both models. Thus the results rendered by the two models concur strongly.

A striking difference between the models is the level of understanding they provide about exactly how these factors act and interact. The statistical model merely tells one which factors reduce the population, and more or less by how much. It gives us no indication of how these factors can optimally be applied in controlling the population. It also gives no indication of how the factors may, or may not, interact with one another. In contrast, the mathematical model allows one to clearly see under exactly what circumstances each factor is effective, how they can optimally be applied and how they interact with each other. This is a clear strength of mechanistic mathematical modelling over statistical regression analyses. It should be mentioned, however, that statistical modelling holds the advantage of being much easier to apply, requiring less specialised expertise and that there are many easily used software packages that assist in this process.

Constructing these models provided many interesting insights into these two different approaches. Mathematical models are constructed in a much less structured manner. The modeller identifies a pattern or phenomenon and tries to explain its formation. Mathematical models are generally tested by plotting graphs of the observed and expected values and visually examining their agreement. At first, this method appears rather subjective and makes statistical modelling seem more objective or scientifically sound. After all, statistical models are constructed by set techniques with very clear statistical indices to tell one how good the model is.

One does not have to look far to find criticisms of the objective statistics that science often clings to. Anderson *et al.* (2000), Johnson (1999) and Parkhurst (2001) all give substantial criticisms of the use of statistical hypothesis testing and statistical significance levels in ecology. For example Johnson (1999) points out that using a no effect null hypothesis that is known to be false (which is often the case in ecology) is erroneous because altering the sample size can cause the null hypothesis to be accepted or rejected. Furthermore, using fixed alpha levels for when hypotheses are accepted/rejected as so-called objective tests is often problematic because not all the requirements of the tests are met and so the test results are somewhat inaccurate.

Statistical hypothesis testing or significance is not the issue here. These are merely examples of how techniques that are widely seen as reliable can indeed be problematic. It is true that many of the criticisms of statistical tests stem from their misuse rather than their intrinsic value (Johnson 1999). However, it quickly becomes clear that avoiding such misuses in sciences like ecology can be very difficult.

In ecology, which deals with highly interconnected complex systems, which are innately non-linear, the use of statistical techniques that are often essentially linear can be highly unsatisfactory. Furthermore, our data sets tend to be relatively small in statistical terms, precluding the use of many techniques. Thus, more non-linear, mechanistic techniques should be given reasonable consideration, even if they are slightly more subjective. Johnson (1999) points

out that traditional hypothesis tests are ideally suited to the hard sciences like physics and chemistry and must be applied differently in soft sciences like ecology, psychology and education. According to Anderson *et al.* (2000) the ecological sciences have lagged behind in the discussion of null hypotheses and their statistical significance. This is something that should surely be rectified, that some of the myths about statistics in general can be rectified.

Johnson (1999) is of the opinion that statistical hypotheses tests should be regarded only as a piece of evidence in deciding about a scientific hypothesis. Results that are not statistically significant should also be reported, as non-significant effects can also be important (Parkhurst 2001). Many of the statistical techniques used regularly are in fact poorly understood and easily misused. Would an easily understood technique like drawing a graph not sometimes be preferable? Even if it is somewhat subjective?

REFERENCES

- ANDERSON, D.H., BURNHAM, K.P. & THOMPSON, W.L. 2000. Null hypothesis testing: Problems, prevalence, and alternative. *Journal of Wildlife Management* 64:912-923.
- JOHNSON, D.H. 1999. The insignificance of statistical significance. *Journal of Wildlife Management* 63:763-772.
- PARKHURST, D.F. 2001. Statistical significance tests: Equivalents and reverse tests should reduce misinterpretation. *BioScience* 51:1051-1057.

Summary:

Modelling population dynamics of *Leysera gnaphalodes* in Namaqualand, South Africa

by

Jessica Kate Conradie

Supervisor: Prof. M.W. van Rooyen

Submitted in partial fulfilment of the requirements for the degree Magister Scientiae

Department of Botany, University of Pretoria, Pretoria

Namaqualand is world renowned for its mass displays of annual wildflowers occurring in highly disturbed areas. *Leysera gnaphalodes* is a short-lived perennial shrub that encroaches into this wildflower display, lessening the aesthetic appeal. For this reason populations of *L. gnaphalodes* need to be kept as small as possible. This is usually achieved by tilling the area regularly, but a less disruptive method would be preferable. Alternatives to this approach are explored.

The effect of many interacting factors needed to be examined over long periods of time so that alternative management strategies could be evaluated. Ecological modelling was used as it is ideally suited to this purpose. A review of modelling and its application in ecology is given, which includes a description of the modelling process and a discussion of different types of models and their applications.

It was hypothesised that grazing and low rainfall, in addition to tilling, could control the population size of *L. gnaphalodes*. Data was used from an eight-year study conducted to determine the effects of tilling, grazing and environmental factors on the seedbank and population size of *L. gnaphalodes*.

A rule-based mechanistic mathematical model based on the logistic growth curve was constructed to describe the population dynamics of this species. The model-fit was evaluated using Pearson's correlation coefficients and graphs, and it proved to be a good model. Tilling and low rainfall were both

found to be effective in reducing populations of *L. gnaphalodes* but grazing had no reducing effect. Simulations based on the model were run to test three different basic management strategies under stochastic rainfall conditions. The management strategy, which most effectively controlled the population was to till the lands whenever the population of *L. gnaphalodes* reaches or exceeds a relative frequency of 45%.

Multivariate statistical models were constructed to determine the effects of all of these factors on the population of *L. gnaphalodes*. Tilling was confirmed to be effective in reducing the population, but grazing was found to have no effect. Low rainfall was also effective in controlling the population but has the disadvantages of being out of management control and also affecting the desirable wildflowers.

Acknowledgements

I would like to thank the National Research Foundation and the University of Pretoria for funding. I would further like to thank the University of Pretoria, and in particular the Botany department for the use of their facilities and for providing a stimulating and enjoyable environment in which to work.

I would like to thank my supervisor professor Gretel van Rooyen for sharing her wealth of knowledge and experience so freely and with such humility. I would also like to thank her for supplying the experimental data I used to construct my models. Also for her unending support and encouragement and her wonderful sense of humour.

I would like to thank all of the staff and postgraduate students in the Vetman building for all of their assistance and input, and for being wonderful colleagues and friends whose company and camaraderie I have much enjoyed. Specifically, I would like to thank Miranda Deutschlander for doing the layout on a poster on this work for me.

I would like to thank Hermi Borain and Rina Owen of the Department of Statistics at the University of Pretoria for their technical input and assistance with the statistical analyses.

I would like to thank the staff at Namaqua National Park, and particularly Matthew Norval for hosting the experimental plots and providing rainfall data and other information.

I would like to thank my friend, Marc' Ground for his unending support, emotional and statistical. For all of the hours he patiently listened to my wanderings over how I should do things and my complaints when they didn't work. I hope I shared enough of the successes too! His friendship is invaluable.

I would also like to thank my friend Ina Venter for her assistance and encouragement. For making me laugh and always being available to sympathise with my frustrations. Her friendship too, is a blessing to me.

I would like to thank my boyfriend, Andre' Grobler for his tolerance, love and support. I believe I was nothing less than intolerable at times while I was writing this dissertation, and he just kept on relentlessly trying to make me feel better. Also for encouraging me when I was despondent, always believing in me and for our wonderful discussions about ecological theory and practise. I want him to know that I really appreciate it and love him deeply.

I would like to thank my dear father Simon Conradie and brother James Conradie for their support and tolerance too. And my father in particular for board, lodging and supplementary funding!

Last, but definitely not least I would like to thank all of the rest of my friends and family for their support and encouragement, whether big all small. I really appreciate all of it, and love you all dearly.

References

- ANDERBERG, A.A. & BREMER, K. 1991. Parsimony analysis and cladistic reclassification of the Rephalis generic group *Asteraceae, Gnaphalieae . *Annals of the Missouri Botanical Gardens* **78**:1061-1072.
- BALZTER, H. 2000. Markov chain models for vegetation dynamics. *Ecological Modelling* **126**:139-154..
- BALZTER, H., BRAUN, P.W. & KOHLER, W. 1998. Cellular automata models for vegetation dynamics. *Ecological Modelling* **107**:113-125.
- BASSON, M., REDDINGTON, J. R. & MAY, R. 1991. An assessment of the maximum sustainable yield of ivory from African elephant populations. *Mathematical Biosciences* **104**:73-95.
- BOLKER, B.M. & PACALA, S.W. 1998. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. *The American Naturalist* **153**:575-602.
- BREWER, J.A., BURNS, P.& CATO, Q.V. 1985. Short-term projection accuracy of five asymptotic height-age curves for Loblolly Pine. *Forest Science* **31**:414-418.
- BUGMANN, H.K.M. 1996. A simplified forest model to study species composition along climate gradients. *Ecology* **77**:2055-2074.
- BURDEN, R.L. & FAIRES, J.D. 2001. *Numerical Analysis* (7th ed.), Brooks/Cole Publishing Company, Pacific Grove.
- CALOIN, M. & YU, O. 1982. An extension of the logistic model of plant growth. *Annals of Botany* **49**:599-607.
- CANTRELL, R.S. & COSTER, C. 1989. Diffusive logistic equations with indefinite weight: population models in disrupted environments. *Proceedings of the Royal Society of Edinburgh, Section A: Mathematics* **112**:293-318.
- CASEBOLT, D. 1986. Analysis of primate population data using logistic regression and loglinear models. *American Journal of Primatology* **10**:383.
- CHUINE, I., COUR, P. & ROUSSEAU, D. D, 1999. Selecting models to predict the timing of flowering of temperate trees: Implications for tree phenology modelling. *Plant, Cell & Environment* **22**:1-13.
- CROSS, M. & MOSCARDINI, A.O. 1985. *Learning the art of mathematical modelling*. Ellis Horwood Ltd., Chichester.
- CUI, J. & CHEN, L. 1998. The effect of diffusion on the time varying logistic population growth. *Computational Mathematics and Applications* **36**:1-9.

- DE GEE, M. & GRASMAN, J. 1998. Sustainable yields from seasonally fluctuating biological populations. *Ecological Modelling* **109**:203-212.
- DEAN, W.R.J. & MILTON, S.J. 1991a. Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: Mammal diggings as germination sites. *African Journal of Ecology* **29**:11-16.
- DEAN, W.R.J. & MILTON, S.J. 1991b. Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* **20**, 231-237.
- DEAN, W.R.J. & MILTON, S.J. 1995. Plant and insect assemblages on old fields in the arid southern Karoo, South Africa. *African Journal of Ecology* **33**:1-13.
- EKSCHMITT, K. & BRECKLING, B. 1994. Competition and coexistence, the contribution of modelling to the formation of ecological concepts. *Ecological Modelling* **75/76**:71-82.
- ERIKSON, O. 1997. Colonization dynamics and relative abundance of three plant species (*Antennaria dioica*, *Hieracium pilosela* and *Hypochoeris maculata*) in dry semi-natural grasslands. *Ecography* **20**:559-568.
- FULDA, J.G. 1981. The logistic equation and population decline. *Journal of Theoretical Biology* **91**:255-259.
- GINO, H. & SENO, H. 1997. Transition matrix modelling on disturbance-controlled persistence of plant population. *Ecological Modelling* **94**:207-219.
- GOPALSAMY, K. 1980. Optimal stabilisation and harvesting in logistic population models. *Ecological Modelling* **11**:67-69.
- GOTELLI, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.
- GRIMM, V. 1994. Mathematical modelling and understanding in ecology. *Ecological Modelling* **15**:641-651.
- GUJJURATI, D. N. 1995. *Basic Econometrics* (3rd ed.) pp. 77 & 767. McGraw-Hill Book Co., Singapore.
- HALLAM, T.G., & LEVIN, S.A. (eds.). 1986. *Biomathematics volume 1: Mathematical Ecology*. Springer-Verlag, Berlin, Heidelberg.
- HANSEN, T.F., STENSETT, N.C., HUNTONEN, H. & TAST, J. 1999. Interspecific and intraspecific competition as causes of direct and delayed density-dependence in a fluctuating vole population. *Proceedings of the National Academy of Science of the United States of America* **96**:986-991.
- HANSON, F.B. & TUCKWELL, H.C. 1997. Population growth with randomly distributed jumps. *Journal of Mathematical Biology* **26**:169-187.
- HAYDON, D.T. 2000. Maximally stable model ecosystems can be highly connected. *Ecology* **81**:2631-2636.

- HOBBS, R.J. & LEGG, C.J. 1983. Markov models and initial floristic composition in heathland vegetation dynamics. *Vegetatio* **56**:31-43.
- HUGHES-HALLETT, D., GLEASON, A.M., LOCK, P.F., FLATH, D., GORDON, S.P., LOMEN, D.O. & LOVELOCK, D. 1997. *Brief calculus for business, social sciences and life sciences* (preliminary edition) pp. 234-248. John Wiley & sons Ltd., Brisbane.
- HUISMAN, J. & WEISSING, F.J. 2001. Biological conditions for oscillations and chaos generated by multi-species competition. *Ecology* **28**:2682-2695.
- INGHE, O. 1990. Computer simulations of flowering rhythms in perennials – is there a new area to explore in the quest for chaos? *Journal of Theoretical Biology* **147**:449-469.
- JELTSCH, F., MILTON, S. J., DEAN, W. R. J. & VAN ROOYEN, N. 1996. Tree spacing and coexistence in semi-arid savannahs. *Journal of Ecology* **84**:583-595.
- JELTSCH, F., MILTON, S.J., DEAN, W.R.J. & VAN ROOYEN, N. 1997a. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* **8**:177-188.
- JELTSCH, F., MILTON, S.J., DEAN, W.R.J. & VAN ROOYEN, N. 1997b. Analysing shrub encroachment in the southern Kalahari: a grid-based approach. *Journal of Applied Ecology* **34**:1497-1508.
- JOHNSON, D.H. 1999. The insignificance of statistical significance. *Journal of Wildlife Management* **63**:763-772.
- JOLICOEUR, P. & PONTIER, J. 1989. Population growth and decline: a four-parameter generalization of the logistic curve. *Journal of Theoretical Biology* **141**:563-571.
- JORGENSEN, S.E. 1994. *Developments in environmental modelling 19 – Fundamentals of ecological modelling*. Elsevier, Amsterdam.
- KENNEDY, P, 1992. *A Guide to Econometrics* (3rd edition) pp. 271. MIT Press, Cambridge.
- KINGSLAND, S. 1982. The refractory model: The logistic curve and the history of population ecology. *Quarterly Review of Biology* **57**:29-51.
- LE ROUX, A. & VAN ROOYEN, G. 1999. Succulent Karoo. In: J. Knobel (ed.) *The Magnificent Natural Heritage of South Africa*, pp. 94-107. Sun Bird Publishing, Cape Town.
- LEFEVER, R., LEJEUNE, O. & COUTERON, F. 1998. Generic modelling of vegetation patterns: A case study of *Tiger Bush* in sub-saharian Sahel. *Proceedings of the workshop on pattern formation and morphogenesis: Model systems*. University of Minnesota, Minneapolis.
- LEKANG, S., DEHARVENG, L. & LEK, S. 1999. Predictive models of the Collembolan diversity and abundance in a riparian habitat. *Ecological Modelling* **120**:247-260.
- LOVEGROVE, B. 1993. *The living deserts of Southern Africa*, Longmans, London.
- MARCATI, P. 1982. On the global stability of the logistic age-dependent population growth. *Journal of Mathematical Biology* **15**:215-226..

- MCALLISTER, M.K & KIRKWOOD, G.P. 1998. Bayesian stock assessment – a review and example application using the logistic model. *ICES Journal of Marine Science* **55**:1031-1060.
- MICKENS, R.E. 1988. Exact solutions to a population model: The logistic equation with advection. *SIAM Review* **30**:629-633.
- MILTON, S. & DEAN, R. 1991. Disturbances in dune grassland: Colourful consequences of clearing. *African Wildlife* **45**:199-203.
- MILTON, S.J., YEATON, R.I., DEAN, W.R.J. & VLOK, J.H.J. 1997. *Succulent Karoo*. In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.) *Vegetation of Southern Africa*, pp. 131-166, Cambridge University Press, Cambridge
- NORDEN, R.H. 1982. On the distribution of the time to extinction in the stochastic logistic population model. *Advances in Applied Probability* **14**:687-708.
- O'CONNOR, T.G. 1993. The influence of rainfall and grazing on the demography of some African savannah grasses: A matrix modelling approach. *Journal of Applied Ecology* **30**:119-132.
- PARKHURST, D.F. 2001. Statistical significance tests: Equivalents and reverse tests should reduce misinterpretation. *BioScience* **51**:1051-1057.
- PAUSAS, J.G. 1999b. Mediterranean vegetation dynamics: Modelling problems and functional types. *Plant Ecology* **140**:27-39.
- PAUSAS, J.G. 1999a. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems – A simulation approach. *Journal of Vegetation Science* **10**:717-722.
- POULSEN, E.T. 1979. A model for population regulation with density- and frequency-dependent selection. *Journal of Mathematical Biology* **8**:325-343.
- PRAJNESHU 1980. Time-dependent solution of the logistic model for population growth in random environments. *Journal of Applied Probability* **17**:1083-1086.
- RODIN, E.Y., MURTHY, D.N.F. & PAGE, N.N. 1990. *Mathematical modelling*. Pergamon Press, New York.
- RÖSCH, H., VAN ROOYEN, M.W. & THERON, G.K. 1997. Community-level competition between five Namaqualand pioneer plant species. *South African Journal of Botany* **63**:1-3.
- ROSEN, G. 1984. Characterising conditions for generalised Verhulst logistic growth of a biological population. *Bulletin of Mathematical Biology* **64**:963-965.
- SEALBLOOM, E.W., MOLONEY, K.A. & VAN DER VALK, A.G. 2001. Constraints on the establishment of plants along a fluctuating water depth gradient. *Ecology* **82**:2216-2232.
- TOGNETTI, K. & WINLEY, G. 1980. Stochastic growth models with logistic mean population. *Journal of Theoretical Biology* **82**:167-169.

- TUCKWELL, H.C. & KOZIOL, J.A. 1987. Logistic population growth under random dispersal. *Bulletin of Mathematical Biology* **49**:495-506.
- VAN DER BOSCH, F. & GABRIEL, W. 1997. Cannibalism in an age-structured predator-prey system. *Bulletin of Mathematical Biology* **59**:551-567.
- VAN ROOYEN, G., STEYN, H. & DE VILLIERS, R. 1999. *Cederberg, Clanwilliam & Biedouw Valley: South African Wild Flower Guide 10*. Botanical Society of South Africa, Kirstenbosch.
- VAN ROOYEN, M.W. 1999. Functional aspects of short-lived plants. In: W.R.J. Dean & S.J. Milton (eds.) *The Karoo – ecological patterns and processes pp. 107-122*. Cambridge University Press, Cambridge.
- VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N.. 1996. Skilpad Wildflower Reserve – A flower-lover's paradise. *Veld & Flora* **82**:40-42.
- VONHULST, R. 1987. Invasion models of vegetation dynamics. *Vegetatio* **69**:123-131.
- WESTOBY, M., WALKER, B.H. & NOY-MEIR, I. 1989. Range management on the basis of a model which does not seek to establish equilibrium. *Journal of Arid Environments* **17**:235-239.
- WIEGAND, T. & KELLNER, K. 2000. *Workshop at the 26th annual congress of the South African Association of Botanists: The role of models in long-term ecological research*, Unpublished report of abstract, January 2000, Potchefstroom University for Christian Higher Education, Potchefstroom.
- WIEGAND, T., MOLONEY, K.A., NAVES, J. & KHAUER, F. 1999. Finding the missing link between landscape structure and population dynamics: A spatially explicit perspective. *The American Naturalist* **154**:605-627.