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Computational
and
Mathematical Modelling
of
Plant Species Interactions
in a
Harsh Climate

Thesis submitted in accordance with the
requirements of the University of Liverpool for
the degree of Doctor in Philosophy by Enu-Obari
Nwamue Ekaka-a

July 2009

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Declaration

No part of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other institution of learning. However some parts of the material contained herein have been previously sent out for publication and some parts of the material contained herein have been previously published:

1. Parts of Chapters 1, 2, and 4 were presented at HERCMA, Athens, September, 2007.
2. Parts of Chapter 4 were presented at the International Research Meeting on Stochastic Evolutionary Problem: Theory, Modelling, and Numerics at the University of Chester, Department of Mathematics, Chester, October, 2007.
3. Parts of Chapters 3, 5, and 6 were presented at the University of Chester Annual Postgraduate Conference, Chester, November, 2008.
4. Parts of Chapter 1, Chapter 2, and Chapter 6 form part of our joint paper on 'Mathematical Modelling of Plant Species Interactions in a Harsh Climate' by (Professor Neville J. Ford, Dr Patricia M. Lumb, Enu Ekaka-a) which has already been accepted for publication in the Journal of Computational and Applied Mathematics.

Dedication

I wish to dedicate this thesis to my parents who had my education as one of their major life goals, to my Wife (Nton-Obari) who has always been extremely supportive of my work, and my Son (Ebenezer Obaribenjun Awiate), and my Sister (Edith Nneka blessed memory). Also dedicated to my mentors Elder Benson Ikini and Mrs Joyce Ikini.

I also recognise the very important contributions of several of my teachers over many years who have helped provide direction in my education.

All Glory Be to Almighty God.

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Abstract

This thesis will consider the following assumptions which are based on a few insights about the arctic climate ([169], [69])

1. the arctic climate can be characterised by a growing season called summer and a dormant season called winter.
2. in the summer season growing conditions are reasonably favourable and species are more likely to compete for plentiful resources.
3. in the winter season there would be no further growth and the plant populations would instead be subjected to fierce weather events such as storms which is more likely to lead to the destruction of some or all of the biomass.

Under these assumptions, is it possible to find those changes in the environment that might cause mutualism (see section 1.9.2) from competition (see section 1.9.1) to change?

The primary aim of this thesis is to provide a prototype simulation of growth of two plant species in the arctic that:

1. takes account of different models for summer and winter seasons.
2. permits the effects of changing climate to be seen on each type of plant species interaction.

Introduction

0.1 Aim

The aim of this thesis is to demonstrate that we can use a mathematical approach to identify qualitative types of plant species interactions in a harsh climate. This methodology is cost effective and efficient can be obtained with a fairly less computational cost than was thought with the traditional plant ecological experiments in a harsh climate.

0.2 Lotka-Volterra Systems: A brief history

From the literatures, the classical theory of ecological competition between two species which is usually modelled by a system of nonlinear ordinary differential equations of first order which is associated with Volterra ([193]) and Lotka ([128]). Their work is an extension of the logistic model of single species dynamics originally due to Verhulst ([190]). Verhulst logistic model does primarily two things:

1. It introduces nonlinearity into the model of self or intraspecific interaction coefficient.
2. It models the growth of a single species when self or intraspecific interaction coefficient is introduced into the dynamics.

Lotka-Volterra systems of equations are usually described by a set of deterministic equations involving a small number of variables which are characteristics of complex systems in physics, chemistry, and biology.

0.3 Numerical simulation of changes in qualitative interactions of plant species

Ecology is a complex scientific field ([143], [134]). An ecological simulation is a detailed specific model that requires much to enable its application. An example of this type of numerical simulation concerns the numerical simulation of changes in qualitative interactions of plant species ([71]).

It is this type of numerical simulation over a 10 year period and a 20 year period of one trajectory that this thesis is seeking to use to study the changes in the qualitative interactions of plant species in both harsh and relatively benign environments.

0.4 The dilemma of unused relevant ecological data in an interdisciplinary research

The notion of unused relevant information in research and development is not new ([201]). For example, the analysis of determinate growth of some agricultural crops ([203]) is partly based on the data provided by ([118]).

The time series plant growth data provided by Blackman ([35]) which our analysis in this thesis uses were published in 1919. However, some other researchers have cited the notion of the assumption behind the experimental analysis of Blackman without a further analysis ([197]). Other similar experimental works have been cited by ([191]) and ([175]).

However, as far as we know, these useful biological experimental results are yet to be further analysed mathematically. These data sources represent a domain of unused data in research and development ([201]). We would fairly say that the reasons for unused relevant ecological data in an interdisciplinary research are still subjective depending on the objectives of the researcher's agenda and key objectives. Therefore, an application of unused ecological data in an interdisciplinary research would face a dilemma. We propose to manage this dilemma satisfactorily.

Although, we have used old plant growth data ([35]), their use provide good ecological insights which we have not seen elsewhere. We would simply mention that for many years, other researchers were aware of Blackman's data but never knew a satisfactory method of analysing these important data mathematically. Hence, we intend to propose a novel approach of analysing and making sense from these time series plant growth data.

0.5 Content

In this work we are concerned with the computational and mathematical modelling of plant species interactions in a harsh climate. It is organised into the following seven chapters:

Chapter 1

In chapter 1, we shall first review a few ecological notions, ecological hypotheses, mathematical questions, and types of plant species interactions which are relevant to the study of computational and mathematical modelling of plant species interactions in a harsh climate

Chapter 2

In chapter 2, we shall introduce the mathematical analyses of the types of species interactions which we have identified in chapter one by using some standard mathematical methods.

Chapter 3

In chapter 3, we shall construct a deterministic summer model by using a non-linear optimization method. Our approach is to choose an error or penalty function that measures the agreement between the data and the model. The

parameters are then adjusted within a 0.1 percent relative tolerance error to achieve a minimum in the penalty function that yield the best-fit parameters. These model equations of summer competition between two plant species were analysed using the standard mathematical methods which we have identified in chapter 3.

Chapter 4

In chapter 4, we shall carry out a systematical sensitivity analysis of the model parameters of the model equations of the summer competition model which we have constructed in chapter 3 with a view to selecting the important parameters, that is, parameters which on their variation would produce the biggest effects on the solutions.

Chapter 5

In chapter 5, we shall focus on the simulation of our summer-winter model of plant species interactions in order to decide on a method for calculating the minimum biomass for each plant species over a ten year period of one trajectory and also decide on how we should allow our program to reflect shortened winter and lengthening summer for calculating the minimum biomass for each plant species over a ten year period of one trajectory. We use an example to illustrate the possibility of obtaining mutualism from our summer competition model as a result of a variation of the length of summer.

Chapter 6

In chapter 6, we shall focus on a systematic investigation on how we can obtain cases of mutualism and facilitation from a combination of our summer competition model and our stochastic winter model which are consistent with the mainstream ecological perspective due to a variation of our summer and winter model parameters.

Chapter 7

In chapter 7, we shall concentrate on the key achievements of this thesis and indicate some ideas for further research.

Chapter 8

A few relevant graphs are presented in this chapter for the purpose of understanding the ideas which they represent.

Chapter 1

Ecological and Mathematical Ideas

1.1 Introduction

The topic of this thesis will tackle a challenging interdisciplinary problem by using the tool of mathematical modelling and numerical simulation of plant species interactions in a harsh climate. As a matter of fact, according to the declarations of the 1992 Earth Summit, interdisciplinarity was cited repeatedly as one of the means for increasing our understanding of and developing solutions to pressing environmental issues such as sustainable resource development, climate change, ecosystem rehabilitation to mention a few ([188]). Interesting enough, interdisciplinary approaches have moved on to consider issues other than broad global issues. In this context, interdisciplinarity has facilitated research on subjects which are more narrow in scope. For example, mutualism has been suggested as an important factor of community stability in general ([89], [136], [161], [136], [34], [182]). On the other hand, we know from these authors that population dynamics of mutualistic interactions are rarely described except in the case of positive-density.

In this thesis, we shall attempt to adapt numerical methods to solving this novel ecological problem with the expectation of providing further insights and contributing new knowledge. Driving this motivation is our recognition of the complexity of inhospitable arctic environments and the complex links between ecological and dynamical systems.

One of the well known ecological interpretations of understanding the interaction between plant species is through the process of competition. But in a harsh climate where it takes a longer time to understand if the process of competition is taking place which is very rare, we choose to assume a summer growing season where competition takes place along with a winter season where occasional frequency of storms may affect the biomass.

This chapter will attempt to tackle the following issues that relate to this thesis.

First, we would consider issues relating to global warming, lengthening summer and shortening winter. This would be followed with a brief introduction to the concepts of mathematical modelling and numerical simulation. Then, we

would consider the central purpose of this thesis, a few observations of ecologists that directly relate to our investigation. This will be followed with a list of objectives that this thesis expects to achieve.

Second, we shall consider the main methodology which we have used in the analysis of our summer-winter model.

Third, we shall define and discuss the key ecological hypotheses and other research questions on which this thesis is designed. It is very important to define and discuss in detail other important factors and issues that affect the growth of plant and plant species interactions. For example, we need to understand the concept of the kinetics of plant growth, competitive exclusion and species coexistence among other related ecological concepts that would provide insights to understanding the process of plant growth and the dynamics of plant species interactions.

In this chapter, we would also consider five types of plant species interactions on which our subsequent mathematical analysis and simulations would be based. This introductory chapter ends with a conclusion that points out what we would expect the next chapters to achieve.

1.1.1 Global Warming

One of the effects of a climate change will take the form of a significant global warming. This change is expected to be most pronounced at polar latitudes ([19]). As a result of this, plant species are predicted to change in response to changing climates ([19], [74], [133], [171], [68], [51], [176], [183], [170], [166], [109], [101]). In particular, [176] have shown that a warmer climate could lead to new competitive relationships between plant species that will consequently diminish the reproductive capacity of plant species.

1.1.2 Lengthening summer and shortening winter

Plants require specific growing season lengths to complete their life cycles. These requirements are said to vary significantly with different species ([95]). For example, red raspberries which are produced in Scotland requires a short, cool growing season while in the tropical and subtropical regions, sugarcane requires long, hot, humid growing seasons. On the other hand, other plant species can grow and perform better over a wide range of temperatures and length of season.

The quantification of lengthening a summer season and shortening a winter season has been reported in the literature ([107]). According to these researchers, the summer season is said to be lengthened significantly by 11 days whereas the winter season is said to be contracted or shortened by 30 days. These climate changes could alter the complex interactions between plant species.

According to a global warming resource ([81]), it was reported that summer days without snow cover have increased from fewer than 80 in the 1950's to more than 100 in the 1990's. In the same context, a group of other researchers have reviewed the evidence that global warming has affected the growth period of plants and also reported that the lengthening of the growing season can contribute to the global carbon fixation ([162]). Hence, the lengthening of a summer growing season is more likely to enhance the process of competition than facilitation.

1.1.3 Other factors of a benign environment

The initial biomass is an important benign factor that can play a key role in the shift between positive and negative interactions along environmental gradients ([77], [84], [113], [39]). Another important factor of a benign environment is the intensity of species interactions ([41], [39]).

1.1.4 Regional variation of frequency of storms in the arctic

Just as chronic wind is an important ecological parameter, so is the impact of fierce storms on the biomass ([67]). According to the arctic data source, it was reported that the frequency of storms was greatest during the months of June, July, and August with an average of two or three per month ([12]). This occurrence of storms enables us to choose an annual average of storms to be between 6 and 9.

In this thesis, we propose to use the Poisson distribution to approximate the mean number of storms over a period of 10 years whereas we propose to use the Gamma distribution to approximate the intensity of storms. These distributions are the two most popular models of studying the occurrence of events in an interval and the increasing intensity of storms in particular.

1.1.5 Impact of temperature and other stresses on the growth of plant species

The growth of plant species can be affected by a range of abiotic stresses such as the temperature stress, soil stress, and pH stress to mention a few ([163]). In this thesis, we can investigate the impact of temperature stress on the type of plant species interactions indirectly by changing either the daily intrinsic growth rate or the intra-specific coefficient of an appropriate competition model in a benign climate. This would indirectly provide some important ecological qualitative insights from our expected numerical simulation in this thesis.

1.2 Review of relevant literatures

The idea behind a literature review stems from the concept of research. In this context, research is a diligent investigation to validate and refine existing knowledge and generate new knowledge.

What is a literature review? There is no single definition that fits this concept universally. We would think that a literature review is an important part of developing a research and it involves an analysis and synthesis of research sources to generate a picture of what is known about a particular research problem or a particular field of study. It can also be used to identify the knowledge gaps that exist in a research topic. In a literature review, the researcher who is investigating a scientific problem wants to find out the methods that other researchers have used to tackle his or her proposed problem especially if the problem being investigated is a new research topic in order to avoid duplication of research outputs. Hence, these few reasons reinforce the fact that a literature review is an important part of a research process and development (see, section 3.17 of this thesis).

1.3 Mathematical Modelling

Mathematical modelling is an integral part of attempting to understand the dynamics of a given scientific problem which is familiar in the mathematical literatures ([145], [75], [20], [21], [24], [87]). In general, a mathematical description of a system serves to put our knowledge of that system into a rigorous quantitative form that is subject to rigorous testing. In this sense, we would mention that a mathematical model serves as an embodiment of a hypothesis about how a system is constructed or how it functions. We also think that the model forces one to focus thinking and make inexact ideas more precise.

In the context of this thesis, we intend to use only a system of first order coupled differential equations to study the interaction dynamics between two competing plant species. Other appropriate models involving partial differential equations, difference equations, delay equations, and other types of functional differential equations can be extended by another researcher to model the interaction dynamics between two competing plant species.

1.4 Numerical simulation

A numerical simulation is a satisfactory method of tackling a mathematical model which has complex characteristics and does not have a closed-form solution ([20], [21], [24]). It is an important component of developing a mathematical model. This viewpoint is consistent with the general consensus that as fields of science develop, dissemination of knowledge seems to evolve in theory from analytic to numerical solutions ([73]).

We learn from this author that, as soon as a theoretical formulation is well defined and validated for simple test equations, the next stage of analysis would involve the application of the theory to understanding more complex systems. When the system to be solved becomes very complex, that is, when the model equations that describe the phenomena being considered consist of many many parameters, familiar analytic mathematical techniques will in most scenarios fail to provide precise solutions. It is at this point that numerical simulation or computational science becomes an important mathematical technique.

For example, to study the mathematical modelling of plant species interactions in a harsh climate which is motivated by a system of complex model equations, the application of a numerical simulation is inevitable in order to draw useful ecological insights ([69]).

1.5 Purpose of this Thesis

Our primary goal in this thesis is to use the tool of numerical simulation to investigate the effect of climate change on the extent of obtaining cases of mutualism and facilitation from a combination of our summer competition model and our stochastic winter model which are consistent with widely accepted ecological theories. Our other secondary goals are to

- find out how sensitive the environment is to particular model parameters that can be affected by climate change.

- find those model parameters, which when varied, have the biggest effect on the approximate solution of a system of nonlinear deterministic model equations of competition interaction.
- find those winter and summer parameters which when varied will lead to changes in the interaction behaviour.

1.6 Observations of Ecologists

The idea that interactions between plant species are affected by some environmental conditions such as changes in weather conditions in which the species grow is well established ([186],[48], [65], [38]) and several other references which are cited by these authors. According to these authors, the prediction of ways that changes in the environment will affect biodiversity is of particular concern.

Nevertheless, these authors have reported that, in delicate ecosystems, the presence of research scientists may pose a major influence on the environment and on the expected scientific results that would be obtained.

1.7 Objectives of Research

The key objectives of this study are to

- develop a model that will accept as input data details of the environmental factors and the distribution of different plant species.
- develop a model that will provide predictions of future distributions of the interacting plants over time, taking account of various hypotheses regarding climate variations.
- find which model parameters when varied have the biggest effect on the solutions.
- decide on a method of calculating the effect of summer and winter parameters on the biomass.
- investigate the possibility of using an ecological simulation to obtain mutualism and facilitation from a combination of a summer competition model and a stochastic winter model due to a variation of winter model parameters.
- find out the critical environmental factors that can cause mutualism and facilitation to change to other patterns of plant species interactions.

1.8 Research Methodology

A research methodology is an important part of developing a mathematical model ([70], [20], [21]). Our research methodology consists of three main phases namely the modelling phase, the simulation phase, and the review/revisit phase.

1.8.1 Modelling phase

The modelling phase of our research methodology considers three main issues namely

1. Issues about species interactions.
2. Issues about data availability.
3. Issues about parameter estimation problem

Issues about species interactions

In terms of species interactions, we would only consider the competition $(-, -)$ interaction between two competing plant species for resources in combination with a stochastic winter model. Our competition model is characterised by a set of defining parameters such as the intrinsic growth rates for the two plant species, the self or intraspecific interaction coefficients for the two plant species, the interspecific interaction coefficients for the two plant species and the starting biomasses over a long time interval.

Issues about data availability

In terms of data availability, we have only analysed the given plant growth data provided by ([35]) because the results which we obtain by analysing these data provide useful ecological insights which are consistent with the key objective of this thesis.

Moreover, we could not find a set of plant growth data because of the constraint of the inhospitability of the arctic climate and lack of funding. In the literature, we are yet to see any other analysis of these data using our method of analysis. Despite the problem of data paucity which is characteristic of most interdisciplinary studies, our analysis of these available data forms a background for other further analyses.

Issues about Parameter Estimation Problem

The problem of parameter estimation to be considered in this thesis is described by a system of m nonlinear ordinary differential equations of first order

$$\frac{dx}{dt} = f(t, x, p) \quad (1.1)$$

that depend on a set of parameters $p \in \mathfrak{R}^p$ where $x \in \mathfrak{R}^m$ and $t \in [0, T]$.

The initial values $x_0 = x(0)$ are usually treated as additional unknown parameters and these are included in the parameter set p ([24]). We consider the observed quantity y_i as a function of the system state x which are sampled at discrete times t_i such that

$$y_i = g(x(t_i, p)) \quad (1.2)$$

for $i = 1, 2, \dots, N$.

If $\hat{x}(t, p)$ is the approximate solution of the above equation for a given set of parameters p . The objective function $\Phi(\hat{p})$ is defined as the sum of squared residues between the data and the model such that

$$\Phi(\hat{p}) = \sum_{i=1}^N |y_i - g(\hat{x}(t_i, p))|^2 \quad (1.3)$$

In this thesis, our approach is to choose an error function which is also called the penalty function that measures the agreement between the data and the model. The parameters are then slightly varied to achieve a minimum in the 2-norm penalty function which will yield the "best-fit" parameters. With nonlinear dependencies, however, the minimization must proceed incrementally/iteratively, that is, given trial values for the parameters, we develop a procedure that improves the trial solution. Our procedure is then repeated until $\Phi(\hat{p})$ stops decreasing and starts increasing again, hence indicating the property of a monotone sequence.

When the measurement points are good, our scheme correctly identifies the minimum point and hence the best fit parameters are chosen subject to a relative error tolerance of 0.1 percent.

We know that the construction of a mathematical model is not a simple task for several reasons. According to [115], it is impossible to identify a single model structure for a natural system since such a system is never closed and more than one model would appropriately provide reliable realistic result. In some circumstances, the modeller is compelled to use one single reliable model which best describes the phenomenon under investigation as long as the construction of this single model can be justified with an appropriate numerical scheme.

Next, models are built under uncertainties in the values of the defining parameters, in the parameterization of the system and in the choice of equations that describe dynamics ([153], [45]).

Lastly, uncertainty can also be related to an inherent stochasticity of the model where the dynamics includes a random term. Issues of parsimony in model identification are discussed in great depth by ([204], [20]).

In an interaction between two dis-similar plant species, a parameter which is numerically characterised as less important could become an important parameter when an interaction between two similar plant species is considered. To avoid this type of contradiction and inconsistency in the interpretation of our analysis, it would be a good idea to simply differentiate those parameters which have the biggest effect on the solutions as important parameters and those which have the smallest effect as less important parameters.

1.8.2 Simulation Phase

Our simulation phase is characterised by two distinct components comprising of the numerical simulation of our summer competition model using fourth order Runge-Kutta methods and the assumptions leading to the stochastic winter model.

Numerical simulation of summer competition model

For our summer season prototype model, we consider

$$\frac{dN_1}{dt} = f(a, b, c, N_1, N_2, N_1(0), N_2(0)) \quad (1.4)$$

$$\frac{dN_2}{dt} = g(d, e, f, N_1, N_2, N_1(0), N_2(0)) \quad (1.5)$$

where

1. a denotes the intrinsic growth rate for the first species N_1 in the absence of interaction with N_2 .
2. b denotes the self or intraspecific interaction coefficient for the first species N_1 .
3. c denotes the interspecific interaction coefficient of the second species with the first species inhibiting the growth of the first species.
4. d denotes the intrinsic growth rate for the second species N_2 in the absence of interaction with N_1 .
5. e denotes the interspecific interaction coefficient of the first species with the second species inhibiting the growth of the second species.
6. f denotes the self or intraspecific interaction coefficient for the second species N_2 .
7. N_1 and N_2 are the given biomasses for the first and second plant species.
8. $N_1(0)$ and $N_2(0)$ are the given starting biomasses for the first and second plant species.

Our summer competition model is characterised by two continuous and differentiable interaction functions in terms of the defining model parameters which we have talked about in the early section of our research methodology. These two interaction functions are solved numerically by the following explicit fourth order Runge-Kutta method ([106], [120]). This numerical method which is well established for solving an initial value problem and also for solving a system of equations is a procedure that produces approximate solutions at particular points.

For a standard system of two equations, we consider

$$\frac{dx}{dt} = f(x, y) \tag{1.6}$$

$$\frac{dy}{dt} = g(x, y) \tag{1.7}$$

with initial conditions

$$x(0) = x_0 \tag{1.8}$$

$$y(0) = y_0 \tag{1.9}$$

We know that to achieve a higher order of accuracy when applying the Taylor series, one is expected to find various higher order derivatives. This approach involves tedious algebraic manipulations. However, if the derivatives are replaced by evaluating $f(x, y)$ and $g(x, y)$ at intermediate points, it becomes possible to achieve the same desired accuracy. The methods that are derived in this way are called Runge-Kutta methods but there are numerous variations of

these method. The version which we have used in this study is the one proposed by ([120]).

Our system of model competition equations are analysed using a fourth order Runge-Kutta scheme with which the starting biomasses before the start of our winter season can be calculated under our assumption that in the summer season the growing conditions are reasonably favourable and species will compete for resources.

Numerical simulation of stochastic winter model

The arctic climate is also characterised by a dormant season called winter. We assume that in the winter season there will be no further growth and the plant populations will instead be subjected to various weather events such as storms which lead to destruction of some or all of the biomass. The simplifying assumptions that lead us to set up our winter model will be considered in detail in chapter five of this thesis. Some ecological questions such as how do we approximate the number and intensity of storms can be answered by simulating the Poisson probability distribution and the gamma distribution in order to obtain estimates for the number and intensity of storms. Detailed definition and analysis can be found in chapter five of this thesis.

1.8.3 Review and revisit phase of our summer-winter model

In this section of our research methodology, we used our summer simulation program to obtain solution trajectories over a longer time interval for other variations of the length of summer growing season. This confirms that our program is working correctly.

Summer season prototype model

For our summer season prototype model, we use our Matlab coded Runge-Kutta program to calculate maximum biomass for each plant species. These maximum biomasses for the first and second species form the values at the start of winter dormant season. Then, we would stop our simulation of this summer growing season.

Illustrating our Winter Dormant Season

For our winter season, we follow the following steps in our research methodology

1. Use gamma distribution to model storm intensity.
2. Calculate the proportion of the biomass that remains after storm 1, after storm 2, after storm 3, etc as generated by the Poisson probability distribution for the first year winter 1 for the first and second species.
3. At the end of the first year winter 1, use the biomass that remains for each species to form the starting biomass at the start of the second year summer season and winter season.
4. Continue the process for the second year winter 2 for the first and second species.

5. At the end of the second year winter 2, use the biomass that remains for each species to form the starting biomass at the start of the third year summer season and winter season.
6. The above steps are repeated for winter 3, then summer 4, winter 4, etc for 10 summer growing seasons and 10 dormant winter seasons.

In this thesis, we have used a Matlab program to simulate our summer-winter model.

1.8.4 Application of our research methodology

We have successfully updated our summer-winter program and decided on a method

1. For calculating the minimum biomass for each plant species over a 10 year period of one example trajectory instead of exact solutions.
2. To simulate 1000 ten year periods with the same starting values with which we can calculate our experimental probability of extinction of each plant species.
3. To allow our program to reflect shortened winter and lengthening summer based on ecological literature idea.
4. To obtain cases of mutualism, commensalism, parasitism, competition, and facilitation if possible from a combination of our summer model and stochastic winter model which are consistent with dominant/mainstream ecological theory.

Our next task is to discuss a few types of species interactions which would form the background to this study.

1.9 Types of Plant Species Interactions

From our discussions so far, we know that when two species in an ecosystem have some common activities or requirements, they may interact to some degree. The principal types of species interactions are interspecific competition, mutualism, commensalism, parasitism and predation. Predation is one of these interactions which we have not discussed in this section because parasitism can easily switch to predation.

Three of these interactions namely parasitism, mutualism, and commensalism are symbiotic relationships in which two or more species interacting together benefit from the relationship. In mutualism and commensalism neither species is harmed by the interaction.

In this section, we will define and discuss the four main types of plant species interactions on which this study will be based with a view to illustrating these interactions with a few examples.

1.9.1 Competition

One of the ways in which plants interact and compete for limited resources in the environment is through the process of competition.

The most accepted scientific opinion is to view competition as a process of concurrent use of a limited resource. The concept of competition between plant species could be further broken into interspecific competition and intraspecific competition ([30]). Interspecific competition occurs when individuals of two separate species share a limiting resource (water, light, soil nutrients and growing space) in the same ecological niche whereas intraspecific competition may occur when individuals of two same species share a limiting resource in the same ecological niche. Both types of competition may limit population size but when interspecific competition does affect population size, it could lead to the local extinction of one or more competing species ([31]).

Consider two plant species growing in a desert where the major limiting resource is water. The species whose root growth enables them to acquire much water would have an advantage whereas the species that cannot obtain as much water may find it difficult to persist with limited growth during drought or face the ecological risk of extinction.

Ecologists usually measure competition by using the concept of neighbouring plant density as a factor that affect the growth of plants ([143]). Other things being equal, ecologists are interested to know if the presence of other plants from the same species does affect the growth of individual plants in a predictable pattern. Another question of interest to ecologist is about interspecific competition. Other things being equal, does the presence of other plants from other species affect the growth of individual plants differently than the presence of plants from the same species? Does this difference occur in a predictable pattern?

According to ([134]) and several other ecologists, there is a general unanimous consensus that the concept of competition between two interacting species has been widely studied more than any other type of species interactions.

1.9.2 Mutualism

Mutualism (+,+) is a type of symbiotic interaction in which both species benefit by sharing a common limited resource and contribute to the growth of individual species positively. For example, mycorrhizae are mutualistic interactions between fungi and the roots of almost all plants ([31],[29],[30]). The fungus is said to absorb phosphorus and other essential minerals from the soil and provides them to the plant. In return, the plant provides the fungus with carbohydrates produced by photosynthesis.

According to these authors, this example may be true in nutrient-poor soils, however, when the plant has enough minerals that it does not require the benefit from the fungus, this benefit could become a drain on the plant's resources, thereby the mutualistic interaction could be turned into a parasitic interaction in this context.

According to ([143]), facultative mutualism occurs when either species can grow in the absence of the other, although neither species alone can attain population densities as great as when both species occur together. In obligate mutualism, neither species can grow in the complete absence of the other, however, growth at very low densities is sometimes guaranteed given the required

lower population threshold and availability of limited resources.

Mutualism or symbiosis is considered as one of the major categories of ecological interaction of populations or species. It has also been suggested as an important factor of community stability in general ([89], [136], [161], [34], [136]). According to ([134]), the population dynamics of mutualism relations are less studied when compared with the dynamics of competition. This viewpoint has changed as the notion of mutualism which has a positive-density dependence ([136], [34], [182]) is contributing better insights for scientists. However, ([136]) and ([185]) have argued that positive density-dependence could be problematic since a strong mutualism may lead to the infinite population growth or population explosion.

1.9.3 Commensalism

In a commensalistic (+/0) interaction, species one (called the commensal) benefits while species two (called the host) is not affected. Epiphytes are smaller plants that grow on other plants ([30], [31]). One classic example of commensalism is the interaction between a rain-forest tree and its epiphytes.

1.9.4 Facilitation

Facilitative (mutually positive) interaction between two plant species is an important type of species interaction ([48], [127]). As a matter of fact, theoretical models predict that facilitation generally increases in importance with increasing abiotic stress([127]).

Facilitation which is called the credit column of the ecological ledger has not been frequently studied despite its importance in the plant community ([42]). Despite this setback, more recent research indicates that the impact of facilitation is an important community-level process ([42]).

The importance of integrating facilitation into dominant/mainstream ecological theory as well as the importance of facilitation and environmental gradients has been proposed ([39], [42]).

A few findings that directly relate to this study on modelling plant species interactions in a harsh climate are that

1. Both positive and negative effects occur simultaneously along environmental gradients, affect different variables, and change with time and location ([157]).
2. The net balance between the facilitative and competitive effects represents the magnitude and sign (either positive or negative) of the interaction ([49],[102]).
3. It has been reported from an experimental study that the harsher the ecological conditions, the stronger the facilitative effect of the nurse plants ([157]).
4. Several factors can affect or shift the balance between competition and facilitation, including physiological and developmental traits ([14]).
5. Abiotic conditions seem to be the overriding factor increasing the importance of positive effects in harsher environments ([40], [48]).

6. The net negative competitive effects are more important under relatively benign environmental conditions, whereas positive facilitative effects are more important under harsher conditions ([111]).

1.9.5 Parasitism

Parasitism is another (+, -) symbiotic relationship in which one member, called the parasite, benefits and the other, called the host, is adversely affected ([30]).

In this symbiotic interaction, the parasite obtains nourishment from its host, and in spite of the fact that a parasite may weaken its host, it rarely kills it ([30]). Thus, whilst the parasite benefits from the parasite-host interaction, the host plant may suffer a decrease in fitness through either a decrease in survival, reproduction and /or growth.

It is worth mentioning that many parasites do not cause disease, but some do. When a parasite causes disease and sometimes the death of a host, it is called a pathogen. The mistletoe is one of the best examples of parasitic seed plants ([31],[30]). From an evolutionary perspective, mistletoe is a successful example because as a parasite, it keeps its leaves in winter and so is highly visible in bare trees. Hence, it has become a cultural symbol during Christmas.

1.10 Ecological Hypotheses

In this section, we would define and discuss the following hypotheses which relate directly with the primary aim of this thesis.

1.10.1 Competition Theory

The common ecological paradigm which explains the process of plant species interactions is based on the idea of competition for limited resources ([186]). A few of the existing mathematical models that have been used to explain the plant interactions observed in experiments can be found in the works of ([75], [76], [158]).

1.10.2 Positive Interaction Theory

From studies which were conducted in harsh climates ([48], [65], [64]), it has been observed that there can be positive interactions between plant species. According to these authors, these positive interactions are not explained by previous competition theory and there is an increasing body of evidence obtained by community manipulation that supports the idea that one finds examples of commensalism and mutualism within these ecosystems along declining productivity gradients. For example, temperature changes may lead to other secondary changes, such as, increase in rainfall levels, or the availability of nutrients to plants may change.

Hence, these changes to environmental factors may mean that two plant species may at some point cease to interact positively and begin to compete. In this thesis, we are going to provide a mathematical model that will enable us to predict when this bifurcation in the interacting behaviour will occur.

In another scenario, competition can become greatest in the most stressful and disturbed zone ([72]).

1.10.3 Stress Gradient Hypothesis

From the ecological literatures, the relationship between the harshness of environmental stress and the relative importance of facilitation and competition can be conceptually formalised as a stress gradient hypothesis. It predicts that the net negative competitive effects are more important under relatively benign environmental conditions while positive facilitative effects are more important under harsher conditions ([32], [49], [38]). In this thesis, we would interpret the term stress to mean any benign environmental factor which its manipulation would produce some negative effects on the two interacting plant species such as the length of growing season, the daily intrinsic growth rate, the intra-specific coefficient and the initial biomass. Other benign environmental factors can be high temperature, warmer summers, osmotic pressure, and nutrient level ([32], [176]).

1.11 Other Research Questions

The hypotheses being considered above have both ecological and mathematical components. Hence, we will need to rely on some reliable mathematical techniques to answer the related ecological questions.

1.11.1 Ecological Questions

In this study, we shall attempt to focus on a few important ecological questions. These questions are not exhaustive. As far as we know, these are the ones that relate to our present analysis.

1. Ecologists know how to measure plant interactions experimentally ([13]) but they want to know how to measure some performance variables usually biomass between individual plants interacting together and in isolation by a simulation technique in the absence of actual experimentation.
2. Ecologists want to find out the effect of varying the length of summer growing season and its sensitivity on the probability of extinction of plant species over a longer time interval.
3. In the winter season characterised by occasional fierce storms, ecologists will like to know if shortening the length of winter leads to some degree of extinction of plant species over a longer time interval.
4. Ecologists also want to know if global warming could trigger either the persistence or extinction of two interacting plant species.
5. Ecologists want to know if they can use an alternative mathematical method different from their classical experimental approach to determine mutualism from competition from a combination of a summer competition model and a stochastic winter model.

1.11.2 Mathematical Questions

In this thesis, we would specify the main questions that mathematicians are interested to tackle:

- How do we set up the summer and winter models?
- How do we approximate the number of storms that occur in the winter season?
- For each storm, how do we approximate the intensity of storm in the winter season?
- How do we approximate the quantity of biomass that remains at the end of each storm?
- To find out how to select model parameters of summer model only.

1.12 Other Important Concepts

Our concern in this section is to define and discuss other important concepts relevant to the understanding of competition interaction and the growth of plants.

1.12.1 Kinetics of Plant Growth

It is known that when a plant emerges from its seed, it grows slowly to begin with and then accelerates its growth until it reaches the flowering stage, when the growth slows down again to a limiting value ([191]). The "S" or sigmoid shape of the curve is typical of the growth of the plant as a whole as well as of the growth of living organisms in general. According to ([191]), the three stages which characterise the so-called grand period of growth are:

- An early period of slow growth.
- A central period of rapid growth.
- A final period of slow growth.

1.12.2 Fundamental Niche

According to ([179]), a fundamental niche is defined as a full potential range of physical, chemical, and biological factors that a species could use if there were no competition from other species. When competition emerges, we would expect this fundamental niche to change in response to the factor of competition between plant species. In particular, the fundamental niches for similar and dissimilar interacting plant species differ.

1.12.3 Competitive Exclusion Principle

Experimental scientists have shown that no two species can occupy exactly the same fundamental niche indefinitely in a habitat where there is not enough of a particular resource to meet the needs of both species. This is called the competitive exclusion principle. This principle can be justified mathematically ([145]). When this principle can be justified both in experimental analysis and analytical analysis, one of the species will persist at its carrying capacity while the other species will go extinct over time. This is one of the reasons why the competitive exclusion principle is an important ecological concept. Another reason why this principle is important is that it provides a baseline for studying competition ([30]).

1.12.4 Species Coexistence

Coexistence takes place when two or more plant species live together in a stable environment. In any competition interaction between two species, either one eliminates the other (competitive exclusion), or they both coexist. In essence, competitive exclusion and coexistence are merely opposite sides of the same coin, or at least alternative states derived from the same model of competition ([179]).

1.12.5 A Neighbourhood Modelling of Plant-Plant Interactions

It is worth to mention at this stage that plant-plant interactions are characteristically local in nature ([58]). What this concept means is that, individual plants do not experience global population density per se, however, they can only interact over constrained distances within their neighbourhood ([58], [143]). A detailed discrete model formulation of this problem has been defined and discussed (see, [143], [155], [156]).

1.13 Conclusion

In this chapter, we have identified four main types of plant species interactions namely competition, mutualism, commensalism and parasitism. In a competition ($-/-$) interaction, direct or indirect inhibition of each species is affected by the other. In commensalism ($+/0$), the commensal benefits from the host without harming it whereas in mutualism ($+/+$), interaction is favourable to both species and obligatory. In a parasitic ($+/-$) interaction, one of the species benefits and the other does not. Facilitation is simply a mutually positive interaction which is slightly different from mutualism in the sense that the fast growing plant species with greater access to nutrients is more likely to provide a nursing support to a slow growing plant species.

In this chapter, we have established our research methodology, key ecological hypotheses, and other mathematical questions that underpin this thesis.

Having identified these types of plant species interactions, the question of describing and analysing the dynamics of the processes of competition, mutualism, commensalism and parasitism between plant species borders on the use of mathematical modelling. Our next chapter will discuss the mathematical techniques with which these problems can be tackled.

Without a detailed discussion of what comes next in the sequel, it would be a good idea to mention briefly about the contents of the next five chapters.

In chapter two, we shall be concerned with a detailed mathematical analysis of the model equations of plant species interactions identified in chapter one. This would involve the use of typical mathematical techniques such as steady state and stability.

In chapter three, we intend to tackle the problem of constructing our model equations of interspecific competition ($-,-$) interaction first by estimating the intrinsic growth rate for a single growing plant and optimizing a set of nonlinear logistic model equations with the aim of obtaining the model parameters that minimize the 1-norm.

In chapter four, we shall consider the application of sensitivity analysis and selection of model parameters from our experiments. Subsequent analysis will require the results of this chapter. This chapter is all about the methodology of finding out which model parameters when varied will have the biggest effect on the solution. It is these parameters which we would regard as important parameters and the parameters which would have the smallest effect on the solutions will be categorized as less important.

In chapter five, we shall focus on the numerical simulation of our summer-winter model of plant species interactions with the hope of providing some insights about some important research questions in this interdisciplinary subject of mathematical ecology or mathematical modelling in ecology.

In chapter six, we shall focus on another important aspect of numerical simulation with the the expectation of obtaining mutualism from a combination of our summer competition model and our stochastic winter model under some realistic assumptions and variation of summer and winter model parameters. We would expect to provide some further extentions of this work.

Chapter 2

Mathematical Analysis of Species Interactions

2.1 Motivation

We have introduced four types of species interactions in chapter one. In this chapter, we shall focus on providing a detailed definition and analysis of model competition equations which can also be adapted to other types of species interactions which we have identified in chapter one.

2.2 Introduction

This chapter is organized into five important sections. In section one, we shall consider the idea and the implication of studying the population dynamics of species interactions. This idea will be illustrated with a few examples.

Section two tackles the problem of setting up the model equations of interspecific interaction between two plant species from the typical model of exponential growth. The setting up of other model equations of mutualism, commensalism and parasitism are similarly defined and discussed.

Section three tackles the core problem of using typical mathematical methods of steady states and stability to analyse the four types of species interactions with a view to providing insight into qualitative behaviour of steady state solutions over time. This analysis would be of importance to ecologists who are often interested in possible uniform states where two species coexist. In particular, one is interested with using typical mathematical techniques to analyse general model equations of competition ($-/-$), mutualism ($+/+$), commensalism ($+/0$) and parasitism ($+/-$) between plant species. Although our analyses bear the general procedure of conducting these analyses, we have considered detailed analyses and their ecological implications in this chapter.

In section four, we have attempted to construct three criteria for the coexistence of two plant species competing for a limited resource in the environment assuming that the defining model parameters of model equations of competition do not depend on a variation of time. Similar criteria for the survival and extinction of two competing plant species are derived mathematically which is

followed up with other mathematical analyses. Finally, a few of what we have achieved in this chapter is briefly summarised in section five.

2.3 Population dynamics of species interactions

In this section, we shall consider the classical n -species Lotka-Volterra model. This model defines the time-evolution of a system of n species in which each is characterised by the number N_i of individuals belonging to the i -th species ([145], [134]).

First we introduce a single species model which describes that the rate of growth of the i -th species is proportional to N_i .

On the other hand, such a rate of growth can be decreased by competition among individuals of the same species and is proportional to N_i^2 , and also by competition among individuals of different species, which is proportional to $N_i N_j$.

Central to our understanding of the Lotka-Volterra model is the population law of mass action. It states that the rate of change of one population due to interaction with another population is proportional to the product of the two populations ([36]).

The general form of Lotka-Volterra model can then be written as follows

$$N_i = N_i(t) \tag{2.1}$$

$$\frac{dN_i}{dt} = N_i \left(a_i - \sum_{j=1}^n b_{ij} N_j \right) \tag{2.2}$$

where $i = 1, 2, \dots, n$ and the terms a_i and b_{ij} are assumed to be positive constants.

To be specific,

- a_i stands for the intrinsic growth rate which defines the difference between the birth rate and death rate of species.
- b_{ij} stands for the competition coefficient with respect to the interaction between the i -th and the j -th species.

In the absence of both intraspecific and interspecific interactions between species,

$$\frac{dN}{dt} = aN \tag{2.3}$$

subject to $N(0) = \alpha > 0$.

The dynamics for this one species population in the absence of interspecific interaction can be described by a first order initial value problem

$$\frac{dN}{dt} = N(a - bN) \tag{2.4}$$

subject to $N(0) = \alpha > 0$.

Similarly, the dynamics for a two species population in the presence of intraspecific and interspecific interactions can be described by a system of two

first order nonlinear ordinary differential equations ([167]), otherwise called the Lotka-Volterra system

$$\frac{dN_1}{dt} = N_1(a - bN_1 - cN_2) \quad (2.5)$$

$$\frac{dN_2}{dt} = N_2(d - eN_1 - fN_2) \quad (2.6)$$

subject to $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$.

Hence, the exponential growth model and the logistic model are special cases of the Lotka-Volterra model.

A further detailed analysis of this model can be found in the works of ([134], [167], [117]).

Therefore, our discussion up to this point has the following common points:

1. The state variable N which is indexed by $N = (N_1, N_2)$ represents the set of the number of individuals belonging to each species.
2. Normalise each N_i with respect to

$$N_0 = \sum_{i=1}^n N_i(0) \quad (2.7)$$

represents the total number of individual species when the initial time $t = 0$.

3. The set P is defined by the set $P = (a, d, b, f, c, e, N_1(0), N_2(0))$.
4. The mathematical model is a continuous dynamic model which is described by a system of nonlinear ordinary differential equations of first order. Its matrix form can be written as

$$\frac{dN}{dt} = f(N; P) \quad (2.8)$$

where

$$f = (f_i) \quad (2.9)$$

where $i = 1, 2$.

$$f_i = N_i a_i - N_i \left(\sum b_{ij} N_j \right) \quad (2.10)$$

In this case, the linear and nonlinear parts are characterised by

$$L_i = \frac{dN_i}{dt} - a_i N_i \quad (2.11)$$

and

$$H_i = N_i \left(\sum_{j=1}^n b_{ij} N_j \right) \quad (2.12)$$

1. If one or more model parameters in set P are random variables, then we would expect the system to be stochastic. If all the parameters are deterministic, then the model is deterministic.

2. If

$$\frac{dN_i}{dt} = 0 \quad (2.13)$$

when $i=1,2,\dots,n$, then the model is in a stable state and the number of steady state solutions can be found from a nonlinear algebraic system of the form

$$f(N; P) = 0. \quad (2.14)$$

In this thesis, we shall only focus on nonlinear deterministic competition model equations.

Next, consider an ecosystem which consists of two interacting plant species $N = (N_1, N_2)$. In general, the presence of a second species has either a positive or negative effect on the first one and vice versa:

- If the species enhance the growth of each other, then this $(+, +)$ interaction is called mutualism or symbiosis which we have defined in chapter one.
- If the species negatively affect each other, then they are said to be in a $(-, -)$ interaction called competition for the same limited resource which we have defined in chapter one.
- If one of the species called parasite benefits and the other, called the host, is adversely affected, then this $(+, -)$ interaction is called parasitism which we have also defined in chapter one.
- If one of the species benefits and the other remains unharmed, then commensalism is the outcome of this $(+, 0)$ interaction which we have also defined in chapter one.

We shall consider a detailed mathematical analyses of these types of interaction later on in this chapter.

In summary, the theory of nonlinear ordinary differential equations of first order is a powerful mathematical approach for describing the interactions between two competing species ([134], [88],[97], [189]).

In this chapter, we shall focus on defining, analysing, and discussing a few relevant coupled nonlinear first order ordinary differential equations of $(-, -)$ species interactions of the form

$$\frac{dN_1}{dt} = F(a, b, c, N_1, N_2) \quad (2.15)$$

$$\frac{dN_2}{dt} = G(d, e, f, N_1, N_2) \quad (2.16)$$

where a,b,c,d,e,f are positive constants whilst $N_1(0) = N_{10} > 0$ and $N_2(0) = N_{20} > 0$ are called the initial conditions or starting values when time $t = 0$. N_1 and N_2 represent the population biomass of species one and species two.

In particular,

1. The model parameter a represents the intrinsic growth rate of species 1 in the absence of interaction.
2. The model parameter b represents the intraspecific interaction coefficient of species 1 with species 1.
3. The model parameter c represents the interspecific interaction of species 2 with species 1.
4. The model parameter d represents the intrinsic growth rate of species 2 in the absence of interaction.
5. The model parameter e represents the interspecific interaction of species 1 with species 2.
6. The model parameter f represents the intraspecific interaction coefficient of species 2 with species 2.

We shall assume that the two plant species in question are interacting for a limited resource within the environment.

Most model equations of plant species interactions do not have any closed-form solutions. Hence, we shall seek to find the steady state solutions which exist for all time ([189]), study their stability properties and numerical simulations of these model equations. The corresponding ecological implications of our mathematical analysis will be discussed.

Under some simplifying assumptions, general model equations of plant species interactions shall be formulated and analysed. It is expected that the analysis of our model equations would provide a basis for improved understanding of these complex plant species interactions.

The parameters that define our model equations are not known precisely, in the sequel we are proposing to find those parameters which, when varied, have the biggest effect on the solutions.

Therefore, in this chapter, we shall analyse the model equations of plant species interactions which are similar to Lotka-Volterra models.

2.4 Model assumptions

In order to analyse the model equations of competition interaction between two plant species, we shall consider the following assumptions:

1. There are plentiful resources and a mild climate that promote continuous growth of two plant species.
2. Consider the population of plant or grass species N_1 and N_2 living together and competing with each other for the same limiting resource.
3. Each population is inhibited not only by members of its own species but also by those of the other population.
4. Linear growth rates and the intraspecific or self competition parameters are the logistic parameters for species N_1 and N_2 if they were growing in isolation of other plant species .

5. The environmental parameters involved with the model formulation are all constants irrespective to time and environmental fluctuations.
6. That the environmental parameters involved with the model formulation are all positive constants without time delays.
7. The dynamics of a system of competition equations or any other type of interaction are independent of diffusion terms.

In order to set up appropriate model equations of interaction, we would require the application of these assumptions.

2.5 Setting up Model Equations of Interactions

In this section, we shall focus on defining and discussing the formulation of the growth of one plant species, then introduce the formulation of interaction of species 1 with itself which we would extend into interspecific interaction between species 2 and species 1.

2.5.1 Exponential growth model

From chapter one, the exponential growth model for one species in the absence of competition is

$$\frac{dN_1}{dt} = aN_1 \quad (2.17)$$

subject to $N_1(0) = \alpha > 0$.

The closed-form solution of this simple standard first order differential equation is

$$N_1(t) = \alpha e^{at} \quad (2.18)$$

This equation implies an exponential growth of population which is also called the law of Malthus ([190]). We can say that this equation is the simplest differential equation and also one of the most important. What does it mean? Here $N_1 = N_1(t)$ is an unknown real-valued function of a real variable t . The function $\frac{dN_1}{dt}$ is its derivative. What else does this equation tell us? This equation tells us that for every value of t , the equality (2.18) is true where the parameter a is a constant, that is if a is positive, zero, and negative.

How are the solutions of this equation obtained? The solutions are obtained by separating the variables technique and integrating both sides of this equation. Hence, if K is any arbitrary constant, the function $f(t) = Ke^{at}$ will obey the first order ordinary differential equation

$$\dot{f}(t) = aKe^{at} = af(t). \quad (2.19)$$

It would be misleading to think that there are other solutions. To prove that there are no other solutions, we shall consider $u(t)$ to be any solution. We want to compute the derivative of $u(t)e^{-at}$. By the product rule differentiation, we know that

$$\frac{d}{dt}(u(t)e^{-at}) = \frac{du}{dt}e^{-at} + u(t)(-ae^{-at}) \quad (2.20)$$

By simplifying this equation further, we would obtain

$$\frac{d}{dt}(u(t)e^{-at}) = au(t)e^{-at} - au(t)e^{-at} = 0. \quad (2.21)$$

By integrating the above equation with respect to t , we know that $u(t)e^{-at}$ is a constant K , so that $u(t) = Ke^{at}$. This proves our assertion.

For a second plant species, we would expect its growth in the absence of intraspecific and interspecific interactions to take the form of

$$\frac{dN_2}{dt} = dN_2 \quad (2.22)$$

subject to $N_2(0) = \beta > 0$ whose general solution is similarly

$$N_2(t) = \beta e^{dt} \quad (2.23)$$

Summarising our discussion so far, the dynamics of unrealistic unlimited growth of two plant species are

$$\frac{dN_1}{dt} = aN_1 \quad (2.24)$$

$$\frac{dN_2}{dt} = dN_2 \quad (2.25)$$

with initial conditions or starting plant biomasses $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$.

Next, we would like to modify the exponential growth assumption in order to model the fact that plant species populations cannot grow unboundedly.

2.5.2 Intra-specific model of a single species

To modify the exponential growth model, we simply add a term that will reduce $\frac{dN}{dt}$ as the population increases.

The term $-bN_1^2$ would be included to represent a self limiting growth of a single first species. Hence, the initial value problem or equation that governs the growth of a single species is

$$\frac{dN_1}{dt} = aN_1 - bN_1^2 \quad (2.26)$$

with initial condition $N_1(0) = \alpha > 0$.

We can rewrite the above logistic equation as

$$\frac{dN_1}{dt} = N_1(a - bN_1) \quad (2.27)$$

where the value of the carrying capacity K_1 is $\frac{a}{b}$.

The growth of another species is modelled by the corresponding logistic equation

$$\frac{dN_2}{dt} = N_2(d - fN_2) \quad (2.28)$$

with initial condition $N_2(0) = \beta > 0$ where the value of the carrying capacity K_2 is $\frac{d}{f}$.

In summary, in the absence of interspecific interaction, the growth of two plant species or grass species can be modelled by

$$\frac{dN_1}{dt} = N_1(a - bN_1) \quad (2.29)$$

$$\frac{dN_2}{dt} = N_2(d - fN_2) \quad (2.30)$$

where the initial conditions or starting biomasses are $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$ and the carrying capacities of the species are $K_1 = \frac{a}{b}$ and $K_2 = \frac{d}{f}$.

In summary, it was Verhulst ([190]) who proposed a theory which is contrary to the the view of Malthus and reported that the growth in a population was not unbounded as modelled by Malthus. He provided a mechanism which accounted for the retardation of population growth. The equation which he constructed is

$$\frac{dN(t)}{dt} = aN(t)\left[1 - \frac{N(t)}{K}\right] \quad (2.31)$$

which limits the growth of the population to the level K which is called the carrying capacity.

The above equation can be solved analytically to obtain

$$N(t) = \frac{KN(0)}{(N(0) + [K - N(0)]exp(-at))} \quad (2.32)$$

We note that for any initial data $N(0)$, $N(t) = K$ is the analytic solution as $t \rightarrow \infty$.

If we assume that a saturated growth will take place at some point during the period of growth, then the initial data can be used to determine the largest population K that would be supported by the environment and the rate of growth of the population.

Other ecologists ([29], [30]) have utilised these ideas to formulate the dynamics of intraspecific interaction between plants of the same species. Our analysis in chapter three will build on this idea.

Our next task is to define and discuss the effect of adding interspecific interaction terms.

2.5.3 Inter-specific model of competition

The effect of (-/-) competition between plant species N_1 and N_2 modelled by the addition of the term $-cN_1N_2$ represents the reduction due to the ecological competition interaction between these two plant species. Therefore, the appropriate model equation is

$$\frac{dN_1}{dt} = aN_1 - bN_1^2 - cN_1N_2 \quad (2.33)$$

We note that the term $-cN_1N_2$ is an empirical correction that is similar to the law of mass action (which states that the rate of change of a population over time is proportional to the product of the two interacting populations)

The effect of $(-/-)$ competition between plant species N_2 and N_1 can also be modelled by the addition of the term $-eN_1N_2$. Therefore, another similar model equation is

$$\frac{dN_2}{dt} = dN_2 - eN_1N_2 - fN_2^2 \quad (2.34)$$

Therefore, the dynamics of two competing plant species can be modelled by the following coupled Lotka-Volterra logistic nonlinear ordinary differential equations of first order ([117], [145])

$$\frac{dN_1}{dt} = N_1(a - bN_1 - cN_2) \quad (2.35)$$

$$\frac{dN_2}{dt} = N_2(d - eN_1 - fN_2) \quad (2.36)$$

with initial conditions $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$.

We shall adapt other model equations from this standard Lotka-Volterra model. These models equations can also be found in works of ([88], [97]).

2.5.4 Inter-specific model of mutualism

When two plant species are involved in a $(+/+)$ interaction, their dynamics can be described by

$$\frac{dN_1}{dt} = N_1(a - bN_1 + cN_2) \quad (2.37)$$

$$\frac{dN_2}{dt} = N_2(d + eN_1 - fN_2) \quad (2.38)$$

with initial conditions $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$.

2.5.5 Inter-specific model of commensalism

In a commensalistic $(+/0)$ interaction between two plant species, their dynamics can be described by

$$\frac{dN_1}{dt} = N_1(a - bN_1 + cN_2) \quad (2.39)$$

$$\frac{dN_2}{dt} = N_2(d - fN_2) \quad (2.40)$$

with initial conditions $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$.

2.5.6 Inter-specific model of parasitism

In the case of a parasitic $(+/-)$ interaction between two plant species, the dynamics that describe this type of symbiotic interaction are

$$\frac{dN_1}{dt} = N_1(a - bN_1 + cN_2) \quad (2.41)$$

$$\frac{dN_2}{dt} = N_2(d - eN_1 - fN_2) \quad (2.42)$$

with initial conditions $N_1(0) = \alpha > 0$ and $N_2(0) = \beta > 0$.

From chapter one, each type of plant species interaction which we have formulated in this section makes sense because we can find their examples in ecology.

Next, we shall attempt to tackle the mathematical analysis of each type of species interaction starting with the (-/-) competition interaction.

2.6 Different Types of Mathematical Techniques

In this section, we shall consider the mathematical analysis of the general model equations which we have formulated in the last section. This analysis is important as it would provide key qualitative behaviour of solutions.

2.6.1 Mathematical techniques

In this study, our main mathematical techniques will include steady state solutions and the characterizations of the stability properties of the types of species interactions being considered in this study. A detailed definition and mathematical analysis of the concepts of steady state and its stability can be found in the works of ([80], [145], [135], [150], [93], [87]).

2.6.2 Background to understanding steady state

When does a system of equations reach a state of equilibrium or steady state? A system is said to reach a state of equilibrium or steady state when it shows no further tendency to change its properties with time.

Stability theory is a fundamental topic in mathematics. There are several concepts of stability such as asymptotic stability, absolute stability, Lyapunov stability, and stability of periodic solutions. These stability concepts have extensive literatures. Readers who are interested in a detailed and comprehensive mathematical treatment of stability theory are referred to references ([93], [80], [87], [150]) and several other references which are also cited by these authors.

We know that many systems in ecological theory ([143], [145], [134], [167], [64], [147]) can be described in the form

$$\dot{x} = F(x, t). \quad (2.43)$$

Here the function $F(\cdot)$ is a function of only x and t . If $F(x, t)$ does not explicitly depend on t , then the system is called autonomous, otherwise is nonautonomous.

In a state space \mathfrak{R}^n , there is a special set that corresponds to equation (2.43) with a given function $F(x, t)$. If we start at any point x_e in this special set such that for all t that belongs to the interval $[t_0, \infty)$

$$F(x_e, t) = 0. \quad (2.44)$$

Such a point, x_e , is called an equilibrium point or a steady state solution.

Next, we shall introduce the methodology of linearization around a steady state.

2.6.3 Linearization in the neighbourhood of a steady state

A standard method of defining the concept of linearization in the neighbourhood of a steady state can be seen in the work of ([80]). Linearization around a steady state is an important analytical method for checking if the steady state is either stable or unstable. This method can be described as follows:

1. We assume that our interaction functions $F(N_1, N_2)$ and $G(N_1, N_2)$ are continuous and differentiable at each steady state.
2. Determine the four partial derivatives of F and G with respect to N_1 and N_2 .
3. Evaluate these partial derivatives at each steady state and set up a 2 by 2 Jacobian matrix consisting of only four elements.
4. If the determinant of the Jacobian matrix at a steady state is strictly positive, then the steady state will be stable. If the determinant of the Jacobian matrix is strictly negative, then the steady state will be unstable. If the determinant of the Jacobian matrix is zero, then the steady state is neither stable nor unstable, hence it is said to be sitting on the cusp.
5. If the eigenvalues which are determined from the Jacobian matrix are two negative real numbers, then the corresponding steady state is said to be stable indicating that the two solutions will decay over time.
6. If the eigenvalues are two positive real numbers, then the corresponding steady state is said to be unstable indicating that the two solutions will grow unboundedly over time.
7. If the eigenvalues are two real numbers of opposite signs, then the corresponding steady state is said to be unstable as the positive eigenvalue contributes more to the growing behaviour of solutions over time than the negative eigenvalue.

It is possible to discuss and analyse a more general case of the linearization in the neighbourhood of a given solution ([150]) but we cannot embark on this level of analysis in this chapter.

2.6.4 Problem: does the perturbation from the steady state grow or decay?

The stability and instability of a steady state can also be studied by the method of a small perturbation from the steady state apart from the method of linearization just discussed in the last section.

The defined model equations of competition as formulated by equation 1 and equation 2 can be rewritten in the following two-dimensional systems

$$\frac{dN_1}{dt} = F(N_1, N_2) \tag{2.45}$$

$$\frac{dN_2}{dt} = G(N_1, N_2) \quad (2.46)$$

Suppose that (N_{1s}, N_{2s}) is a steady state, that is, $F(N_{1s}, N_{2s}) = 0$ and $G(N_{1s}, N_{2s}) = 0$. We consider a small perturbation from the steady state, that is,

$$N_1 = N_{1s} + u \quad (2.47)$$

$$N_2 = N_{2s} + v \quad (2.48)$$

where $u \ll 1$ and $v \ll 1$.

What are we looking for? We want to find whether the perturbation grows or decays. The starting point to achieving this at all is to derive the differential equations for u and v . We would conduct this analysis as follows. Since N_{1s} and N_{2s} are positive constants independent of the time variable, it follows from elementary calculus that

$$\frac{du}{dt} = \frac{dN_1}{dt} \quad (2.49)$$

$$\frac{dv}{dt} = \frac{dN_2}{dt} \quad (2.50)$$

By using our earlier definitions, we would obtain

$$\frac{du}{dt} = F(N_1, N_2) \quad (2.51)$$

$$\frac{dv}{dt} = F(N_{1s} + u, N_{2s} + v) \quad (2.52)$$

By using the Taylor series expansion on the right hand side of this equation, we obtain

$$\frac{du}{dt} = F(N_{1s}, N_{2s}) + \frac{\partial F}{\partial N_1}(N_{1s}, N_{2s})u + \frac{\partial F}{\partial N_2}(N_{1s}, N_{2s})v + O(u^2, v^2, uv) \quad (2.53)$$

Since $F(N_{1s}, N_{2s}) = 0$, it follows that

$$\frac{du}{dt} = \frac{\partial F}{\partial N_1}(N_{1s}, N_{2s})u + \frac{\partial F}{\partial N_2}(N_{1s}, N_{2s})v + O(u^2, v^2, uv) \quad (2.54)$$

By a similar line of analysis, we can also obtain

$$\frac{dv}{dt} = \frac{\partial G}{\partial N_1}(N_{1s}, N_{2s})u + \frac{\partial G}{\partial N_2}(N_{1s}, N_{2s})v + O(u^2, v^2, uv) \quad (2.55)$$

We learn that the higher order terms will be extremely small because u and v are assumed to be small. In summary, knowing whether the perturbation is growing or decaying can be studied by using these equations

$$\frac{du}{dt} = \frac{\partial F}{\partial N_1}(N_{1s}, N_{2s})u + \frac{\partial F}{\partial N_2}(N_{1s}, N_{2s})v. \quad (2.56)$$

$$\frac{dv}{dt} = \frac{\partial G}{\partial N_1}(N_{1s}, N_{2s})u + \frac{\partial G}{\partial N_2}(N_{1s}, N_{2s})v. \quad (2.57)$$

2.7 Model equations of competition interaction

In this section, we are interested to tackle the analysis of a two species competition $(-, -)$ interaction.

The dynamics of a two species competition model has been described by a system of coupled nonlinear ordinary differential equations of first order where the intrinsic growth rates (a, d) are assumed to be positive and the interspecific/intraspecific interaction coefficients are assumed to be positive subject to the initial conditions

$$N_1(t_0) = N_{10}. \quad (2.58)$$

$$N_2(t_0) = N_{20}. \quad (2.59)$$

The biomasses of plant species are represented by N_1 and N_2 .

In this section, we are interested to determine the steady states or equilibria of this model and investigate their stability or instability. We shall show under the assumption of this model that this system of equations has a unique positive equilibrium which is locally asymptotically stable. Our first task is to calculate the steady states or equilibria.

2.7.1 Characterization of steady states of competition

The ecologist is interested in possible uniform states where the two-species co-exist ([143], [58], [179]).

The qualitative behaviour of a dynamic system may depend on its steady state behaviour. The calculation of the values of the state variables at which the dynamic system reaches a steady state is of particular importance in our mathematical analysis and ecological simulation.

In this section, we shall study the characterization of the steady states and their ecological implications.

According to ([80], [145], [135], [150]) and several other mathematical literatures which we can not cite at this stage, that at a steady state

$$\frac{dN_1}{dt} = 0. \quad (2.60)$$

and

$$\frac{dN_2}{dt} = 0. \quad (2.61)$$

If the bracket of the right hand side of equation (2.35) is not equal to zero, then

$$N_1 = 0. \quad (2.62)$$

If the bracket of the right hand side of equation (2.36) is not equal to zero, then

$$N_2 = 0. \quad (2.63)$$

Hence, the point $(0, 0)$ is a steady state solution. At this steady state, species 1 and species 2 will be extinct.

If $N_1 = 0$ is substituted into the second equation and N_2 is substituted into the first equation, we shall obtain

$$d - fN_2 = 0. \quad (2.64)$$

$$a - bN_1 = 0. \quad (2.65)$$

From these two equations, we know that

$$N_2 = \frac{d}{f}. \quad (2.66)$$

$$N_1 = \frac{a}{b}. \quad (2.67)$$

Hence, the points $(0, \frac{d}{f})$ and $(\frac{a}{b}, 0)$ are steady state solutions. At the steady state $(0, \frac{d}{f})$, only N_2 species will survive at its carrying capacity while the N_1 species will be extinct whereas at the steady state $(\frac{a}{b}, 0)$, it is only the N_1 species that will survive at its carrying capacity while the N_2 species will be extinct.

Next, we shall assume that $N_1 \neq 0$ and $N_2 \neq 0$ such that

$$bN_1 + cN_2 = a. \quad (2.68)$$

$$eN_1 + fN_2 = d. \quad (2.69)$$

From equation (2.68),

$$bN_1 = a - cN_2. \quad (2.70)$$

By multiplying equation (2.69) by b and substituting into equation (2.68), we would obtain

$$e(a - cN_2) + bfN_2 = bd. \quad (2.71)$$

By solving this equation, we would obtain

$$N_2 = \frac{bd - ae}{bf - ce}. \quad (2.72)$$

provided $bd > ae$ and $bf > ce$

Next by substituting for the value of N_2 and multiplying out the bracket, we shall obtain

$$bN_1 = \frac{abf - ace - dbc + ace}{bf - ce}. \quad (2.73)$$

If we simplify this equation further, we shall obtain

$$N_1 = \frac{af - dc}{bf - ce}. \quad (2.74)$$

provided $af > dc$ and $bf > ce$.

Let $N_{1s} = N_1$ and $N_{2s} = N_2$. Then (N_{1s}, N_{2s}) is a positive steady state. At this steady state, both species will coexist and it is particularly interesting to ecologists.

In summary, we have similarly derived the steady state solutions as other researchers like ([134]) and several others have done: For example, apart from the trivial solution $(0, 0)$, the Lotka-Volterra competition model studied by ([134]) presents steady states in two fashions: as coexistence, where both N_{1s} and N_{2s} are positive internal solutions or as exclusion, where only one species survives at its carrying capacity and the other species will go extinct.

In the next section, we are interested to find out how the stability properties of these steady states are characterised.

2.7.2 Characterization of stability properties of competition

In the section, we shall characterize the stability properties of competition by using equations (2.35) and (2.36).

In this section, our objective is to investigate the characterization of the stability properties of the steady states which we have determined in the previous section.

Consider the linearization of these interaction functions by assuming that these functions of N_1 and N_2 are continuous and differentiable ([43])

$$F(N_1, N_2) = aN_1 - bN_1^2 - cN_1N_2. \quad (2.75)$$

$$G(N_1, N_2) = dN_2 - eN_1N_2 - fN_2^2. \quad (2.76)$$

We shall differentiate these functions partially with respect to N_1 and N_2 to obtain

$$J_{11} = \frac{\partial F}{\partial N_1} = a - 2bN_1 - cN_2. \quad (2.77)$$

$$J_{12} = \frac{\partial F}{\partial N_2} = -cN_1. \quad (2.78)$$

$$J_{21} = \frac{\partial G}{\partial N_1} = -eN_2. \quad (2.79)$$

$$J_{22} = \frac{\partial G}{\partial N_2} = d - eN_1 - 2fN_2. \quad (2.80)$$

Next, by following [80], we shall evaluate these functions at each steady state starting with the zero steady state $(0, 0)$.

At the steady state $(0, 0)$, the above partial derivatives are evaluated and we found that

$$J_{11} = a. \quad (2.81)$$

$$J_{12} = 0. \quad (2.82)$$

$$J_{21} = 0. \quad (2.83)$$

$$J_{22} = d. \quad (2.84)$$

The Jacobian matrix is defined by

$$J = \begin{pmatrix} a & 0 \\ 0 & d \end{pmatrix} \quad (2.85)$$

In this scenario, the eigenvalues are

$$\lambda_1 = a. \quad (2.86)$$

$$\lambda_2 = d. \quad (2.87)$$

Hence, the steady state $(0, 0)$ is unstable because the two eigenvalues have positive signs. These positive eigenvalues contribute to the unbounded growth of solutions over time.

Next, we shall characterize the stability property of the steady state solution $(0, \frac{d}{f})$. Similarly, we shall evaluate the above functions to obtain

$$J_{11} = a - \frac{cd}{f} = a(1 - \frac{cd}{af}). \quad (2.88)$$

$$J_{12} = 0. \quad (2.89)$$

$$J_{21} = -\frac{ed}{f}. \quad (2.90)$$

$$J_{22} = d - \frac{2df}{f} = -d. \quad (2.91)$$

Let $\Delta = 1 - \frac{cd}{af}$.

The Jacobian matrix J is defined by

$$J = \begin{pmatrix} a\Delta & 0 \\ -\frac{de}{f} & -d \end{pmatrix} \quad (2.92)$$

In this scenario, the corresponding eigenvalues are

$$\lambda_1 = a\Delta. \quad (2.93)$$

$$\lambda_2 = -d. \quad (2.94)$$

provided all the parameters are positive and $\Delta > 0$. Hence, the steady state $(0, \frac{d}{f})$ is unstable because the eigenvalues have opposite signs, one negative and the other positive provided $\frac{c}{f} < \frac{a}{d}$.

The positive eigenvalue contributes to the unbounded growth of solution whereas the negative eigenvalue contributes to the decaying behaviour of solution over time.

Next, we shall characterize the property of the steady state $(\frac{a}{b}, 0)$. In the same manner, we shall evaluate the linearized functions about this steady state to obtain

$$J_{11} = a - \frac{2ab}{b} = -a. \quad (2.95)$$

$$J_{12} = -\frac{ac}{b}. \quad (2.96)$$

$$J_{21} = 0. \quad (2.97)$$

$$J_{22} = d\left(1 - \frac{ae}{bd}\right). \quad (2.98)$$

Let $\Delta = 1 - \frac{ae}{bd}$.

The Jacobian matrix is defined by

$$J = \begin{pmatrix} -a & \frac{ac}{b} \\ 0 & d\Delta \end{pmatrix} \quad (2.99)$$

In this scenario, the corresponding eigenvalues are

$$\lambda_1 = -a. \quad (2.100)$$

$$\lambda_2 = d\Delta. \quad (2.101)$$

If all parameters defined by these eigenvalues are positive and $\Delta > 0$, then the steady state solution is unstable because the eigenvalues have opposite signs provided $\frac{e}{b} < \frac{d}{a}$.

Next, we shall evaluate the linearized functions at the positive steady state and investigate its stability. In this case,

$$J_{11} = a - 2bN_{1s} - cN_{2s} = a - 2b\left(\frac{af - cd}{bf - ce}\right) - c\left(\frac{bd - ae}{bf - ce}\right). \quad (2.102)$$

On multiplying out the brackets and simplifying, we shall obtain

$$J_{11} = \frac{abf - ace - 2abf + 2bcd - bcd + ace}{bf - ce}. \quad (2.103)$$

By a further simplification, we would obtain

$$J_{11} = \frac{bcd - abf}{bf - ce}. \quad (2.104)$$

Let $\Delta = bf - ce$ and $\alpha = bcd - abf$.

Next, we shall evaluate another function to obtain

$$J_{12} = -cN_{1s} = -c\left(\frac{af - cd}{bf - ce}\right). \quad (2.105)$$

By multiplying out the bracket, we shall obtain

$$J_{12} = \frac{c^2d - acf}{bf - ce}. \quad (2.106)$$

Let $\beta = c^2d - acf$. Similarly, at the positive steady state solution, we shall evaluate the function to obtain

$$J_{21} = \frac{ae^2 - bde}{bf - ce}. \quad (2.107)$$

Let $\delta = ae^2 - bde$.

Next, at the positive steady state solution, we shall evaluate another linearized function to obtain

$$J_{22} = d - e\left(\frac{af - cd}{bf - ce}\right) - 2f\left(\frac{bd - ae}{bf - ce}\right). \quad (2.108)$$

By multiplying out the brackets and simplifying, we shall obtain

$$J_{22} = \frac{aef - dbf}{bf - ce}. \quad (2.109)$$

Let $\gamma = aef - dbf$.

On substituting for these notations in the appropriate equations, we shall obtain the matrix

$$J - \lambda I = \begin{pmatrix} v_1 & v_2 \\ v_3 & v_4 \end{pmatrix} \quad (2.110)$$

where

$$v_1 = \frac{\alpha - \Delta\lambda}{\Delta} \quad (2.111)$$

$$v_2 = \frac{\beta}{\Delta} \quad (2.112)$$

$$v_3 = \frac{\delta}{\Delta} \quad (2.113)$$

$$v_4 = \frac{\gamma - \Delta\lambda}{\Delta} \quad (2.114)$$

By applying the characteristic equation $\det(J - \lambda I) = 0$, we shall obtain the following quadratic equation

$$\Delta^2\lambda^2 - \Delta(\alpha + \gamma)\lambda + (\alpha\gamma - \delta\beta) = 0. \quad (2.115)$$

On using the quadratic formula to solve this equation, we shall obtain two eigenvalues

$$\lambda_{1,2} = \frac{1}{2\Delta}[(\alpha + \gamma) \pm \sqrt{((\alpha + \gamma)^2 - 4(\alpha\gamma - \delta\beta))}]. \quad (2.116)$$

If $(\alpha + \gamma) < 0$ and $\sqrt{((\alpha + \gamma)^2 - 4(\alpha\gamma - \delta\beta))} < (\alpha + \gamma) < 0$, and provided $\Delta > 0$, then we shall obtain two eigenvalues with negative signs. Hence, the positive steady state (N_{1s}, N_{2s}) is stable provided

$$(\alpha + \gamma)^2 > 4(\alpha\gamma - \delta\beta). \quad (2.117)$$

These two negative eigenvalues contribute to the decaying behaviour of solutions over time. Hence, the positive steady state is stable. At this coexistence

steady state, neither species will go extinct. This conclusion has important ecological insights.

Therefore for the competition model equations, we would have four steady states out of which only three steady states are unstable. It is only the positive steady state that is stable under the constraints being specified.

If the model parameters of model equations of competition are slightly changed, we would likely observe a different qualitative behaviour of steady state solutions. We have done this level of analysis with a view to providing good insights on the criteria at which the two species can coexist and become stable. However, its detailed content would not be presented because it does not relate with the focus of this section.

In our next level of analysis, we are interested to use an alternative analytical method to check for the stability and instability properties of these model equations of competition.

2.7.3 Another characterization of stability properties of competition: the method of a small perturbation from the steady state

In this section, we shall use the method of a small perturbation from the steady state which we have defined early in this chapter to investigate the stability and instability of each steady state as a sort of a reality check to see whether we would obtain the same conclusions about the qualitative behaviour of steady state solutions as those obtained by using the linearization about each steady state.

We consider the following interaction functions

$$F(N_1, N_2) = aN_1 - bN_1^2 - cN_1N_2 \quad (2.118)$$

$$G(N_1, N_2) = dN_2 - eN_1N_2 - fN_2^2 \quad (2.119)$$

First, does a small perturbation from the trivial steady state grows or decays?

For the purpose of clarity, we can see that at the trivial steady state, $F(0, 0) = 0$ and $G(0, 0) = 0$. By partial differentiation with respect to N_1 , we know that

$$\frac{\partial F}{\partial N_1} = a - 2bN_1 - cN_2 \quad (2.120)$$

where $\frac{\partial F}{\partial N_1}(N_{1s}, N_{2s}) = \frac{\partial F}{\partial N_1}(0, 0) = a$

By partial differentiation with respect to N_2 , we obtain

$$\frac{\partial F}{\partial N_2} = -cN_1 \quad (2.121)$$

where $\frac{\partial F}{\partial N_2}(0, 0) = 0$

Similarly, we obtain

$$\frac{\partial G}{\partial N_1} = -eN_2 \quad (2.122)$$

where $\frac{\partial G}{\partial N_1}(0, 0) = 0$

and

$$\frac{\partial G}{\partial N_2} = d - eN_1 - 2fN_2 \quad (2.123)$$

where $\frac{\partial G}{\partial N_2}(0, 0) = d$

Hence, the qualitative behaviour of a small perturbation from the trivial steady state over time is described by $\frac{du}{dt} = au$ and $\frac{dv}{dt} = dv$.

In a general case, for a competition system of equations, since a and d are positive constants, it follows that the perturbations from the trivial steady state will grow. In this case, both N_1 and N_2 will move away from the steady state. Therefore, the trivial steady state is unstable which is consistent with the qualitative behaviour of solutions over time when we used the method of linearization.

For other steady state solutions, we would simply summarise our findings as

1. The qualitative behaviour of a small perturbation from the steady state $(0, \frac{d}{f})$ over time is described by $\frac{du}{dt} = (a - \frac{cd}{f})u$ and $\frac{dv}{dt} = -d(\frac{eu}{f} + v)$ indicating that u will grow over time provided $a > \frac{cd}{f}$ and v will decay provided $\frac{eu}{f} + v > 0$. In this case, N_1 will move away from the steady state whereas N_2 will move towards the steady state. Therefore, the steady state $(0, \frac{d}{f})$ is unstable. This conclusion is consistent with the qualitative behaviour of solutions over time when we used the method of linearization.
2. The qualitative behaviour of a small perturbation from the steady state $(\frac{a}{b}, 0)$ over time is described by $\frac{du}{dt} = -a(u + \frac{c}{b}v)$ and $\frac{dv}{dt} = (d - \frac{ae}{b})v$ indicating that u will decay over time provided $(u + \frac{c}{b}v) > 0$ and v will grow over time provided $d > \frac{ae}{b}$. In this case, N_1 will move towards the steady state whereas N_2 will move away from the steady state. Therefore, the steady state solution $(\frac{a}{b}, 0)$ is unstable. This conclusion is consistent with the qualitative behaviour of solutions over time when we used the method of linearization.
3. The qualitative behaviour of a small perturbation from a positive steady state $(\frac{af-cd}{bf-ce}, \frac{bd-ae}{bf-ce})$ over time is described by

$$\frac{du}{dt} = -\alpha_1(bu + cv) \quad (2.124)$$

$$\frac{dv}{dt} = -\alpha_2(eu + fv) \quad (2.125)$$

where $\alpha_1 = \frac{af-cd}{bf-ce}$ and $\alpha_2 = \frac{bd-ae}{bf-ce}$ provided

1. $bf > ce$
2. $af > cd$.
3. $bd > ae$

These information indicate that both u and v will decay over time provided the above inequalities are true. Similarly, both N_1 and N_2 will move toward the steady state. Therefore, the positive steady state (α_1, α_2) is stable. Our conclusion is consistent with the qualitative behaviour of solutions over time when we used the method of linearization.

Due to the constraint of the length of this thesis, we cannot apply this method to checking for the stability and instability of other types of species interactions such as mutualism, commensalism, and parasitism.

2.7.4 Uniqueness of steady state solutions of model equations of competition

Is the steady state solution (N_{1s}, N_{2s}) unique? For the model equations of competition, we would obtain

$$bN_1 + cN_2 = a \quad (2.126)$$

$$eN_1 + fN_2 = d \quad (2.127)$$

or we can recast the above equations in matrix form

$$AX = H \quad (2.128)$$

where the coefficient matrix is defined by

$$A = \begin{pmatrix} b & c \\ e & f \end{pmatrix} \quad (2.129)$$

where the determinant of matrix A denoted by $\det A$ is $bf - ce$. and the matrix of the right hand side of the simultaneous system is defined by

$$H = \begin{pmatrix} a \\ d \end{pmatrix} \quad (2.130)$$

By the principle of the Cramer's rule, we know that

$$A_1 = \begin{pmatrix} a & c \\ d & f \end{pmatrix} \quad (2.131)$$

where the determinant of matrix A_1 is $af - cd$.

By using a similar approach, we would obtain

$$A_2 = \begin{pmatrix} b & a \\ e & d \end{pmatrix} \quad (2.132)$$

where the determinant of matrix A_2 is $bd - ae$.

Hence, the unique solution of this system of two equations is (N_{1s}, N_{2s}) where

$$N_{1s} = \frac{\det A_1}{\det A} = \frac{af - cd}{bf - ce} \quad (2.133)$$

and

$$N_{2s} = \frac{\det A_2}{\det A} = \frac{bd - ae}{bf - ce}. \quad (2.134)$$

provided

1. $bf > ce$.
2. $af > cd$.
3. $bd > ae$.

In summary, through this procedure, we have shown that the steady state solution to the system of model equations of competition is unique. This unique solution can not be generalised to other model equations of species interactions. For other types of species interactions, we can similarly show that their steady state solutions are unique.

2.8 Model equations of mutualism

In this section, we shall be studying the dynamics of a mutualistic interaction (+, +) model. By modifying model equations of competition to include a (+, +) interaction, we shall obtain the following model equations of mutualism:

$$\frac{dN_1}{dt} = N_1(a - bN_1 + cN_2). \quad (2.135)$$

$$\frac{dN_2}{dt} = N_2(d + eN_1 - fN_2). \quad (2.136)$$

where the model parameters are all positive and their meanings are as defined in the previous section subject to the same initial conditions $N_1(0) = N_{10} > 0$ and $N_2(0) = N_{20} > 0$.

We are interested to characterize the steady state solutions and stability or instability properties of these model equations of mutualism.

In our next analysis, we shall focus on characterizing the steady states and stability properties of model equations of mutualism as we did for model equations of competition.

2.8.1 Characterization of steady states of mutualism

By using the standard method of calculating the steady states, we found

1. The trivial steady state solution is $(0, 0)$.
2. Another steady state solution is $(0, \frac{d}{f})$.
3. Another steady state solution is $(\frac{a}{b}, 0)$.

2.8.2 Uniqueness of steady state solutions of model equations of mutualism

If $N_1 \neq 0$ and $N_2 \neq 0$ are assumed, then we shall obtain two linear simultaneous equations in two unknowns N_1 and N_2

$$bN_1 - cN_2 = a. \quad (2.137)$$

$$-eN_1 + fN_2 = d. \quad (2.138)$$

By using the Cramer's rule, we can solve these equations to obtain

$$N_1 = \frac{af + cd}{bf - ce}. \quad (2.139)$$

and

$$N_2 = \frac{bd + ae}{bf - ce}. \quad (2.140)$$

provided

1. $bf > ce$.
2. $af + cd > 0$.
3. $bd + ae > 0$.

This positive steady state solution is unique and can not be generalised to other model equations of species interactions.

Let $N_1 = N_{1s}$ and $N_2 = N_{2s}$. Hence, (N_{1s}, N_{2s}) is a positive steady state where both species populations coexist.

This unique positive steady state can only be positive provided $bf > ce$, $af + cd > 0$ and $bd + ae > 0$. Since, all the constants are positive, it is unlikely to have a negative steady state as discussed by [134].

Our next task is to investigate the characterization of the stability or instability property of the positive steady state solution only. We shall simply summarise our calculations for the stability or instability properties of the other three steady state solutions.

2.8.3 Characterization of stability of mutualism

Let the positive steady state be (N_{1s}, N_{2s})

Consider the following differentiable and continuous functions

$$F(N_1, N_2) = aN_1 - bN_1^2 + cN_1N_2. \quad (2.141)$$

$$G(N_1, N_2) = dN_2 + eN_1N_2 - fN_2^2. \quad (2.142)$$

By differentiating these functions partially, we would obtain

$$J_{11} = \frac{\partial F}{\partial N_1} = a - 2bN_1 + cN_2. \quad (2.143)$$

$$J_{12} = \frac{\partial F}{\partial N_2} = cN_1. \quad (2.144)$$

$$J_{21} = \frac{\partial G}{\partial N_1} = eN_2. \quad (2.145)$$

$$J_{22} = \frac{\partial G}{\partial N_2} = d + eN_1 - 2fN_2. \quad (2.146)$$

Next, we shall evaluate these linearized equations at the positive steady state solution.

At the point (N_{1s}, N_{2s}) , we shall obtain

$$J_{11} = a - 2b\left(\frac{af + cd}{bf - ce}\right) + c\left(\frac{bd + ae}{bf - ce}\right). \quad (2.147)$$

On multiplying out these two brackets and simplifying, we would obtain

$$J_{11} = -\left(\frac{abf + bcd}{bf - ce}\right). \quad (2.148)$$

Let

$$\Delta = bf - ce. \quad (2.149)$$

$$\alpha = abf + bcd. \quad (2.150)$$

$$J_{12} = cN_1 = \frac{acf + dc^2}{bf - ce}. \quad (2.151)$$

Let

$$\beta = acf + c^2d. \quad (2.152)$$

$$J_{21} = eN_2 = \frac{bde + ae^2}{bf - ce}. \quad (2.153)$$

Let

$$\delta = bde + ae^2. \quad (2.154)$$

$$J_{22} = d + e\left(\frac{af + cd}{bf - ce}\right) - 2f\left(\frac{bd + ae}{bf - ce}\right). \quad (2.155)$$

Let

$$\gamma = bdf + aef. \quad (2.156)$$

By using these notations, we shall construct the following matrix

$$J - \lambda I = \begin{pmatrix} v_5 & v_6 \\ v_7 & v_8 \end{pmatrix} \quad (2.157)$$

where

$$v_5 = -\left(\frac{\alpha + \Delta\lambda}{\Delta}\right) \quad (2.158)$$

$$v_6 = \frac{\beta}{\Delta} \quad (2.159)$$

$$v_7 = \frac{\delta}{\Delta} \quad (2.160)$$

$$v_8 = -\left(\frac{\gamma + \Delta\lambda}{\Delta}\right) \quad (2.161)$$

By using the characteristic equation $\det(J - \lambda I) = 0$, we would obtain the quadratic equation

$$\Delta^2\lambda^2 + \Delta(\alpha + \gamma)\lambda + (\alpha\gamma - \delta\beta) = 0. \quad (2.162)$$

By solving the quadratic equation, we would obtain the two eigenvalues

$$\lambda_{1,2} = \frac{1}{2\Delta} [\pm\sqrt{((\alpha + \gamma)^2 - 4(\alpha\gamma - \delta\beta))} - (\alpha + \gamma)] < 0. \quad (2.163)$$

provided

$$\sqrt{((\alpha + \gamma)^2 - 4(\alpha\gamma - \delta\beta))} < (\alpha + \gamma). \quad (2.164)$$

Hence, the positive steady state (N_{1s}, N_{2s}) is stable because the two eigenvalues have negative signs. These eigenvalues contribute to the decaying behaviour of solutions over time.

In summary, our calculations for the instability of the steady states are as follows:

1. For the trivial steady state solution $(0, 0)$, the two eigenvalues are $\lambda_1 = a$ and $\lambda_2 = d$. Hence, the trivial steady state solution is unstable because the eigenvalues are both positive.
2. For the steady state solution $(\frac{a}{b}, 0)$, the two eigenvalues are $\lambda_1 = -a$ and $\lambda_2 = d + \frac{ae}{b}$. Hence, this steady state solution is unstable because the eigenvalues are of opposite signs.
3. For the steady state solution $(0, \frac{d}{f})$, the two eigenvalues are $\lambda_1 = (a + \frac{cd}{f})$ and $\lambda_2 = -d$. Hence, this steady state solution is unstable because the eigenvalues are of opposite signs.

According to [134] and [145], there are certain forms of model equations of mutualism that have problematic features in the sense of its steady state having negative values. These model equations shall be defined, analysed, and discussed in our next section.

2.9 Orgy of mutual benefaction

In this section, we would like to define and explain the notion of an "orgy of mutual benefaction" as discussed by [134] and [145].

Up till now, we have only seen cases of positive steady states. But in a special type of $(+, +)$ interaction between two species, one can observe a case of negative steady states. These typical model equations are

$$\frac{dN_1}{dt} = aN_1 + cN_1N_2 \quad (2.165)$$

$$\frac{dN_2}{dt} = dN_2 + eN_1N_2 \quad (2.166)$$

with $N_1(0) = N_{10} > 0$ and $N_2(0) = N_{20} > 0$

We can see that the point $(0, 0)$ is a steady state solution. If $N_1 \neq 0$ and $N_2 \neq 0$, $N_{2s} = -\frac{a}{c}$ and $N_{1s} = -\frac{d}{e}$. [134] has described this behaviour as "an orgy of mutual benefaction". According to this author, realistic models of mutualism must at least show a mutual benefit to both species or as many as are involved, and have positive steady state or limit cycle type oscillation.

For these typical model equations of mutual benefaction,

$$F(N_1, N_2) = aN_1 + cN_1N_2 \quad (2.167)$$

$$G(N_1, N_2) = dN_2 + eN_1N_2 \quad (2.168)$$

We shall similarly construct the partial derivatives of these functions with respect to N_1 and N_2 and evaluate each function at these two steady states. By doing this, we shall obtain

$$J_{11} = a + cN_2 \quad (2.169)$$

$$J_{12} = cN_1 \quad (2.170)$$

$$J_{21} = eN_2 \quad (2.171)$$

$$J_{22} = d + eN_1 \quad (2.172)$$

At the trivial steady state, $J_{11} = a$, $J_{12} = 0$, $J_{21} = 0$, $J_{22} = d$. Hence, the two eigenvalues will definitely have two positive signs. In this scenario, the trivial steady state will be unstable contributing to unbounded growth of solutions over time.

To avoid the possibility of not obtaining a negative steady state, [134] has suggested a set of two model equations that describe the dynamics of two mutualistically interacting species. This new set of model equations of mutualism has also been presented in the work of Murray (2002). As far as one knows, this is an open problem. This problematic feature shall be tackled next.

2.9.1 Another model of mutualism

Consider the following nonlinear ordinary differential equation model between two species with populations N_1 and N_2 ([145])

$$\frac{dN_1}{dt} = r_1N_1\left[1 - \frac{N_1}{K_1 + b_{12}N_2}\right]. \quad (2.173)$$

$$\frac{dN_2}{dt} = r_2N_2\left[1 - \frac{N_2}{K_2 + b_{21}N_1}\right]. \quad (2.174)$$

If the terms $b_{12}N_2$ and $b_{21}N_1$ are equated to zero, the two species populations will obey the well known logistic equation. In this context, the rate of change of each species population will be saturated by the carrying capacities of K_1 and K_2 . The corresponding model is

$$\frac{dN_1}{dt} = r_1N_1\left[1 - \frac{N_1}{k_1}\right]. \quad (2.175)$$

$$\frac{dN_2}{dt} = r_2N_2\left[1 - \frac{N_2}{k_2}\right]. \quad (2.176)$$

If these equations are modified, so as to include the effect of increasing the carrying capacity for each species by the presence of the other species, then we can obtain the present model (Murray, 2002) that we want to study if

$$k_1 = K_1 + b_{12}N_2. \quad (2.177)$$

$$k_2 = K_2 + b_{21}N_1. \quad (2.178)$$

2.9.2 Characterization of steady states

In this section, we shall be concerned with determining the steady states of the the model formulated in the previous section. By equating the rate of change for each population to zero, we can determine four steady states or equilibria. The first of these is the trivial zero equilibria. If r_1N_1 and r_2N_2 are not equal to zero, then the following equations are valid

$$N_1 - b_{12}N_2 = K_1. \quad (2.179)$$

$$-b_{21}N_1 + N_2 = K_2. \quad (2.180)$$

The matrix of the coefficients of the unknowns N_1 and N_2 is defined by

$$A = \begin{pmatrix} 1 & -b_{12} \\ -b_{21} & 1 \end{pmatrix} \quad (2.181)$$

Since $\det A \neq 0$, several non-trivial solutions exist depending on the value of the parameters. On using either the Cramer's rule method or any other method, the positive steady state solution is (N_{1s}, N_{2s}) where

$$N_{1s} = \frac{K_1 + b_{12}K_2}{1 - b_{12}b_{21}}. \quad (2.182)$$

and

$$N_{2s} = \frac{K_2 + b_{21}K_1}{1 - b_{12}b_{21}}. \quad (2.183)$$

provided

1. $K_1 + b_{12}K_2 > 0$.
2. $K_2 + b_{21}K_1 > 0$.
3. $1 > b_{12}b_{21}$.

By using a similar method of calculating the border steady state, the next steady state solution is (N_{1s}, N_{2s}) where

$$N_{1s} = 0. \quad (2.184)$$

$$N_{2s} = \frac{K_2 + b_{21}K_1}{1 - b_{12}b_{21}}. \quad (2.185)$$

provided

1. $K_2 + b_{21}K_1 > 0$.
2. $1 > b_{12}b_{21}$.

Similarly, another border steady state solution is (N_{1s}, N_{2s}) where

$$N_{1s} = \frac{K_1 + b_{12}K_2}{1 - b_{12}b_{21}}. \quad (2.186)$$

$$N_{2s} = 0. \quad (2.187)$$

provided

1. $K_1 + b_{12}K_2 > 0$.
2. $1 > b_{12}b_{21}$.

2.9.3 Characterization of stability

We shall linearise the above interaction functions and evaluate the partial derivatives at the positive steady state only. In this regard, we shall consider

$$F(N_1, N_2) = (r_1 N_1) \left(\frac{K_1 + b_{12}N_2 - N_1}{K_1 + b_{12}N_2} \right) \quad (2.188)$$

$$G(N_1, N_2) = (r_2 N_2) \left(\frac{K_2 + b_{21}N_1 - N_2}{K_2 + b_{21}N_1} \right) \quad (2.189)$$

To find the partial derivatives of these functions with respect to N_1 and N_2 , we shall apply the product rule differentiation. To enable this partial differentiation, consider

$$u = r_1 N_1. \quad (2.190)$$

$$v = \left(\frac{K_1 + b_{12}N_2 - N_1}{K_1 + b_{12}N_2} \right). \quad (2.191)$$

$$w = r_2 N_2. \quad (2.192)$$

$$h = \left(\frac{K_2 + b_{21}N_1 - N_2}{K_2 + b_{21}N_1} \right). \quad (2.193)$$

Hence,

$$F(N_1, N_2) = uv. \quad (2.194)$$

$$G(N_1, N_2) = wh. \quad (2.195)$$

By partial differentiating these interaction functions with respect to N_1 and N_2 , we shall obtain

$$J_{11} = \frac{\partial F}{\partial N_1} = \frac{r_1 K_1 + r_1 b_{12} N_2 - 2r_1 N_1}{K_1 + b_{12} N_2} \quad (2.196)$$

$$J_{12} = \frac{\partial F}{\partial N_2} = \frac{b_{12} r_1 N_1^2}{(K_1 + b_{12} N_2)^2} \quad (2.197)$$

$$J_{21} = \frac{\partial G}{\partial N_1} = \frac{r_2 b_{21} N_2^2}{(K_2 + b_{21} N_1)^2} \quad (2.198)$$

$$J_{22} = \frac{\partial G}{\partial N_2} = \frac{r_2 K_2 + r_2 b_{21} N_1 - 2r_2 N_2}{K_2 + b_{21} N_1} \quad (2.199)$$

Next, we evaluate these partial derivatives to obtain

$$J_{11} = -r_1 \quad (2.200)$$

$$J_{12} = b_{12} r_1 \quad (2.201)$$

$$J_{21} = r_2 b_{21} \quad (2.202)$$

$$J_{22} = -r_2 \quad (2.203)$$

Hence, the Jacobian matrix is defined by

$$J = \begin{pmatrix} -r_1 & b_{12} r_1 \\ r_2 b_{21} & -r_2 \end{pmatrix} \quad (2.204)$$

We know that another method of checking whether the steady state is stable or unstable or neither stable nor unstable is to calculate the determinant of the Jacobian matrix ([92]). By applying this method, we will obtain

$$\det(J) = r_1 r_2 (1 - b_{12} b_{21}) \quad (2.205)$$

Hence, we shall differentiate three criteria for the stability or instability of a given steady state solution namely

1. If $\det(J) > 0$ at a given steady state solution, then this steady state solution is said to be stable provided $r_1 r_2 > 0$ and $1 > b_{12} b_{21}$.
2. If $\det(J) = 0$ provided $b_{12} b_{21} = 1$, then this steady state solution is said to be sitting on the 'cusp', that is, it is neither stable nor unstable.
3. If $\det(J) < 0$ at a given steady state solution, then this steady state solution is said to be unstable provided $r_1 r_2 > 0$ and $1 < b_{12} b_{21}$.

Next, we will investigate the criteria for the stability of the positive steady state. Consider the matrix $(J - \lambda I)$ from which the characteristic quadratic equation $(J - \lambda I = 0)$ is

$$\lambda^2 + (r_1 + r_2)\lambda + r_1 r_2(1 - b_{12}b_{21}) = 0. \quad (2.206)$$

The two roots of this quadratic equation are

$$\lambda_{1,2} = \frac{-(r_1 + r_2) \pm \sqrt{[(r_1 + r_2)^2 - 4r_1 r_2(1 - b_{12}b_{21})]}}{2} \quad (2.207)$$

Let $D = [(r_1 + r_2)^2 - 4r_1 r_2(1 - b_{12}b_{21})]$. By simplifying this formula, we can rewrite it as $D = r_1^2 + r_2^2 + 2r_1 r_2(2b_{12}b_{21} - 1)$. We observe that the value of D will have a positive sign provided $r_1 > 0$, $r_2 > 0$, $2b_{12}b_{21} > 1$.

Hence

$$\lambda_{1,2} = \frac{-(r_1 + r_2) \pm \sqrt{D}}{2} \quad (2.208)$$

For the purpose of our next discussion about the stability of the positive steady state, we will split these eigenvalue roots into two namely

$$\lambda_1 = \frac{-(r_1 + r_2 + \sqrt{D})}{2} \quad (2.209)$$

$$\lambda_2 = \frac{\sqrt{D} - (r_1 + r_2)}{2} \quad (2.210)$$

- Claim 1: If $(r_1 + r_2 + \sqrt{D}) > 0$, then $\lambda_1 < 0$ provided $r_1 > 0$, $r_2 > 0$, $2b_{12}b_{21} > 1$.
- Claim 2: If $\sqrt{D} > (r_1 + r_2)$, then $\lambda_2 > 0$ provided $r_1 > 0$, $r_2 > 0$, $2b_{12}b_{21} > 1$.
- Claim 3: If $\sqrt{D} < (r_1 + r_2)$, then $\lambda_2 < 0$ provided $r_1 > 0$, $r_2 > 0$, $2b_{12}b_{21} > 1$.
- Claim 4: If $\sqrt{D} = (r_1 + r_2)$, then $\lambda_1 < 0$ and $\lambda_2 = 0$ provided $r_1 > 0$, $r_2 > 0$, $b_{12}b_{21} > 1$.

On the basis of claim 1 and claim 2, our positive steady will be unstable (or saddle) because the eigenvalues will have opposite signs whereas on the basis of claim 1 and claim 3, our positive steady state will be stable, otherwise called a stable node or sink. We also observe that our positive steady state is neither stable nor unstable, that is, it is sitting on the cusp on the basis of claim 4.

In summary, we know that the trivial steady state is a saddle point (unstable) because the two eigenvalues have positive signs while the two steady states $(0, K_2)$ and $(K_1, 0)$ are unstable saddle points because the two eigenvalues have opposite signs. We did not present this analysis in this section because we have done similar analyses in this chapter. The only useful conclusion of our analysis in this section is to report that our positive steady state is stable provided the criteria of claim 1 and claim 3 are satisfied.

So far, we have analysed model equations of competition and mutualism. We have similarly defined and analysed the notion of the model of mutual benefaction. Next, we shall tackle the analysis of the model equations of commensalism. This is $(+, 0)$ interaction.

2.10 Another model of commensalism

Our task in this section is to analyse the model equations of commensalism (+, 0) interaction between two plant species. The coupled ordinary differential equations that describe this process take the following form

$$\frac{dN_1}{dt} = N_1(a - bN_1 + cN_2) \quad (2.211)$$

$$\frac{dN_2}{dt} = N_2(d - fN_2) \quad (2.212)$$

with $N_1(0) = N_{10} > 0$ and $N_2(0) = N_{20} > 0$ where the model parameters are positive.

2.10.1 Steady state solutions of commensalism

Following our previous mathematical technique, we found

1. The trivial steady state solution is $(0, 0)$.
2. Another steady state solution is $(\frac{a}{b}, 0)$.
3. The positive steady state solution is $(\frac{cd+af}{bf}, \frac{d}{f})$.

Since we have shown in the cases of competition and mutualism how to investigate the stability properties of the steady state solutions, we shall simply summarise our calculations for the case of commensalism in this section.

2.10.2 Uniqueness of steady state solutions of model equations of commensalism

In this section, our task is to study the uniqueness of the steady state solutions of model equations of commensalism. For $N_1 \neq 0$ and For $N_2 \neq 0$, we obtain

$$bN_1 - cN_2 = a \quad (2.213)$$

$$fN_2 = d \quad (2.214)$$

From these two simple linear equations, the two solutions are solved to obtain

$$N_2 = \frac{d}{f} > 0 \quad (2.215)$$

$$N_1 = \frac{cd + af}{bf} > 0 \quad (2.216)$$

Therefore, under these simplifying assumptions, we would say that the steady state solution (N_1, N_2) of the model equations of commensalism is unique and it can not be generalised to other model equations of species interactions.

2.10.3 Stability properties of commensalism

In this section, we shall present our calculations as follows

1. For the trivial steady state solution $(0, 0)$, the two eigenvalues are $\lambda_1 = a$ and $\lambda_2 = d$. Hence, the trivial steady state solution is unstable because the eigenvalues are both positive.
2. For the steady state solution $(\frac{a}{b}, 0)$, the two eigenvalues are $\lambda_1 = -a$ and $\lambda_2 = d$. Hence, this steady state solution is unstable because the eigenvalues are of opposite signs.
3. For the steady state solution $(\frac{cd+af}{bf}, \frac{d}{f})$, the two eigenvalues are $\lambda_1 = -(a + \frac{cd}{f})$ and $\lambda_2 = -d$. Hence, this steady state solution is stable because the eigenvalues are both negative.

Up to this stage of our analysis, we have studied the mathematical analyses of model equations of competition, mutualism, and commensalism. The pending model equations of parasitism (which is a $(+, -)$ interaction) shall be analysed next.

2.11 Another model of parasitism

Our task in this section is to analyse the model equations of parasitism $(+, -)$ interaction between two plant species. The coupled ordinary differential equations that describe this $(+, -)$ interaction are

$$\frac{dN_1}{dt} = N_1[a - bN_1 + cN_2] \quad (2.217)$$

$$\frac{dN_2}{dt} = N_2[d - eN_1 - fN_2] \quad (2.218)$$

with $N_1(0) = N_{10} > 0$ and $N_2(0) = N_{20} > 0$ where the model parameters are positive constants.

2.11.1 Steady state solutions of parasitism

In this section, we found these steady state solutions

1. The trivial steady state solution is $(0, 0)$.
2. Another steady state solution is $(0, \frac{d}{f})$.
3. Another steady state solution is $(\frac{a}{b}, 0)$.
4. The positive steady state solution is $(\frac{af+cd}{bf+ce}, \frac{bd-ae}{bf+ce})$. This positive steady state will have positive values only provided $af + cd > 0$, $bf + ce > 0$, $bd > ae$.

2.11.2 Uniqueness of steady state solutions of model equations of parasitism

In this section, our task is to study the uniqueness of the steady state solutions of model equations of parasitism. For $N_1 \neq 0$ and For $N_2 \neq 0$, we obtain the following linear simultaneous equations in two unknowns N_1 and N_2

$$bN_1 - cN_2 = a \quad (2.219)$$

$$eN_1 + fN_2 = d \quad (2.220)$$

From the theory of elementary algebra, we know that

$$J = \begin{pmatrix} b & -c \\ e & f \end{pmatrix} \quad (2.221)$$

$$H = \begin{pmatrix} a \\ d \end{pmatrix} \quad (2.222)$$

$$A_1 = \begin{pmatrix} a & -c \\ d & f \end{pmatrix} \quad (2.223)$$

$$A_2 = \begin{pmatrix} b & a \\ e & d \end{pmatrix} \quad (2.224)$$

Hence, $\det J = bf + ce$, $\det A_1 = af + cd$, $\det A_2 = bd - ae$. By using the Cramer's rule, we shall obtain

$$N_1 = \frac{af + cd}{bf + ce} > 0 \quad (2.225)$$

$$N_2 = \frac{bd - ae}{bf + ce} > 0 \quad (2.226)$$

provided

1. $af + cd > 0$
2. $bf + ce > 0$
3. $bd > ae$

Therefore, under these simplifying assumptions, we would say that the steady state solution (N_1, N_2) of the model equations of parasitism is unique and it can not be generalised to other model equations of species interactions.

2.11.3 Stability properties of parasitism

In this section, we shall similarly summarise our calculations as follows

1. For the trivial steady state solution $(0, 0)$, the two eigenvalues are $\lambda_1 = a$ and $\lambda_2 = d$. Hence, the trivial steady state solution for the model equations of parasitism is unstable because the eigenvalues are both positive.

2. For the steady state solution $(0, \frac{d}{f})$, the two eigenvalues are $\lambda_1 = a + \frac{cd}{f}$ and $\lambda_2 = -d$. Hence, this steady state solution is unstable because the eigenvalues are of opposite signs.
3. For the steady state solution $(\frac{a}{b}, 0)$, the two eigenvalues are $\lambda_1 = -a$ and $\lambda_2 = d - \frac{ae}{b}$. Hence, this steady state solution is unstable because the eigenvalues are of opposite signs provided $d > \frac{ae}{b}$.
4. For the steady state solution $(\frac{a}{b}, 0)$, if the two eigenvalues are $\lambda_1 = -a$ and $\lambda_2 = d - \frac{ae}{b}$ provided $d < \frac{ae}{b}$, then this steady state solution will be stable. If $d > \frac{ae}{b}$, then this steady state solution will become unstable.

However, we shall investigate the stability of the positive steady state solution.

In this section, we shall linearise the following two continuous and differentiable functions of N_1 and N_2

$$F(N_1, N_2) = aN_1 - bN_1^2 + cN_1N_2 \quad (2.227)$$

$$G(N_1, N_2) = dN_2 - eN_1N_2 - fN_2^2 \quad (2.228)$$

Following the same standard mathematical technique, we would obtain

$$J_{11} = a - 2bN_1 + cN_2 \quad (2.229)$$

$$J_{12} = cN_1 \quad (2.230)$$

$$J_{21} = -eN_2 \quad (2.231)$$

$$J_{22} = d - eN_1 - 2fN_2 \quad (2.232)$$

By evaluating the linearised functions at the positive steady state $(\frac{af+cd}{bf+ce}, \frac{bd-ae}{bf+ce})$, we would obtain

$$J_{11} = -\left(\frac{abf + bcd}{bf + ce}\right) \quad (2.233)$$

$$J_{12} = \frac{c^2d + acf}{bf + ce} \quad (2.234)$$

$$J_{21} = \frac{ae^2 - bde}{bf + ce} \quad (2.235)$$

$$J_{22} = -\frac{aef - bdf}{bf + ce} \quad (2.236)$$

Next, we would use the following expressions to simplify our analysis:

$$\Delta = bf + ce \quad (2.237)$$

$$\alpha = abf + bcd \quad (2.238)$$

$$\beta = acf + c^2d \quad (2.239)$$

$$\gamma = ae^2 - bde \quad (2.240)$$

$$r = aef - bdf \quad (2.241)$$

Hence, the stability of the positive steady state is governed by the eigenvalues of the Jacobian matrix

$$J = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \quad (2.242)$$

where

$$a_{11} = -\left(\frac{\alpha}{\Delta}\right) \quad (2.243)$$

$$a_{12} = \frac{\beta}{\Delta} \quad (2.244)$$

$$a_{21} = \frac{\gamma}{\Delta} \quad (2.245)$$

$$a_{22} = \frac{r}{\Delta} \quad (2.246)$$

By forming the characteristic equation and finding the eigenvalues, we would obtain

$$\lambda_{1,2} = \frac{1}{2\Delta}[s \pm \sqrt{D}] \quad (2.247)$$

where $s = r - \alpha$ and $D = \sqrt{(s^2 + 4(r\alpha + \beta\gamma))}$.

Claim 1: If $\lambda_1 < 0$.

In this case, $(s + D) < 0$ provided $D < -s$, $r > \alpha$.

Claim 2: If $\lambda_2 < 0$.

In this case, $(s - D) < 0$ provided $s < D$, $r < \alpha$.

Under the assumptions of these claims, we can state that the positive steady state of the model equations of parasitism is stable because the two eigenvalues will have negative signs that contribute to the decaying behaviour of solutions over time.

In summary, the procedure for determining the stability of the steady state (N_{1s}, N_{2s}) is as follows:

1. Compute all partial derivatives of the right-hand side of the original system of model equations, and construct the Jacobian matrix.
2. Evaluate the Jacobian matrix at a given steady state solution (N_{1s}, N_{2s}) .
3. Calculate the eigenvalues for a given steady state solution.
4. Hence, conclude the stability or instability of the model equations of interaction based on the real parts of the eigenvalues.

The steady state solutions can be classified further by the eigenvalues of the Jacobian at the steady state (N_{1s}, N_{2s}) in the following way:

- $\lambda_i \in \mathbb{R}, \lambda_{1,2} < 0 \implies (N_{1s}, N_{2s})$ is a stable node (or sink).
- $\lambda_i \in \mathbb{R}, \lambda_{1,2} > 0 \implies (N_{1s}, N_{2s})$ is an unstable node (or source).
- $\lambda_i \in \mathbb{R}, \lambda_1 < 0 < \lambda_2 \implies (N_{1s}, N_{2s})$ is a saddle point (unstable).
- $\lambda_i = \alpha \pm i\beta, \alpha < 0 \implies (N_{1s}, N_{2s})$ is a stable spiral (or stable focus).
- $\lambda_i = \alpha \pm i\beta, \alpha > 0 \implies (N_{1s}, N_{2s})$ is an unstable spiral (or unstable focus).
- $\lambda_i = \alpha \pm i\beta, \alpha = 0 \implies (N_{1s}, N_{2s})$ is a centre (or neutrally stable).

For the four model equations which we have analysed in this chapter, the stability and instability properties do not show qualitative behaviour for stable focus, unstable focus, and neutral stability.

In summary, we have observed two outcomes of a species interaction: coexistence or competitive exclusion. It would be a good idea to derive general criteria for the existence of coexistence, survival, and extinction. Our next analysis shall tackle this.

2.12 Criteria for Coexistence, Survival and Extinction

So far, we have only established the conditions for the coexistence of two interacting plant species. In this section, we shall define and derive some criteria for the existence of coexistence, survival, and extinction for model equations of competition, mutualism, commensalism, and parasitism.

2.12.1 Competition Interaction

We think that not all competing species can coexist. How then do we set up the criteria for the coexistence of two competing species when model parameters are independent of time? In this section, we shall use the following alternative formulation of competition equations which takes the following form:

$$\frac{dN_1}{dt} = aN_1 \left(\frac{K_1 - N_1 - \alpha_{12}N_2}{K_1} \right) \quad (2.248)$$

where $K_1 = \frac{a}{b}$ and $\alpha_{12} = \frac{c}{b}$.

$$\frac{dN_2}{dt} = dN_2 \left(\frac{K_2 - N_2 - \alpha_{21}N_1}{K_2} \right) \quad (2.249)$$

where $K_2 = \frac{d}{f}$ and $\alpha_{21} = \frac{e}{f}$.

When we analysed the competition model, we mentioned that a positive steady state will be guaranteed provided the following inequalities hold:

$$af > cd \quad (2.250)$$

$$bd > ae \quad (2.251)$$

$$bf > ce \quad (2.252)$$

If we divide the first inequality by b , we would obtain

$$\frac{a}{b} > \left(\frac{c}{b}\right)\left(\frac{d}{f}\right) \quad (2.253)$$

which implies that $K_1 > \alpha_{12}K_2$. This means that the ratio of the carrying capacity of the first plant species to the carrying capacity of the second plant species will be greater than a positive constant α_{12} .

Next, if we divide the second inequality by f , we would obtain

$$\frac{d}{f} > \left(\frac{e}{f}\right)\left(\frac{a}{b}\right) \quad (2.254)$$

which implies that $K_2 > \alpha_{21}K_1$. This means that the ratio of the carrying capacity of the second plant species to the carrying capacity of the first plant species will be greater than a positive constant α_{21} .

Finally, $bf > ce$ implies that

$$\frac{b}{c} > \frac{e}{f} \quad (2.255)$$

Therefore, we would obtain

$$\frac{b}{c} > \alpha_{21} \quad (2.256)$$

Since the inverse of $\frac{b}{c}$ is $\frac{1}{\frac{b}{c}}$, it follows that

$$\frac{1}{\alpha_{12}} > \alpha_{21} \quad (2.257)$$

Therefore, we would obtain the inequality

$$1 > \alpha_{12}\alpha_{21} \quad (2.258)$$

In summary, the three inequalities that will guarantee the coexistence of two interacting species when the model parameters are independent of time are

1. $K_1 > \alpha_{12}K_2$
2. $K_2 > \alpha_{21}K_1$
3. $1 > \alpha_{12}\alpha_{21}$

where $K_1 > 0, K_2 > 0, \alpha_{12} > 0, \alpha_{21} > 0$.

If these inequalities are satisfied, it means that the two competing species will coexist and neither of them will go extinct. If one of them violates say the second inequality, the second species will be extinct whereas the first species will survive or persist. If two of the species do not satisfy the above inequalities, the two species will be extinct under our present assumption.

It is worth mentioning at this stage of our analysis that the coexistence criteria which we have derived above are consistent with the viewpoint of other ecological experiments ([30]).

The advantage of these criteria is that it helps us to avoid the lengthy calculations as suggested by ([199]). What this means is that for any two competing plant species during a summer season, we can use these criteria to find out if these two species will coexist, survive or go extinct.

These inequality criteria may change for other types of interactions such as mutualism, parasitism, and commensalism. However, the conditions for the coexistence of two similar plant species and two dis-similar plant species which we did not derive at this stage have been provided by other ecologists ([30]). We shall define and explain these ideas next.

2.12.2 Coexistence Criteria for Two Similar Species

From our experimental analysis, the more similar two species are ecologically, the more similar their carrying capacities must be for the two species to coexist. If these similar species use the same resources, their carrying capacities are expected to satisfy the inequality $0.95 < \frac{K_1}{K_2} < \frac{1}{0.95}$ where the positive constants K_1 and K_2 are the carrying capacities for species 1 and species 2. By this criterion, it was reported that two similar plant species would require a small range for their coexistence.

2.12.3 Coexistence Criteria for Two Dis-Similar Species

In the same manner, the more dis-similar two species are ecologically, the more dis-similar their carrying capacities must be for the two species to coexist. If the species are very dis-similar ecologically in resource use, their carrying capacities are expected to satisfy the inequality $0.05 < \frac{K_1}{K_2} < \frac{1}{0.05}$.

Similarly, the positive constants K_1 and K_2 stand for the carrying capacities for species 1 and species 2. In this case, it was reported that two dis-similar plant species require a large range for their coexistence.

We would verify these coexistence criteria for two similar and two very dis-similar plant species in chapter three of this thesis after we have derived a typical prototype model equations of competition.

In this chapter, we have only focused on constructing the co-existence, survival and extinction criteria for the competition interaction. Similar criteria for other types of species interactions can be attempted which we did not embark on in this chapter.

2.13 Conclusion

In this chapter, we have used some typical mathematical techniques of steady state, stability and instability to analyse model equations of competition, mutualism, commensalism and parasitism between plant species. The expected ecological implications of our analyses were also discussed quantitatively.

We observe that it is only the positive steady state that is stable irrespective of the type of species interaction. Since the effect of the environment may

have some effect on these complex types of interactions, sometimes these stable steady states may switch to being unstable in the real ecological situation.

We have defined and discussed in detail the problematic features that have prompted the occurrence of the notion of "orgy of mutual benefaction". This phenomenon presents a strange mathematical formulation of $(+, +)$ interaction that would create negative steady state solutions. Alternative models of mutualism which do not have these problematic features have been defined and discussed in this chapter.

We have also defined and discussed the inequalities that provide conditions for the survival, extinction, and coexistence of two competing plant species for a limited resource in an environment.

The standard methods of analysing a two dimensional system of competition will be useful in chapter three to study the qualitative behaviour of our prototype model equations of competition.

Chapter 3

Estimation of the Parameters for Model Equations of Interspecific Competition

3.1 Motivation

Central in the development of a system of nonlinear first order ordinary differential equations that describe the interaction between two competing plant species are the concepts of the intrinsic growth rates, intraspecific interaction coefficients, interspecific interaction coefficients, and their starting plant biomasses.

Moreover, the growth of a plant species varies due to the uncertainty of the environment and other factors. In this chapter, we propose to use the combination of a nonlinear optimization and penalty function methods to estimate the model parameters of interspecific competition between two dis-similar plant species for a limited resource in an environment under some simplifying assumptions.

In the parametric modelling of data, we are often faced with a task to condense or summarise data points by fitting them to a model which has adjustable parameters. In some cases, the modelling could be a curve-fit of functions such as polynomials in which case the fit would determine the coefficients. In other cases, the model parameters would come from some underlying theory that the data are supposed to satisfy. An example is the plant growth data ([35]) under the assumption that the growth of a plant species over a time interval is exponential.

In other situations, one encounters a few data points which are to be extended into a continuous function but with some underlying idea of what that function would look like. This is similar to a curve-fitting idea except that the fit in this situation is more likely to be biased.

The approach which we shall adopt in this chapter is to choose an error or penalty function that measures the agreement between the data and the model. It is the concept of the metric-induced 2-norm over a solution vector space that

we will apply in this chapter. The parameters are then adjusted to achieve a minimum in the penalty function which yields the best fit parameters.

We must also bear in mind that data are not exact, they are subject to measurement uncertainties and therefore may not perfectly fit the model even when the model is correct. In this situation, [20] have suggested a number of approaches with which to characterize the confidence in the best-fit parameter estimates particularly with respect to a given family of models (each one with a best-fit set of parameters). We did not follow this line of analysis in this thesis because we are not dealing with a family of models.

The trade-off between goodness of fit and complexity is the key idea of the principle of Occam's razor (William of Occam, 1290-1349) otherwise called the principle of parsimony ([148]). This principle states that entities should not be multiplied beyond necessity ([148]). It is simply a criterion which can be used to decide among scientific theories or explanations. As far as the basic idea of this concept is concerned, selection methods can implement this principle in one way or another without necessarily plunging into the philosophy of this law.

3.2 Introduction

We intend to focus on the construction and mathematical analysis of model equations of competition for a few reasons. First, other types of interactions such as mutualism, commensalism, and parasitism may be adapted from the competition system. Second, we need only to consider a competition model for the primary aim of this thesis as mentioned in chapter one, that is, to develop a continuous dynamic model in combination with a stochastic winter model in order to find out if we can obtain a few cases of mutualism. Third, as mentioned in chapter one, the mathematical modelling of plant species interactions usually relies on competition models ([134]).

So far we have talked about the general formulation of model equations of competition interaction in chapters one and two. It would be important to switch from the classical approach which we now know to look at the methodology of constructing our own model equations of competition $(-, -)$ interaction between two species. As far as we know, this stage of our analysis is very important in the context of our present novel investigation based on some simplifying assumptions as mentioned in chapter two.

For the case of time series plant growth data, it has been shown that during the initial phase, the growth of seedlings follows an exponential law fairly closely and is given by the equation

$$W = W_0 e^{rt} \tag{3.1}$$

where

1. W denotes the weight of plant after time t in days.
2. W_0 denotes the initial weight of plant.
3. r denotes the intrinsic rate of growth.
4. e denotes the exponential coefficient 2.7182 ...

If we take the logarithm to base e of the above equation, we shall obtain

$$\log_e\left(\frac{W(t)}{W(0)}\right) = rt \quad (3.2)$$

where $t = t_2 - t_1$. The intrinsic growth rate r can be estimated by using this formula.

If we assume that the initial weight of plant doubles in two weeks' time, we can use the above formula to estimate the intrinsic growth rate of plant for a given growing period. This fourth night growth assumption can be made clearer in this manner. If the starting biomass is 0.0454 grams per area of grass cover for the first week and the starting value of the second week biomass is 0.064, the daily intrinsic growth rate in this example would be 0.049. With this example, it explains that the starting biomass would double in a fourth night only.

Apart from the data provided by [35], some other related data are those of [191] (and also that by Linehan which was cited by [191]) and [2]. These sources of data similarly assumed that the growth of plant species over time follows an exponential law.

For us to extend the idea of Blackman and apply it to develop a continuous competition model between two plant species, we will start our discussion in this chapter by estimating the intrinsic growth rate based on week 1.

In our next section, we defined and discussed how we set up the logistic model equations and how we can obtain our 10 logistic data points from the standard Blackman's time series data of five successive weeks biomass growth data.

Next, how do we make sense of these huge logistic data for a set of varying steady state and constant intrinsic growth over a given growth period. We think that the appropriate way of choosing the best model parameters that optimise the logistic data is by calculating the 2-norm penalty function and justifying that this non-negative number satisfies the characteristic of a monotone sequence. With a further finer grid around the minimum penalty function, we can realistically select the model parameters that provide a best fit between our simulated logistic data and Blackman's data. Under some simplifying assumptions between the intraspecific interaction coefficient and the interspecific interaction coefficient as suggested by [134], we were able to set the dynamics of model equations of competition between two similar plant species and that between two dis-similar interacting plant species.

A further mathematical analysis of these model equations is tackled and our results are quantitatively discussed in subsequent sections of this chapter by using the earlier ideas introduced in chapter one and chapter two. We would end this core chapter of this thesis with a clear conclusion pointing to what we hope to achieve in chapter four.

First, our numerical method being used in this chapter stems from the idea behind the concept of least squares approximation. For this reason, we would briefly define and discuss the application of this concept.

3.3 Least squares approximation problems

Central to our chosen methodology of nonlinear optimization of logistic model parameters is the concept of least squares approximation. There are other im-

portant applications in the field of acoustics ([116], [112], [125], [8]). Some other practical scientific problems where least squares approximations have been successfully applied are in the selected aspects of applied engineering sciences and mathematical physics ([17], [121], [18]).

We would briefly use a few examples to define and discuss the central idea behind the concept of the least squares approximation.

3.3.1 Example

This example is taken from the field of mathematical physics. Let $S(x)$ be the axial strain distribution in a uniform rod that lies along the x -axis from $x = 0$ to $x = \ell$ ([144], [124]). The strain energy (se) in the rod is proportional to the integral $\int_0^\ell |S(x)|^2 dx$. That is,

$$se = K \int_0^\ell |S(x)|^2 dx \quad (3.3)$$

where K is a positive constant of proportionality. We know that the closeness of an approximation $q(x)$ to $S(x)$ can be known according to the strain energy of the difference of the two strain distributions. That is,

$$V = K \int_0^\ell |S(x) - q(x)|^2 dx \quad (3.4)$$

This formula is called a least squares criterion. The least squares criterion can be approximated by using any of the three popular norms such as the 1-norm, 2-norm, and ∞ -norm.

Other examples where the principle of least squares approximation is being applied are in the electrical theory ([56]), in the analysis and processing of signals ([131]) and in immunology ([20]).

3.4 Estimation of the intrinsic growth rate of plant species populations

In this section, we shall focus on the estimation of the intrinsic growth rate of plant species populations. Then, we would use the value of the intrinsic growth rate and the steady state solution under some simplifying assumption to derive a nonlinear model for two interacting plant species.

Before we consider doing these, we would illustrate the idea behind the calculation of intrinsic growth rates with a few examples.

We shall also assume that, the period of growth will also affect the intrinsic growth rate per day of the plant species. Given the information on the yearly intrinsic growth rates of particular plant species, how do we estimate the intrinsic growth rate per day. By assuming that the plant species could double its weight in a temperate (summer, spring, autumn) climate over a fourth night, how do we estimate its intrinsic growth rate? This idea could also be considered for other types of climates.

3.5 Estimation of the intrinsic growth rate per day

In this section, we shall estimate the intrinsic growth rate using a few examples.

3.5.1 Example 1

Suppose the plant doubles its initial biomass, then $\log_e 2 = 0.69315 \dots$. Therefore, for a short growing season of 10 days, the plant species would produce new biomass assuming there is available resources for growth at the estimated rate of 0.0693 (0.69315 divided by 10), that is, 6.93 percent per day. If the period of growth is 5 days, the estimated intrinsic growth rate would be 0.13863, that is, 13.8 percent per day. If the period of growth is 14 days, the estimated intrinsic growth rate is 0.0495 which is 4.95 percent per day.

If the period of growth is 30 days, the estimated intrinsic growth rate is 0.023105, which is equivalent to 2.3 percent per day. If the period of growth is 70 days, the estimated intrinsic growth rate is 0.0099, which is equivalent to 0.99 percent per day. If the period of growth is 90 days, the estimated intrinsic growth rate is 0.0077, which is equivalent to 0.77 percent per day.

Hence, if the plant doubles its weight in terms of the period of growth, the estimated rate of growth will fall as the period of growth increases.

3.5.2 Example 2

Suppose a plant species increases its biomass by 2.5 per cent. In this example, $\log_e 1.025 = 0.0247 \dots$

Therefore, for a short growing season of 10 days, our estimated intrinsic growth rate per day is 0.00247 which is equivalent to 0.247 percent per day. If the period of growth were 5 days, the estimated intrinsic growth rate per day is 0.00494 which is equivalent to 0.494 percent per day. Similarly, if the period of growth is 14 days, the estimated intrinsic growth rate per day is 0.00176 which is equivalent to 0.176 percent per day.

If the period of growth is 30 days, the estimated intrinsic growth rate is 0.00082 which is equivalent to 0.082 percent per day.

Table 3.1 summarizes the estimated intrinsic growth rate of a single plant species when the periods of growth are 5 days, 10 days, and 14 days. Our rationale is based on the fact that the growth of the plant species depends on the varying patterns of the period of growth.

We can observe that as the percentage plant biomass increases, the estimated intrinsic growth rate r will increase irrespective of the length of the period of growth. The intrinsic growth rate after a period of 5 days is approximately 2 times bigger than the intrinsic growth rate after a period of 10 days when the percentage change in biomass is 3. Similarly, the intrinsic growth rate after a period of 5 days is approximately 2.8 times bigger than the intrinsic growth rate after a period of 14 days when the percentage change in biomass is 3.

The notation pcb stands for the percentage change in biomass.

If the biomass is being varied in the same pattern, how would the intrinsic growth rate after a period of 5 days when the percentage change in biomass is 3 compared with the intrinsic growth rates when the periods of plant growths are

Increase in biomass pcb	Growth Rate		
	5 days	10 days	14 days
1.025	0.00494	0.00247	0.00176
1.05	0.00976	0.00488	0.003486
1.1	0.01906	0.00953	0.0068
1.2	0.03664	0.01823	0.013
1.5	0.081	0.0405	0.02896
2	0.138	0.0693	0.0495
3	0.219	0.109	0.0785

Table 3.1: Estimated intrinsic growth rate per day for a growing period of 5 days, 10 days, and 14 days

30 days, 90 days, 180 days, and 365 days?. We summarise these calculations in Table 3.2.

Increase in biomass pcb	Growth Rate			
	30 days	90days	180days	365 days
1.025	0.00082	0.00027	0.000137	0.000068
1.05	0.00163	0.00054	0.00027	0.013
1.1	0.0032	0.00106	0.00053	0.00026
1.2	0.00608	0.002026	0.001013	0.00049
1.5	0.0135	0.0045	0.00225	0.0011
2	0.023	0.0077	0.00385	0.0019
3	0.037	0.012	0.006	0.003

Table 3.2: Estimated intrinsic growth rate per day for a growing period of 30 days, 90 days, 180 days, and 365 days

In the above calculations of intrinsic growth rate, we observe that the intrinsic growth rate after a period of 5 days is approximately 6 times bigger than the intrinsic growth rate after a period of 30 days when the percentage change in biomass is 3 whereas the intrinsic growth rate after a period of 5 days is approximately 18 times bigger than the intrinsic growth rate after a period of 90 days when the percentage change in biomass is 3.

Similarly, the intrinsic growth rate after a period of 5 days is approximately 36 times bigger than the intrinsic growth rate after a period of 180 days when the percentage change in biomass is 3 whereas the intrinsic growth rate after a period of 5 days is approximately 73 times bigger than the intrinsic growth rate after a period of 365 days when the percentage change in biomass is 3.

For the growing periods of 42 days, 150 days, and 191 days, the intrinsic growth rates are similarly calculated. These results are presented in Table 3.3.

In summary, the intrinsic growth rate of a single plant species decreases as the period of growth varies from 5 days to 365 days.

Next, we want to find out how the percentage intrinsic growth rate of a single plant species per day would change when the period of growth is varied. These results are presented in Table 3.4 and Table 3.5.

Increase in biomass	Growth Rate			
	pcb	42 days	150 days	191 days
1.025		0.00059	0.000165	0.00013
1.05		0.00116	0.000325	0.000255
1.1		0.00227	0.000635	0.000499
1.2		0.0043	0.0012	0.00095
1.5		0.00965	0.0027	0.002
2		0.0165	0.0046	0.0036
3		0.026	0.0073	0.00575

Table 3.3: Estimated intrinsic growth rate per day for a growing period of 42 days, 150 days, and 191 days

Increase in biomass	Growth Rate			
	pcb	5 days	10 days	14 days
1.025		0.494	0.247	0.176
1.05		0.976	0.488	0.3486
1.1		1.9	0.953	0.68
1.2		3.66	1.82	1.3
1.5		8.1	4.06	2.89
2		13.8	6.93	4.95
3		21.9	10.9	7.85

Table 3.4: Estimated daily percentage intrinsic growth rate for a growing period of 5 days, 10 days, and 14 days

In summary, the percentage intrinsic growth rate of a single plant species decreases from a big figure of 21.9 percent when the percentage change in biomass is 3 for a growth period of 5 days to a small figure of 0.3 percent when the percentage change in biomass is 3 for a growth period of 365 days.

3.5.3 The estimation of the intrinsic growth rate per $\frac{1}{4}$ day

If the biomass is increased by a certain percent in 5 days, 10 days, and 14 days, and a $\frac{1}{4}$ day step length is applied, the intrinsic growth rate can be estimated. We shall use a few examples to illustrate this idea.

For example, assume that the biomass is doubled. Consider a 10 percent increase in biomass in 14 days. Therefore, if $\frac{1}{4}$ day is taken as step length, this would be equal to 56 times $\frac{1}{4}$ days. In this scenario,

$$e^{56r} = 2 \tag{3.5}$$

By solving this equation for r , we shall obtain the intrinsic growth rate per quarter of a day as

$$r = \frac{\log_e 2}{56} = 0.0124 \tag{3.6}$$

This value of intrinsic growth rate could possibly mimic the temperate (summer, autumn, spring) British growing season. On the other hand if the weight of

Increase in biomass	Growth Rate			
	30 days	90 days	180 days	365 days
pcb				
1.025	0.082	0.027	0.0137	0.0068
1.05	0.00163	0.00054	0.00027	0.013
1.1	0.32	0.106	0.053	0.026
1.2	0.608	0.2026	0.1013	0.049
1.5	1.35	0.45	0.225	0.11
2	2.3	0.77	0.385	0.19
3	3.7	1.2	0.6	0.3

Table 3.5: Estimated daily percentage intrinsic growth rate for a growing period of 30 days, 90 days, 180 days, and 365 days

the plant species is 1.1, under this fourth night scenario and a quarter day step length assumption,

$$r = \frac{\log_e 1.1}{56} = 0.0017 \quad (3.7)$$

Using the above technique, it is possible to estimate the intrinsic growth rate given the length of growing season and the increase in biomass. The results of our calculations are presented in Table 3.6.

Percentage change in weight	Estimated 100r per $\frac{1}{4}$ day		
	5 days	10days	14days
pcb			
1.025	0.1235	0.062	0.044
1.05	0.244	0.122	0.087
1.1	0.4765	0.2382	0.170
1.2	0.9116	0.45558	0.325
1.5	2.027	1.0136	0.720
2	3.465	1.73	1.24
3	5.493	2.746	1.96

Table 3.6: The Estimation of the percentage intrinsic growth rate per $\frac{1}{4}$ day

Hence, when the weight of plant species increases, the corresponding estimated intrinsic growth rate r per quarter of a day will increase irrespective of the length of the growing season.

3.6 The estimation of daily intrinsic growth rate from a yearly growth rate

Given the yearly intrinsic growth rate for each pair of three species of prairie grasses ([2]), how do we estimate the intrinsic growth rate per day. This problem shall be tackled by using plant growth equation where $(1 + r)^t$ represents the yearly intrinsic growth rate and r represents the intrinsic growth rate per day for individual plant species and t represents time in days.

For example, if the yearly intrinsic growth rate is α , then

$$(1 + r)^t = \alpha \tag{3.8}$$

By solving for the value of r , we would have

$$r = (\alpha)^{\frac{1}{t}} - 1 \tag{3.9}$$

where α is the yearly intrinsic growth rate and t is equivalent to 365 days.

For example, if the yearly intrinsic growth rate is 1.5 ([2]), then the estimated intrinsic growth rate using the above formula is $r = (1.5)^{\frac{1}{365}} - 1$. By hand calculation, the value of $(1.5)^{\frac{1}{365}}$ is 1.0011. Therefore, the estimated intrinsic growth rate per day is 0.0011 (that is, 1.0011 minus 1).

Alternatively, we can simply use the same formula which we have used in the previous sections of this chapter by assuming an exponential growth model. For example, if the biomass changes by 2.7, then in a year, the intrinsic growth rate per day for a growing period of 365 days is simply

$$r = \frac{\log_e 2.7}{365} = 0.0027 \tag{3.10}$$

Hence, the estimated intrinsic growth rate per quarter of a day and the estimated intrinsic growth rate in percentage are 0.000275 and 0.11 respectively. For other yearly intrinsic growth rates, the estimated intrinsic growth rates per day and other related calculations are displayed in Table 3.7.

Yearly rate	Estimated intrinsic growth rate		
r	r per day	r(percent)	r per 0.25 day
1.2	0.0005	0.05	0.000125
1.5	0.0011	0.11	0.000275
1.8	0.0016	0.16	0.0004
2.1	0.002	0.2	0.0005
2.4	0.0024	0.24	0.0006
2.7	0.0027	0.27	0.00068

Table 3.7: The estimation of the daily intrinsic growth rate from a yearly growth rate

In summary, as the yearly intrinsic growth rate changes, the corresponding intrinsic growth rate per day also changes.

In this experimental mathematical analysis, we have provided a few examples with which to illustrate how the intrinsic plant growth rate can be estimated under some realistic simplifying assumptions. The results of our analysis are discussed quantitatively.

Subsequent analysis and application of intrinsic plant growth rate will be based on our calculations in this section.

3.7 Data fitting techniques

We consider the basic logistic model for the case when r is a scalar parameter. Then we can select r by minimizing the distance

$$d(u, v) = \| u - v \| \quad (3.11)$$

between the information u on the behaviour of the system and the prediction $v = v(r)$ of the model which depends on the choice of r . In this scenario, the search of the minimum is in one variable only.

In our numerical method, a penalty function measuring the distance between the model approximate solution and our observations is minimized.

3.7.1 Formulation of a penalty function

Our penalty function is defined only in terms of three common norms namely 1-norm, 2-norm and ∞ -norm. The formulation of a 1-norm penalty function is defined as follows. We minimize the penalty function

$$J = \sum_{t=0}^{r-1} | N_t - S_t | \quad (3.12)$$

This positive number is subject to the dynamics of the logistic model where the distance between time series data, that is, the plant biomass N_t ([35]) and our simulated data S_t which we obtain from the logistic model is measured using the 1-norm. The 2-norm and ∞ -norm can be defined in a similar manner.

The 1-norm is simply the sum of differences at specified points whereas the 2-norm is the root mean square of the sum of differences at specified points. The infinity norm is the maximum difference at any time. We remark that our simulated data follow an exponential growth pattern.

At the model parameters where the penalty function is minimized, we take a finer grid around the dominant logistic model parameter that provides a local minimum to find a set of best fit model parameters where the penalty function is further minimized.

In fitting two similar data sets, there is usually an error assigned for overfitting or underfitting. This error is measured by using the concept of a penalty function. In the above equation, N_t and S_t are called solution trajectories of the provided data and our simulated data which we assume have exponential growth characteristic.

3.8 Construction of Model Equations of Competition Interaction

The core part of this chapter concerns how to construct model equations that describe the interaction between two very similar interacting plant species and also that between two dis-similar interacting plant species.

Our primary task in this chapter is to construct a possible set of model equations that describe the dynamics of two interacting plant species by using the experimental data which are provided by ([35]).

From these model equations, we would use an appropriate penalty function to select our candidate model equation which is expected to correspond to the model parameters of the defining logistic model equation in which its parameters provide a best fit for the data being used.

3.8.1 The estimation of week 1 intrinsic growth rate and daily growth rate

According to ([35]), the average weight in grams of a number of plants were 0.0454, 0.147, 0.508, 1.653, 5.868, 17.33, 30.35, 46.2, 66.1, 88.9. The limiting value for this important sequence of time series plant growth data is 88.9. We do not know the value of the steady state. In this chapter, we would choose an appropriate steady state interval and consider varying the values of the steady state upon which we would develop a set of candidate model equations.

If the second weight is divided by the first weight and so on, we would obtain a sequence of nine biomass data 3.24, 3.46, 3.25, 3.55, 2.95, 1.75, 1.52, 1.43, 1.35,

Hence, the intrinsic growth rate based on week 1 is $\log_e\left(\frac{0.147}{0.0454}\right)$ or 1.176 approximately. Based on week 1 growth rate, our daily intrinsic growth is 0.168.

For example, if the steady state g is 100 grams per m^2 and the week 1 intrinsic growth rate gh is 1.176, then the intraspecific interaction or self- interaction coefficient h is 1.176 divided by 100. In this example, the value of h is 0.01176. Other values of h can be obtained using the same technique for varying values of the steady state g .

3.8.2 Formulation of another logistic model

Consider the case of one species N_1 growing in isolation of another species, that is, $N_2 = 0$. The logistic equation describing this phenomenon would have a form which can be written as

$$\frac{dN_1(t)}{dt} = hN_1(t)(g - N_1(t)) \quad (3.13)$$

where $N_1(0) = N_{10} > 0$.

In this situation, the positive steady state is given by g if $N_1 \neq 0$ and the intrinsic growth rate is given by gh . We know that there are other ways of formulating this where the constants h and g would mean slightly different things ([123]). But this is the easiest way to think about it for now.

Therefore, all our models with the same limiting state will have the same value for g . The different values of h will determine how quickly the steady state is reached. The bigger the value of h , the faster the steady state is attained.

Consider the case of species N_2 when $N_1 = 0$. The corresponding logistic equation has the form that we can write as

$$\frac{dN_2}{dt} = sN_2(t)(\ell - N_2(t)) \quad (3.14)$$

where $N_2(0) = N_{20} > 0$.

In this case, the positive steady state is given by ℓ if $N_2 \neq 0$ and the intrinsic growth rate is given by $s\ell$. Hence, all our models with the same limiting state will have the same value for ℓ . The different values of s will determine how quickly the steady state is reached. The bigger the value of s , the faster the steady state is attained.

In summary, the two logistic intraspecific or self-interaction model equations are

$$\frac{dN_1}{dt} = hN_1(t)(g - N_1(t)) \quad (3.15)$$

$$\frac{dN_2}{dt} = sN_2(t)(\ell - N_2(t)) \quad (3.16)$$

where where $N_1(0) = N_{10} > 0$ and $N_2(0) = N_{20} > 0$.

The development of our model competition equations which we will derive later on in this chapter will use the forms of these logistic equations.

3.9 How do we obtain the 10 logistic data points?

First, we use the time scale of $T = 0 : 1 : 70$ to simulate the 10 week summer competition model.

Since, we are interested in the week 1, week 2, week 3, week 4, week 5, week 6, week 7, week 8, week 9 and week 10 data points, we define a subset of the weekly data points on the approximate competition solution of the 10 week model equation.

That is, if Y is the approximate solution of the competition model, our weekly biomass data points are $Y(1), Y(8), Y(15), Y(22), Y(29), Y(36), Y(43), Y(50), Y(57)$ and $Y(64)$ because week 1 starts on day 1, week 2 starts on day 8, week 3 starts on day 15 and ends with week 10 which starts on day 64. We end on week 10 because the data of [35] are based on the growth period of 10 weeks.

The calculation of 1-norm which is the sum of the difference at specified points and the application of the penalty function will be based on the 10 week logistic simulated data and the actual 10 biomass data points provided by ([35]).

We will use the 2-norm in our analysis, hence it is appropriate at this stage to define its corresponding penalty function.

3.10 The calculation of our error function using 2-norm penalty function

In terms of 2-norm, our penalty function is defined as

$$P = \min\left(\sum_{t=1}^{10} [|N_t - S_t|]^2\right)^{\frac{1}{2}} \quad (3.17)$$

where S_t are the 10 data points which we obtain from the logistic model when the time scale is $T = 0 : 1 : 70$ and week 1 starts on day 1, week 2 starts on day 8, week 3 starts on day 15, and so on. The values of N_t are the 10 week time series biomass data points provided by [35].

3.11 Monotone sequence

Central to the concept of penalty function as used in this chapter is the property of a monotone sequence. A sequence a_n such that $a_{n+1} \geq a_n$ for all $n \geq 1$ is called an increasing monotone whereas the sequence such that $a_{n+1} \leq a_n$ for

all $n \geq 1$ is called a decreasing monotone. These definitions are familiar ones which can be found in several real analysis and calculus literatures.

3.12 The calculation of the intra-specific interaction coefficient h

In this section, we shall calculate the intraspecific or self-interaction coefficient h . The first column of the table below is calculated for varying values of the steady state g and the intrinsic growth rate gh for species 1.

We will only consider the corresponding calculation of the 2-norm penalty function in this chapter because the model parameters that minimize the 2-norm penalty function and the ∞ -norm penalty function are within the same range whereas the model parameters that minimize the 1-norm penalty function are outside this range. We have used a starting value of 0.0454. Our calculations are presented in Table 3.8.

Example Number	The calculation of h for a chosen steady state						
	h	g	gh	n	h	g	gh
1	0.0021132	79.5	0.168	8	0.002024	83	0.168
2	0.0021	80	0.168	9	0.002012	83.5	0.168
3	0.002087	80.5	0.168	10	0.002	84	0.168
4	0.00207	81	0.168	11	0.001988	84.5	0.168
5	0.00206	81.5	0.168	12	0.0019765	85	0.168
6	0.002049	82	0.168	13	0.001965	85.5	0.168
7	0.002036	82.5	0.168	14	0.001953	86	0.168

Table 3.8: The calculation of the intra-specific coefficient for a chosen steady state and a fixed growth rate

3.13 Comparison of Data Fitting Logistic Model Parameters and the General Methodology of Selecting our Best Fit Parameters

In order to embark on this task, the starting point is to specify the following calculated parameters which are common in these calculations such as

- Parameter 1 is the weekly intrinsic growth rate of 1.176.
- Parameter 2 is the daily intrinsic growth rate of 0.168.
- Parameter 3 is the starting value for the first species which is 0.0454 grams per area of grass cover.
- Parameter 4 is the length of the growing season of 70 days.

The following notations are used in our simulations

- ss stands for our chosen steady state in grams per area of grass cover.
- b stands for our calculated intra-specific coefficient.
- pf stands for our calculated positive 2-norm penalty function which measures the size of the error between the measured data and our simulated data.

For the purpose of clarity in our analysis, we choose to divide our entire parameter space for our simulated data into sub-parameter space.

The scenario 1 parameters which we used for our simulated data 1 and our simulated data 2 are the following

- For our simulated data 1, we used $ss = 79.5$, $b = 0.0021132$, $pf = 15.754$.
- For our simulated data 2, we used $ss = 80$, $b = 0.0021$, $pf = 15.606$.

These parameters concern only the measured data ([35]). All other parameters relate to our simulated data which we have obtained. Our calculations and search for our best-fit model parameters are presented in the following tables and discussed.

Data	Comparison of data		
number	measured data	simulated data 1	simulated data 2
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4735	0.4735
4	1.653	1.5132	1.5133
5	5.868	4.6999	4.7017
6	17.33	13.4417	13.4559
7	30.35	31.5843	31.6627
8	46.2	54.1531	54.3844
9	66.1	69.5139	69.8969
10	88.9	76.4399	76.8986

Table 3.9: The comparison between the measured data and our simulated data for scenario 1

What do we learn from these numbers? We learn that the measured data and our simulated data behave alike: we observe that a slight increase in the value of the chosen steady state and a slight decrease in the value of the intra-specific coefficient would produce a smaller penalty function and also produce an increase in the limiting biomass. Next, we shall consider other simulated data for a varying set of parameters.

Our fundamental task in this section is to search for the best fit parameters, that is, which model parameters would provide a small error between the measured data and our simulated data. We would expect that this small error will correspond to the local minimum in a sequence of penalty function data which will satisfy the property of a monotone sequence.

The scenario 2 parameters which we used for our simulated data 3 and our simulated data 4 are the following

- For our simulated data 3, we used $ss = 80.5$, $b = 0.002087$, $pf = 15.48$.
- For our simulated data 4, we used $ss = 81$, $b = 0.00207$, $pf = 15.36$.

Data number	Comparison of data		
	measured data	simulated data 3	simulated data 4
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4735	0.4736
4	1.653	1.5135	1.5137
5	5.868	4.7034	4.7056
6	17.33	13.4698	13.4881
7	30.35	31.7404	31.8426
8	46.2	54.6141	54.9175
9	66.1	70.2783	70.7835
10	88.9	77.3561	77.9629

Table 3.10: The comparison between the measured data and our simulated data for scenario 2

The scenario 3 parameters which we used for our simulated data 5 and our simulated data 6 are the following

- For our simulated data 5, we used $ss = 81.5$, $b = 0.00206$, $pf = 15.30$.
- For our simulated data 6, we used $ss = 82$, $b = 0.002049$, $pf = 15.25$.

Data	Comparison of data		
	measured data	simulated data 5	simulated data 6
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4736	0.4736
4	1.653	1.5139	1.5140
5	5.868	4.7069	4.7083
6	17.33	13.4989	13.5108
7	30.35	31.9029	31.9694
8	46.2	55.0974	55.2967
9	66.1	71.0797	71.4008
10	88.9	78.3262	78.7445

Table 3.11: The comparison between the measured data and our simulated data for scenario 3

Similarly, the scenario 4 parameters which we used for our simulated data 7 and our simulated data 8 are the following

- For our simulated data 7, we used $ss = 82.5$, $b = 0.00203636$, $pf = 15.2144$.
- For our simulated data 8, we used $ss = 83$, $b = 0.002024$, $pf = 15.22$.

Data	Comparison of data		
	measured data	simulated data 7	simulated data 8
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4736	0.4736
4	1.653	1.5142	1.5143
5	5.868	4.7100	4.7116
6	17.33	13.5245	13.5379
7	30.35	32.0462	32.1217
8	46.2	55.5274	55.755
9	66.1	71.799	72.177
10	88.9	79.2419	79.7024

Table 3.12: The comparison between the measured data and our simulated data for scenario 4

Similarly, the scenario 5 parameters which we used for our simulated data 9 and our simulated data 10 are the following

- For our simulated data 9, we used $ss = 83.5$, $b = 0.002012$, $pf = 15.26$.
- For our simulated data 10, we used $ss = 84$, $b = 0.002$, $pf = 15.31$.

Data number	Comparison of data		
	measured data	simulated data 9	simulated data 10
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4736	0.4736
4	1.653	1.5145	1.5147
5	5.868	4.7131	4.7147
6	17.33	13.5509	13.564
7	30.35	32.1954	32.2694
8	46.2	55.9778	56.2023
9	66.1	72.5479	72.9227
10	88.9	80.154	80.6099

Table 3.13: The comparison between the measured data and our simulated data for scenario 5

The scenario 6 parameters which we used for our simulated data 11 and our simulated data 12 are the following

- For our simulated data 11, we used $ss = 84.5$, $b = 0.001988$, $pf = 15.40$.
- For our simulated data 12, we used $ss = 85$, $b = 0.0019765$, $pf = 15.51$.

Data number	Comparison of data		
	measured data	simulated data 11	simulated data 12
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4737	0.4737
4	1.653	1.5148	1.515
5	5.868	4.7163	4.7178
6	17.33	13.5771	13.5897
7	30.35	32.3437	32.4153
8	46.2	56.4286	56.6472
9	66.1	73.3015	73.6683
10	88.9	81.0705	81.5163

Table 3.14: The comparison between the measured data and our simulated data for scenario 6

Similarly, the scenario 7 parameters which we used for our simulated data 13 and our simulated data 14 are the following

- For our simulated data 13, we used $ss = 85.5$, $b = 0.001965$, $pf = 15.64$.
- For our simulated data 14, we used $ss = 86$, $b = 0.001953$, $pf = 15.81$.

Data	Comparison of data		
	measured data	simulated data 13	simulated data 14
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4737	0.4737
4	1.653	1.5151	1.5153
5	5.868	4.7193	4.7209
6	17.33	13.6023	13.6154
7	30.35	32.4872	32.5625
8	46.2	56.8676	57.0993
9	66.1	74.0394	74.4314
10	88.9	81.9674	82.4439

Table 3.15: The comparison between the measured data and our simulated data for scenario 7

Similarly, the scenario 8 parameters which we used for our simulated data 15 and our simulated data 16 are the following

- For our simulated data 15, we used $ss = 86.5$, $b = 0.0019422$, $pf = 16$.
- For our simulated data 16, we used $ss = 87$, $b = 0.00193$, $pf = 16.256$.

Data number	Comparison of data		
	measured data	simulated data 15	simulated data 16
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4737	0.4737
4	1.653	1.5154	1.5156
5	5.868	4.7223	4.7239
6	17.33	13.6273	13.6407
7	30.35	32.6315	32.7095
8	46.2	57.3099	57.5497
9	66.1	74.8073	75.2249
10	88.9	82.8568	83.2712

Table 3.16: The comparison between the measured data and our simulated data for scenario 8

Similarly, the scenario 9 parameters which we used for our simulated data 17 and our simulated data 18 are the following

- For our simulated data 17, we used $ss = 87.5$, $b = 0.00192$, $pf = 16.456$.
- For our simulated data 18, we used $ss = 88$, $b = 0.0019$, $pf = 16.9$.

Data number	Comparison of data		
	measured data	simulated data 17	simulated data 18
1	0.0454	0.0454	0.0454
2	0.147	0.1468	0.1468
3	0.508	0.4737	0.4738
4	1.653	1.5157	1.516
5	5.868	4.7252	4.7278
6	17.33	13.6518	13.6739
7	30.35	32.7732	32.9013
8	46.2	57.7473	58.1467
9	66.1	75.562	76.245
10	88.9	83.6831	84.5206

Table 3.17: The comparison between the measured data and our simulated data for scenario 9

Similarly, the scenario 10 parameters which we used for our simulated data 19 and our simulated data 20 are the following

- For our simulated data 19, we used $ss = 88.5$, $b = 0.0018983$, $pf = 16.954$.
- For our simulated data 20, we used $ss = 88.9$, $b = 0.0018897$, $pf = 17.175$.

Data	Comparison of data			
	number	measured data	simulated data 19	simulated data 20
1		0.0454	0.0454	0.0454
2		0.147	0.1468	0.1469
3		0.508	0.4738	0.4738
4		1.653	1.516	1.5161
5		5.868	4.7281	4.7292
6		17.33	13.6758	13.6853
7		30.35	32.9122	32.9676
8		46.2	58.1809	58.3545
9		66.1	76.3036	76.6016
10		88.9	84.5926	84.9587

Table 3.18: The comparison between the measured data and our simulated data for scenario 10

3.14 Justification

From this detailed analysis, we know that the minimum 2-norm penalty function is 15.2144 which correspond to the following data fitting parameters:

- Weekly intrinsic growth rate is 1.176.
- Daily intrinsic growth rate is 0.168.
- Chosen steady state is 82.5 grams per area of grass cover.
- Calculated intra-specific coefficient is 0.00203636.
- Starting value for the first plant species is 0.0454 grams per area of grass cover.

By a further gridding around the best fit steady state 82.5, the local minimum is 15.2137 of which the following best fit model parameters are selected

- Weekly intrinsic growth rate is 1.176.
- Daily intrinsic growth rate is 0.168.
- Chosen steady state is 82.6 grams per area of grass cover.
- Calculated intra-specific coefficient is 0.0020339.
- Starting value for the first plant species is 0.0454 grams per area of grass cover.

These results will be clearly presented and discussed in the next section of this chapter. For a compact presentation of our results, we shall adopt the following pattern in our next section.

3.15 Best fit logistic model parameters

In this section, we shall find those logistic model parameters that minimize the 2-norm. Our calculations are presented below. What do we want to find out? We are interested to find a list of best fit model parameters of our logistic model that minimise the agreement between the provided model and our simulated model. Our calculations are presented in Table 3.19.

For the purpose of illustration, the graphical representations of a few of these data points have been presented (see the appendix, Figure 8.1, Figure 8.2, Figure 8.3).

What do we want to find out from this table? We are interested in finding a triple of our logistic parameters which will minimise our 2-norm penalty function. In our analysis, we have found this minimum 2-norm penalty function from a list of 14 different simulations.

The property of the penalty function is satisfied because for $h = 0.00203636$, $g = 82.5$, $gh = 0.168$, the value of the 2-norm is 15.2144 (the minimum of the 2-norm) in the sequence of 2-norm values. The sequence of 2-norm values is a monotone sequence. In other words, we have found the smallest error between

Parameter	Calculation of our 2-norm P_f			
	h	g	gh	2-norm
1	0.0021132	79.5	0.168	15.754
2	0.0021	80	0.168	15.606
3	0.002087	80.5	0.168	15.48
4	0.00207	81	0.168	15.35
5	0.00206	81.5	0.168	15.30
6	0.002049	82	0.168	15.25
7	0.00203636	82.5	0.168	15.2144
8	0.002024	83	0.168	15.22
9	0.002012	83.5	0.168	15.26
10	0.002	84	0.168	15.31
11	0.001988	84.5	0.168	15.40
12	0.0019765	85	0.168	15.50
13	0.001965	85.5	0.168	15.64
14	0.001953	86	0.168	15.81

Table 3.19: The calculation of our 2-norm penalty function from the measured data and our simulated data

the measured data and our 14 simulated data using the starting biomass of 0.0454 grams per area of grass cover

We would think that there can be a possibility of finding a further smaller 2-norm penalty function. To tackle this problem, we would take a further grid around $g = 82.5$. In this scenario, we will present our calculations in Table 3.20.

Since, we are gridding around the steady state 82.5, it would be rare to find our new minimum 2-norm penalty function further away from the value of 82.5.

On the basis of our penalty function calculations, the parameters of the logistic model that would provide a best fit for the weekly average plant growth data will have the precise values of $h = 0.0020339$, $g = 82.6$ grams and $gh = 0.168$ approximately.

Hence, the intraspecific interaction coefficient is 0.0020339. Assuming that the interspecific interaction coefficient, that is, the negative effect of species N_2 on the growth of species N_1 may not be too big compared to the intraspecific coefficient ([134]), the interspecific competition coefficient may be $(0.0020339 - \alpha, 0.0020339 + \alpha)$ where α is a small positive number.

We choose to use the 2-norm in our present analysis because it provides a relatively smaller minimum penalty function of 15.2137.

On the basis of our analysis in this chapter, our constructed model equations of competition between two interacting dis-similar plant species is

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.0005N_2(t)) \quad (3.18)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.002 - 0.00002N_1(t) - 0.000015N_2(t)) \quad (3.19)$$

with initial conditions $N_1(0) = 0.04$ grammes per area and $N_2(0) = 0.045$ grammes per area.

Parameter	2-norm P_f			
	h	g	gh	2-norm
1	0.0020463	82.1	0.168	15.2386
2	0.0020438	82.2	0.168	15.2289
3	0.0020413	82.3	0.168	15.2212
4	0.0020388	82.4	0.168	15.2163
5	0.00203636	82.5	0.168	15.2144
6	0.0020339	82.6	0.168	15.2137
7	0.002031439	82.7	0.168	15.2141
8	0.0020289	82.8	0.168	15.2156
9	0.0020265	82.9	0.168	15.218
10	0.002024	83	0.168	15.22
11	0.00202166	83.1	0.168	15.226
12	0.0020192	83.2	0.168	15.2319
13	0.0020168	83.3	0.168	15.2385
14	0.00201439	83.4	0.168	15.2463
15	0.0020302	83.5	0.168	15.2147

Table 3.20: The calculation of our 2-norm penalty function by gridding around a chosen steady state of 82.5

The value of the intrinsic growth rate for the second species is chosen on the assumption that $d \leq 0.168$. This assumption is based on the idea that the second plant species is a slow growing type.

After a careful thinking and a sensible common sense algebraic manipulation, we arrive at the following conclusion which is just one case out of other choices for the value of the interspecific interaction coefficient.

If (a, b) is an open interval on the real line, we propose to choose our interspecific coefficient so that this value would be bigger than a and smaller than b where $a = 0.0020339 - \alpha$ and $b = 0.0020339 + \alpha$ and α is a small positive number.

For one to choose an appropriate value for the interspecific coefficient for the first plant species, we would expect this number to lie between its lower limit and upper limit which we do not know exactly. If the value we want to choose is $\beta \leq 1$ such that

$$0.0020339 - \alpha = \beta \tag{3.20}$$

$$0.0020339 + \alpha = \beta \tag{3.21}$$

From these two equations, the two values of α are $0.0020339 - \beta$ and $\beta - 0.0020339$. If $\alpha = 0.0018$, then $a = 0.0002339$ and $b = 0.0038339$.

In this first case, our expected value for β could be found in the open interval $(0.000234, 0.003834)$.

If, $\alpha = 0.01$, then $a = -0.0079661$ and $b = 0.0120339$. In this second case, our expected value for β could be found in the open interval $(-0.00796, 0.012034)$.

If, $\alpha = 0.001$, then $a = 0.0010339$ and $b = 0.0030339$. In this third case, our expected value for β could be found in the open interval $(0.001034, 0.003034)$.

If, $\alpha = 0.0002$, then $a = 0.0018339$ and $b = 0.0022339$. In this fourth case, our expected value for β could be found in the open interval $(0.001834, 0.002234)$.

In summary, our choice for the value of interspecific interaction coefficient which will lie in any of these open intervals is subjective. As we can see, $\alpha = 0.0018 > 0.0015$, $\alpha = 0.01 > 0.0015$, $\alpha = 0.001 < 0.0015$, and $\alpha = 0.0002 < 0.0015$.

One out of our several choices for our interspecific interaction coefficient is 0.0005 which holds for the first two cases only.

In this example, we would expect the small positive number α to be strictly greater than 0.0015339 . If the value of interspecific coefficient is 0.0014 , in this case, we would expect the small positive number α to be strictly greater than 0.0006339 .

Whatever is the choice of the interspecific coefficient, it must be smaller than the value of the intraspecific interaction coefficient in our example. We have estimated our intraspecific coefficient but being able to estimate the interspecific coefficient is a matter of choice as long as this choice is appropriate.

By using a similar assumption, the dynamics of competition interaction between two similar plant species are governed by the following systems of initial value nonlinear ordinary differential equations of first order

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.0018N_2(t)) \quad (3.22)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.166 - 0.0015N_1(t) - 0.002N_2(t)) \quad (3.23)$$

where $N_1(0) = 0.04$ grams per m^2 and $N_2(0) = 0.045$ grams per m^2 .

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.002N_2(t)) \quad (3.24)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.167 - 0.00195N_1(t) - 0.002N_2(t)) \quad (3.25)$$

where $N_1(0) = 0.04$ grams per m^2 and $N_2(0) = 0.045$ grams per m^2 .

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.0020339N_2(t)) \quad (3.26)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.166 - 0.0015N_1(t) - 0.0015N_2(t)) \quad (3.27)$$

where $N_1(0) = 0.04$ grams per m^2 and $N_2(0) = 0.045$ grams per m^2 .

Other types of model equations of mutualism, parasitism, and commensalism can be adapted from our model equations of competition between two interacting plant species.

We remark that for other chosen starting values, there could be a change in the value of the minimum 2-norm penalty function.

3.16 Competition between two dis-similar plant species: rationale

In this section, we shall consider the above equations of competition between two dis-similar plant species where the first plant species is growing fastly assuming that the second plant species is growing slowly ([53], [54]). According to this author, the ecological advantage of a high relative growth rate or intrinsic growth rate is that: fast growth enhances the rapid occupation for space, which is beneficial in terms of competition for limiting resources.

The concern for the possible survival value of slow growth has been explained by ([54], [160]): that slow-growing plant species make modest demands and are less likely to exhaust the available nutrients.

In unpredictable but productive environments, where "catastrophes" like occasional occurrence of fierce storm, or other forms of disturbance occur, fast-growing short-lived species are common whereas in more predictable environments with a low incidence of disturbance, longer-lived slow-growing species predominate ([137], [165]).

For this system of model equations between two dis-similar plant species, we shall assume that the two plant species will survive over time. The first plant species is growing fastly whereas the second plant species is growing slowly.

This knowledge on how to set up our model equations of interaction between a fast growing plant species and a slow growing plant species is gained from the above mentioned ecological idea.

We would remark that there are interesting mathematical analyses which we can embark on but these analyses would take us outside the core topic of this chapter.

We would briefly summarise the mathematical techniques as defined and discussed in chapter 2 to list the features of stability, survival and extinction inequalities later on in this chapter.

3.16.1 Steady state solutions and stability/instability properties of competition

For our model equations of competition, we evaluated our linearised interaction functions which are continuous as well as differentiable and found that using our analytical method of determining these steady states (as defined in chapter two of this thesis)

1. The trivial steady state $(0, 0)$ is unstable because $\lambda_1 = 0.168$ and $\lambda_2 = 0.002$.
2. The steady state $(0, 133)$ is unstable because $\lambda_1 = -0.002$ and $\lambda_2 = 0.1$.
3. The steady state $(82.6, 0)$ is unstable because $\lambda_1 = -0.168$ and $\lambda_2 = 0.0003$
4. The coexistence steady state $(74, 34.5)$ is stable because $\lambda_1 = -0.15$ and $\lambda_2 = -0.0003$

We remark that the stability properties of our steady state solutions can also be studied using the method of perturbation which we mentioned in our

last chapter. Unfortunately, we may not repeat the application of this method at this point since the method of linearisation about each steady state and its sign analysis is also satisfactory.

3.16.2 Coexistence, survival and extinction criteria of competition

The analysis of this chapter would not be complete without knowing if the two competing species for a limited resource within the same environment will coexist, survive or go extinct under the assumptions of formulating model equations of competition as said in chapter two.

We have derived the coexistence, survival and extinction criteria in chapter two. We will simply use these criteria to check our few model equations of competition.

3.16.3 Example

We would like to mention that each system of coupled ordinary differential equations of first order is recast in the form as indicated in chapter two. We may not repeat this process in this section. We shall simply check if the inequalities are met.

Consider the following model parameters: $a = 0.168, b = 0.0020339, c = 0.0005, d = 0.002, e = 0.00002, f = 0.000015$. Since $K_1 = \frac{a}{b}, \alpha_{12} = \frac{c}{b}, K_2 = \frac{d}{f}, \alpha_{21} = \frac{e}{f}$, it follows that $K_1 = 82.6, \alpha_{12} = 0.246, K_2 = 133, \alpha_{21} = 1.33$. By using these formulae, we will obtain $\frac{K_1}{K_2} = 0.62$ and $\frac{K_2}{K_1} = 1.61$.

In summary,

$$\alpha_{12} = 0.246 < 0.62 = \frac{K_1}{K_2} \quad (3.28)$$

$$\alpha_{21} = 1.33 < 1.61 = \frac{K_2}{K_1} \quad (3.29)$$

Therefore, the two plant species will survive or persist at their carrying capacities.

3.16.4 Coexistence criteria for two similar plant species

By following our idea which we defined and discussed in chapter two of this thesis that the the more similar two species are ecologically, their carrying capacities must be for the two species to coexist. In this scenario, the carrying capacities for the first and second species for our two similar species competition are $82.6g/m^2$ and $83g/m^2$.

Therefore, $\frac{K_1}{K_2} = 0.995$ is bigger than 0.95 and smaller than 1.05. Hence, our two similar competing species will coexist under the ecological criterion as defined in chapter two. So our two similar plant species would require a small range of (82.6, 83) for their coexistence.

3.16.5 Coexistence criteria for two dis-similar plant species

In the same manner, the more dis-similar two species are ecologically, the more dis-similar their carrying capacities must be for the two species to coexist. Hence, the carrying capacities for the first and second species for our two dis-similar species competition are $82.6g/m^2$ and $133g/m^2$.

Therefore, $\frac{K_1}{K_2} = 0.62$ is bigger than 0.05 and smaller than 20. Hence, our two dis-similar competing species will coexist under the ecological criterion as defined in chapter two. In this situation, our two dis-similar plant species would require a large range of (82.6, 133) for their coexistence.

3.17 Other Interaction Models: Literature Review

On a first thought, this section seems to define and discuss a topic which is different from the focus of this chapter. It is linked to this chapter because it will consider what other researchers have achieved in terms of developing some more complex model equations of competition and mutualism.

This is an important section of this chapter for several reasons. First, as far as we know, science is a coherent body of knowledge which consists of research findings, tested theories, scientific principles, and the laws for a chosen discipline. Second, a review of relevant literature is an analysis and synthesis of the sources of research in order to generate a picture of what is known about a particular field of study (which in our case is computation and mathematical modelling of plant species interactions in a harsh climate) and utilise these information to identify possible knowledge gaps that exist in a particular field of study. Third, because of the disciplinarity feature of this thesis, it is very important to review other relevant literatures in ecological modelling in order to find out if other researchers have previously conducted a similar research.

It is against this motivation that we would consider other types of model equations that have been previously developed, discussed, and analysed.

The following mutualism model was formulated by [83]:

$$\frac{dN_1}{dt} = N_1(0.5 - 2N_1 + N_2 + 0.5N_3). \quad (3.30)$$

$$\frac{dN_2}{dt} = N_2(-3 + 5N_1 - 4N_2 + 2N_3). \quad (3.31)$$

$$\frac{dN_3}{dt} = N_3(4 + N_1 + 2N_2 - 7N_3). \quad (3.32)$$

where $N_i(0) = C_i > 0$ for $i = 1, 2, 3$.

The next set of two species models of mutualism were formulated by [1]:

$$\frac{dN_1}{dt} = \frac{r_1 N_1 (K_1 - N_1 + \alpha_{12})}{K_1 + \alpha_{12} N_2}. \quad (3.33)$$

$$\frac{dN_2}{dt} = \frac{r_2 N_2 (K_2 - N_2 + \alpha_{21})}{K_2 + \alpha_{21} N_1}. \quad (3.34)$$

$$\frac{dN_1}{dt} = r_1(1.0 + \alpha_{12}\frac{N_2}{K_1})\frac{(K_1 - N_1)}{K_1}. \quad (3.35)$$

$$\frac{dN_2}{dt} = r_2(1.0 + \alpha_{21}\frac{N_1}{K_2})\frac{(K_2 - N_2)}{K_2}. \quad (3.36)$$

where $N_i(0) = C_i > 0$ for $i = 1, 2$. All other model parameters are assumed to be positive constants.

The following model describes a special type of mutualistic interaction called obligate mutualism ([143]).

$$\frac{dN_1}{dt} = r_1N_1[1 - \frac{N_1}{K_1(1 - \exp\frac{-(aN_2+C_1)}{K_1})}]. \quad (3.37)$$

$$\frac{dN_2}{dt} = r_2N_2[1 - \frac{N_2}{K_2(1 - \exp\frac{-(aN_1+C_2)}{K_2})}]. \quad (3.38)$$

where where $N_i(0) = C_i > 0$ for $i = 1, 2$. All other model parameters are assumed to be positive constants.

The following four models describe the dynamics of obligate and facultative mutualisms ([98]):

$$\frac{dN_1}{dt} = r_1N_1[1 - \frac{N_1}{K_1} + (\frac{b_1N_2 - c_1N_2^2}{1 + d_1N_2^2})\frac{N_2}{K_1}]. \quad (3.39)$$

$$\frac{dN_2}{dt} = r_2N_2[1 - \frac{N_2}{K_2} + (\frac{b_2N_1 - c_2N_1^2}{1 + d_2N_1^2})\frac{N_1}{K_2}]. \quad (3.40)$$

$$\frac{dN_1}{dt} = r_1N_1[1 - \frac{N_1}{K_1} + (\frac{b_1N_2 - c_1N_2^2}{1 + d_1N_2^2})\frac{N_2}{K_1}]. \quad (3.41)$$

$$\frac{dN_2}{dt} = r_2N_2[1 - \frac{N_2}{K_2} - (\frac{g_2N_1}{1 + h_2N_1})\frac{N_1}{K_2}]. \quad (3.42)$$

$$\frac{dN_1}{dt} = r_1N_1[-1 + (\frac{b_1N_2 - c_1N_2^2}{1 + d_1N_2^2})N_2]. \quad (3.43)$$

$$\frac{dN_2}{dt} = r_2N_2[1 - \frac{N_2}{K_2} + (\frac{b_2N_1 - c_2N_1^2}{1 + d_2N_1^2})\frac{N_1}{K_2}]. \quad (3.44)$$

$$\frac{dN_1}{dt} = r_1N_1[-1 + (\frac{b_1N_2 - c_1N_2^2}{1 + d_1N_2^2})N_2]. \quad (3.45)$$

$$\frac{dN_2}{dt} = r_2N_2[1 - \frac{N_2}{K_2} - (\frac{g_2N_1}{1 + h_2N_1})\frac{N_1}{K_2}] \quad (3.46)$$

where $N_i(0) = C_i > 0$ for $i = 1, 2$. All other model parameters are assumed to be positive constants.

In the absence of interspecific interactions, [97] considered the dynamics of two species with respective densities $N_1(t)$ and $N_2(t)$. They described the interaction between these two species with an uncoupled system of logistic delay differential equations

$$\frac{N_1(t)}{dt} = N_1(t)[r_1 - a_{11}N_1(t - \tau)]. \quad (3.47)$$

$$\frac{N_2(t)}{dt} = N_2(t)[r_2 - a_{22}N_2(t - \tau)]. \quad (3.48)$$

for $r_1 > 0$, $r_2 > 0$, $a_{11} > 0$, $a_{22} > 0$.

It was further assumed that if these two species are permitted to cohabit a common habitat, then each species enhances the average growth rate of the other species such that the interactive dynamics are now governed by the following coupled autonomous delay differential equations

$$\frac{N_1(t)}{dt} = N_1(t)[r_1 - a_{11}N_1(t - \tau) + a_{12}N_2(t - \tau)]. \quad (3.49)$$

$$\frac{N_2(t)}{dt} = N_2(t)[r_2 + a_{21}N_1(t - \tau) - a_{22}N_2(t - \tau)]. \quad (3.50)$$

with $a_{12} > 0$, $a_{21} > 0$. They assumed that this delay system of equations admits initial conditions of the form

$$N_1(s) = \phi(s). \quad (3.51)$$

$$N_2(s) = \varphi(s). \quad (3.52)$$

for $s \in [-\tau, 0]$, $\phi, \varphi \in C([-\tau, 0], \mathfrak{R}_+)$, $\phi(0) > 0$, $\varphi(0) > 0$.

We have simulated these equations and found that qualitatively, we have two patterns of solutions for the coupled and uncoupled models: one oscillatory behaviour of solutions and the other behaves in the form of a cycle.

The stability analysis and boundedness conditions of the solutions to this delay system has been analysed ([97]). Their analysis shows how delay affects the dynamics of a mutualistic system.

The following model describes a nonlinear competition interaction between three species ([135]):

$$\frac{dN_1}{dt} = N_1(1 - N_1 - \alpha_1 N_2 - \beta_1 N_3). \quad (3.53)$$

$$\frac{dN_2}{dt} = N_2(1 - \beta_2 N_1 - N_2 - \alpha_2 N_3). \quad (3.54)$$

$$\frac{dN_3}{dt} = N_3(1 - \alpha_3 N_1 - \beta_3 N_2 - N_3). \quad (3.55)$$

These model equations were studied for the cases when $\alpha_i = \alpha$ and $\beta_i = \beta$ for $i = 1, 2, 3$, $0 \leq \alpha \leq 1 \leq \beta$ and $2 \leq \alpha + \beta$. They showed numerically that the symmetric system exhibits a general class of solutions with non-periodic oscillations of bounded amplitude but ever-increasing cycle time. Their model has only two parameters, α and β . This model demonstrates a complex phenomenon that does not occur in 2-dimensional Lotka-Volterra models. These authors have conducted a detailed analysis with which they determined the equilibria of this model and investigated the stability and qualitative behaviour of their model.

The existence of positive periodic solutions for a class of nonautonomous competitive periodic Kolmogorov systems which generalise the above May-Leonard model has been proved ([26]).

A further extension of the May-Leonard model that incorporates a diffusion rate has been considered by [172]. The dynamics of this new model is described by a system of partial differential equations

$$\frac{\partial N_1}{\partial t} = \mu \Delta N_1 + N_1(1 - N_1 - \alpha N_2 - \beta N_3). \quad (3.56)$$

$$\frac{\partial N_2}{\partial t} = \mu \Delta N_2 + N_2(1 - \beta N_1 - N_2 - \alpha N_3). \quad (3.57)$$

$$\frac{\partial N_3}{\partial t} = \mu \Delta N_3 + N_3(1 - \alpha N_1 - \beta N_2 - N_3). \quad (3.58)$$

in $\Omega \times (0, \infty)$ and $N_1 = N_2 = N_3 = 0$ on $\partial\Omega \times (0, \infty)$ where the diffusion rate μ and the competition coefficients α and β are positive constants and $0 \leq \alpha \leq 1 \leq \beta$.

A detailed mathematical analysis to investigate the global stability of this partial differential model has been discussed.

This model can be extended to investigate the idea behind the stabilization of the unstable steady state by using a powerful numerical technique of constructing a controller which would stabilise an unstable steady state solution ([23]).

The following resource based model has been formulated and analysed ([88]):

$$\frac{dN_1(t)}{dt} = N_1(t)[b_1 - a_{11}N_1(t) - a_{12}N_2(t) - a_{13}N_3(t)]. \quad (3.59)$$

$$\frac{dN_2(t)}{dt} = N_2(t)[b_2N_1(t) - a_{22}N_2(t) - a_{23}N_3(t)]. \quad (3.60)$$

$$\frac{dN_3(t)}{dt} = N_3(t)[b_3N_1(t) - a_{32}N_2(t) - a_{33}N_3(t)]. \quad (3.61)$$

where all the model parameters and initial data are positive constants. A detailed determination of the steady states of this model and a asymptotic behaviour of solutions for $N_1(0) > 0$, $N_2(0) > 0$ and $N_3(0) > 0$ have been investigated and discussed.

An N -dimensional system of autonomous ordinary differential equations that describe the dynamics of interacting species which is slightly more general than the classical Lotka-Volterra system has been considered and stronger persistence for two coexisting species have been analysed in great detail and sophistication ([3]). These equations take the following form

$$\dot{u}_k(t) = u_k(t)[a_k(t) - \sum_{\ell=1}^N b_{k\ell}u_\ell(t)] \quad (3.62)$$

where $k = 1, 2, \dots, N$ under some simplifying assumptions that $b_{k\ell} \geq 0$ and $b_{kk} \geq 0$ for $1 \leq k, \ell \leq N$. Other related models have been developed to analyse the average growth and extinction in a Lotka-Volterra system as well

as conditions for a necessary and sufficient average growth in a Lotka-Volterra system ([5], [4]).

The next model concerns a stochastic analysis of a symmetric model with a simplified initial condition ([132]). The dynamics of this symmetric model for a facultative mutualism is governed by a system of coupled ordinary differential equations with multiplicative noise

$$dx_1 = x_1(t)[(b_1 - a_{11}x_1(t) + a_{12}x_2(t))dt + (\epsilon_{11}x_1(t) + \epsilon_{12}x_2(t))dw(t)] \quad (3.63)$$

$$dx_2 = x_2(t)[b_2 - a_{22}x_2(t) + a_{21}x_1(t) + (\epsilon_{21}x_1(t) + \epsilon_{22}x_2(t))dw(t)] \quad (3.64)$$

By using Ito calculus and a range of other simplifying stochastic definitions, these authors found that the solutions of this symmetric model with additive noise will not explode in a finite time with probability 1 provided the noise intensities $\epsilon_{11}, \epsilon_{22} > 0$ and $\epsilon_{12}, \epsilon_{21} \geq 0$ for arbitrary constants b_i and a_{ij} . Without including noise terms, it was found that the solution will explode in a finite time. One sees here an advantage of using a stochastic differential system to model population dynamics of facultative mutualism.

In the modelling of response of arctic plants, an example of a phenomenological model is the logistic curve of whole-plant growth ([55]) of the form

$$\frac{dW}{dt} = rW(W_{max} - W) \quad (3.65)$$

for $W(0) = W_0$ where W is the dry weight or biomass, r is the intrinsic growth rate, and W_{max} is the maximum biomass attainable.

By finding the complementary solution of the homogeneous part and the particular integral, the general solution is

$$W(t) = W_0 e^{\frac{rt}{W_{max}}} \quad (3.66)$$

where W_0 is the initial condition, W is the dry weight or biomass, r is the intrinsic growth rate, t is the time variable, and W_{max} is the maximum attainable biomass.

In summary, we have identified other complex Lotka-Volterra models that other mathematicians have used to analyse and discuss types of species interactions with the exception of models of commensalism and parasitism or predation. Next we would briefly review these models.

A Lotka-Volterra model of competition between a commensal pair of species and a mutualistic pair has been considered where the species are said to be isolated but compete for resources ([178]). A detailed analysis of the effects of the benefits of mutualism over commensalism was also studied.

The works of Cushing on several aspects of mathematical ecology have contributed to our knowledge in this growing discipline. A few of his mathematical models concern some discrete competition models and the competitive exclusion principle, time delays in single species growth models, the oscillatory nature of general predator-prey models with delays, periodic Lotka-Volterra competition systems, and some examples of Lotka-Volterra systems which are driven by time sharing of ecological niches ([59], [108], [60], [61], [62], [63]).

A complex stochastic model that describes the dynamics of two competing species in an ecosystem has been analysed by using a Monte Carlo simulation technique ([46]). As one would expect, some key characteristics of the stochastic system were found to be different from its deterministic system without a stochastic variation. What this means is that the deterministic characteristics without a stochastic variation are special cases of the characteristics of the stochastic system.

A general description and a detailed mathematical analysis of the dynamics of two interacting populations for prey-predator interactions, for two competing species, and for symbiotic interactions have been done ([6]).

The global behaviour of solutions of classical Lotka-Volterra systems and other highly nonlinear systems that model n interacting mutualistically interacting species has been determined by using other powerful mathematical tools ([180]).

We know that one of the most interesting questions to ask about a dynamic system is: what is the long-term behaviour of its trajectories?. This question has been analysed from a pure functional analysis approach by considering a C^1 system of differential equations in \mathbb{R}^n for either a competitive system or a mutualistic system ([99]). This problem was also extended to study the limiting behaviour of solutions of systems which are either mutualistic or competitive ([100]).

Other simple dynamic model equations that describe plant competition when light is the limiting factor have been formulated ([147]). According to this author, when factors other than light are limiting growth, the representation of competition in crop simulation models is complex. In this paper, it was argued that simple dynamic models should be developed for complex processes such as the process-based simulation models which are detailed specific models that require a lot of information about crop simulation models and the set of equations that describe the distribution of assimilates over plant organs.

Our overall summary in this literature review section is this: we have attempted to construct a prototype model equations of competition which is based on choosing an error or penalty function that measures the agreement between the available data and our simulated model. The parameters were adjusted to achieve a minimum in the penalty function which yields the best fit parameters. We have adopted this numerical approach with a view to contributing to the flow of knowledge in this interdisciplinary thesis and providing insights which we have not seen elsewhere.

3.18 Conclusion and Further Remarks

In this chapter, we have carried out a detailed literature review which can be considered as an important aspect in the development of constructing a prototype competition model.

The main contribution of this chapter is to propose a nonlinear optimization numerical method for calculating the size of the error between the measured data and our simulated data over a time interval. Our proposed method is based on minimising a 2-norm penalty function with which the best fit model parameters were selected in a time interval. The minimum penalty function which we have obtained in this chapter is local and only unique to our data and

should be generalised.

It might be asked why we did not consider using one half of a day and one quarter of a day growth rates in constructing our model equations of competition. Our experimental numerical analysis shows that our calculated error function or 2-norm penalty function between the measured data and our simulated data is so big than expected when these growth rates were applied. This characteristic makes these growth rates as poor fits. This is our reason for choosing to use the daily intrinsic growth rate because it provides a far smaller 2-norm penalty function between the measured data and our simulated data over a 10- week period.

Although our model equations take similar mathematical structure of the well known classical Lotka-Volterra model, as far as one knows, these model equations of competition have not been developed and discussed elsewhere. We hope to use these equations to find out if we can obtain a few cases of mutualism from a combination of a summer competition model and a stochastic winter model which we shall define and discuss in our chapters 5 and 6 of this thesis with a view to comparing our results with experimental ecological studies which we have cited in chapter one.

We reiterate that in chapter one of this thesis, we have defined and discussed a few important components of the ecological and mathematical ideas that are relevant to our mathematical modelling and computational analysis of plant species interactions in a harsh climate. This is followed by a detailed definition, mathematical analysis, and discussions of four main types of plant species interactions, that is, the $(-, -)$, $(+, +)$, $(+, 0)$, $(+, -)$ interactions and their ecological implications. In this chapter, we switch to using the available 10-week plant growth data to develop a prototype model which describes the competition interaction under some simplifying assumptions. Other types of species interaction models can be derived from our competition model. This is how the first three chapters of this thesis are connected.

In this chapter, we have estimated the intrinsic growth rate for a plant species population. We have illustrated how to calculate the intrinsic growth rate under some simplifying assumptions.

The method of choosing the best fit logistic model parameters that minimise the 2-norm has been described and applied in detail. The assumptions that finally lead to our model equations of competition between two dis-similar plant species for a limited resource within the environment have been applied at the appropriate stage of our analysis. We also observed that we can obtain a smaller minimum value of a 2-norm if we consider a growing period of 5 weeks. We did not present our calculations in this chapter because our calculations provide similar qualitative behaviour with a longer growing season of 10 weeks.

Hence, we have constructed the model equations that describe the interspecific interaction between two very similar plant species and that between two dis-similar plant species. These model equations are important to our subsequent analysis in this thesis. This is an important result which one has achieved in this chapter.

Despite what this chapter has achieved by deriving the values of the model parameters such as the intraspecific coefficient and the intrinsic growth rate for the first species, we know that not all the parameters are equally important. How do we know which of the model parameters when varied will have the biggest effect on the solutions? Hence, in chapter four, we would be concerned

with the problem of sensitivity analysis and selection of our model parameters.

Moreover, the trajectories are sensitive to a variation of competition parameters and so it is important to conduct a systematic sensitivity analysis to find out which competition model parameters on a variation have the biggest effect on the solutions. This level of analysis is crucial to our later numerical simulation of plant species interactions in a harsh climate.

Chapter 4

Sensitivity Analysis and Selection of Parameters from Our Experiments

4.1 Motivation

The application of the principle of sensitivity analysis is important in our study because it would be used to find those model parameters whose variation will have a biggest effect on the solution of the model equations. For ecological problems for which data are scarce, sensitivity analysis can indicate which parameters need to be estimated most accurately and which need only be given as rough estimates. Hence, sensitivity analysis can guide effort in parameter estimation.

Our model equations are constructed based on some important parameters namely the intrinsic growth rates, the intraspecific and interspecific interaction coefficients and the initial conditions. It is important to investigate the sensitivity of the behaviour of a model to variations in the values of these parameters because the parameter values can never be known with absolute precision.

We know that norms serve the same purpose on vector spaces that absolute value does on the real line. The concept of a norm on a vector space and that of absolute value on a real line furnish a measure of distance.

What are we looking for? We want to find those model parameters, which when varied, have the biggest effect on the solution. Our present analysis is based on a model which we have constructed in chapter three of this thesis.

4.2 Introduction

In the first two chapters of this thesis, we have defined and discussed the ecological and mathematical questions that are relevant in this study. In chapter three, we have constructed deterministic only model equations of competition $(-, -)$ interaction between two competing plant species for a limited resource within the same environment. The first species is assumed to be growing faster

whereas the second species is growing slowly. Our assumption is based on an ecological insight as mentioned in chapter three.

We know that our model equations of competition are based on seven defining parameters namely: the intrinsic growth rate a for the first species, the intraspecific interaction coefficient b for the first species, the interspecific interaction coefficient c for the first species, the intrinsic growth rate d for the second species, the intraspecific interaction coefficient e for the second species, the interspecific interaction coefficient f for the second species, and the starting values $(N_1(0), N_2(0))$. We know from our own experimental analysis that it would be misleading to judge the sensitivity of the model parameters of competition equations without conducting a detailed methodology of achieving this.

What then is sensitivity? It is simply the generic term for the changes in the output of an initial value problem due to changes in the data. How does this numerical method work? The numerical method of sensitivity or the principle of parsimony (or the Ockham's Raizer) works in the following pattern:

1. Write down some complicated interaction model.
2. Fix the values of each possible model parameter.
3. Take one parameter at a time, vary it and see how much this variation changes the solution.
4. If the variation of one parameter changes the solution a lot, then this parameter would be called a more sensitive parameter.
5. On the other hand, if the variation of another parameter produces a small change in the solution, then this parameter would be called a less sensitive parameter.

We do not necessarily have to remove the less important parameters according to the hypothesis of the principle of parsimony. The notion of sensitivity analysis is a widely applied numerical method often being used in the study of biological, immunological and applied science problems ([16], [154], [94], [122], [10], [114], [20], [177], [25], [7], [130], [50], [202]).

We remark that most of these applied sensitivity analyses are considered at a particular time when a solution is reasonably constant whereas our method as proposed in this chapter will consider data points over a period of time where we only consider approximate solution.

Sensitivity analysis is a standard method for studying mathematical models especially if a further numerical simulation is required to analyse a particular research problem. It aims to find the dependency between model predictions and the particular set of parameter values being used ([104]). This knowledge is useful in process control models to find the optimum set of conditions for running a process ([104], [37]).

In the models of biological systems, a knowledge of a sensitivity analysis can assist the modeller to decide whether the parameter estimates are sufficiently accurate for the model to give reliable results ([105]). Otherwise, a further work can be suggested in order to obtain improved estimation of those parameters which would give rise to the greatest uncertainty in model predictions.

As far as we know, a sensitivity analysis is a general procedure which entails changing parameter values and observing the corresponding changes in the

model predictions. It seems easy to describe this procedure, but conducting a detailed sensitivity analysis in any specific case is a daunting task. Problems may include

1. How much to vary each parameter by.
2. What combinations of parameter values are acceptable.
3. What values of the explanatory variables to use.
4. Which model parameters when varied will have the biggest or smallest effect on the solutions
5. How to interpret the results.

The application of a sensitivity analysis is an important component of this study. This powerful numerical technique will be applied to the competition interaction model between two very dis-similar plant species which was formulated and discussed in the chapter three.

The organization of this chapter is as follows. In section 1, we briefly introduce the idea behind the concept of sensitivity analysis. In section 2, our motivation for using our methodology would be discussed. In section 3, we would discuss the application of sensitivity analysis to a few examples of model equations of two interacting dis-similar plant species. In section 4, we would apply an alternative numerical method of selecting the model parameters that have the biggest effect on the solutions. In section 5, we would briefly discuss a few results which we have achieved in this chapter.

4.3 Model Equations of Competition: Dis-Similar Case

Consider another slowly growing second species represented by N_2 . In this section, we shall discuss the sensitivity analysis of a system of competition model equations which we derived in chapter three. These equations describe the dynamics of two dis-similar interacting plant species. The equations are

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.0005N_2(t)) \quad (4.1)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.002 - 0.00002N_1(t) - 0.000015N_2(t)) \quad (4.2)$$

with $N_1(0) = 0.04$ grams per square metres and $N_2(0) = 0.045$ grams per square metres.

Our aim is to use these model equations to find which of the parameters when varied will have the biggest cumulative effect on the N_1 and N_2 approximate solutions.

We shall tackle this problem numerically and discuss our results quantitatively with a view of providing further insights into the central objective of this chapter in the overall context of this study.

The starting point to achieving our goal is to embark on the calculation of percentage variation in solution compared with the original percentage variation in parameters. Our next task is to define, apply this stage of analysis and discuss our results quantitatively.

4.3.1 Calculation of Percentage Variation in Solution Compared with the Original Percentage Variation in Parameters

In these calculations, we shall use a growing season which has a length of 60 days. Consider two approximate solutions N_1 and N_2 . Consider two other approximate solutions N_{1m} and N_{2m} due to a variation of model parameters of the model equations of competition. In this section, we shall be concerned with the calculation of the difference between two solutions. That is, we will calculate the 1-norm of $(N_1 - N_{1m})$, the 2-norm of $(N_1 - N_{1m})$, and the ∞ -norm of $(N_1 - N_{1m})$. We also calculate 1-norm of $(N_2 - N_{2m})$, the 2-norm of $(N_2 - N_{2m})$, and the ∞ -norm of $(N_2 - N_{2m})$.

Example

The sizes of the N_1 and N_2 solution trajectories as well as the sizes of the difference of the solutions are measured using three popular norms. Our calculations are:

1. For N_1 solution, its 1-norm, 2-norm, and ∞ -norm are 12453, 809.3879, and 76.1093.
2. For N_2 solution, its 1-norm, 2-norm, and ∞ -norm are 28.602, 1.1672, and 0.0495.
3. For F_1 solution, its 1-norm, 2-norm, and ∞ -norm are 8730.1, 501.0639, and 37.3859.
4. For F_2 solution, its 1-norm, 2-norm, and ∞ -norm are 0.1268, 0.0085, and 0.00084918.

If $a = 0.2016$, we want to calculate the cumulative effect of this variation of parameter a on the solutions. For this example, our 1-norm percentage effect of this variation on the N_1 solution is 70.1044 which we obtain by dividing 8730.1 by 12453 while our 2-norm and ∞ -norm percentage effects on the N_1 solution are 61.9065 and 49.1213 which we obtain by dividing 501.0639 by 809.3879 and also by dividing 37.3859 by 76.1093.

Similarly, the effects of varying our parameter a on the N_2 solution are:

1. Our 1-norm percentage effect of varying parameter a by 1.2 percent on the N_2 is 0.4433.
2. Our 2-norm percentage effect of varying parameter a by 1.2 percent on the N_2 is 0.7282.
3. Our ∞ -norm percentage effect of varying parameter a by 1.2 percent on the N_2 is 1.7155.

From these figures, we can see that the magnitude of these effects on the N_1 solution is going in a different direction from the magnitude of these effects on the N_2 solution. For the purpose of a clear uniform interpretation, we would prefer to calculate the cumulative effect of any parameter variation on the N_1 and N_2 solutions.

In this example, our cumulative effects on the solutions are:

1. Our 1-norm cumulative percentage effect if $a = 0.2016$ is 70.5.
2. Our 2-norm cumulative percentage effect if $a = 0.2016$ is 61.9.
3. Our ∞ -norm cumulative percentage effect if $a = 0.2016$ is 50.8.

We remark that this method has been used to calculate our cumulative percentage effects due to a variation of other model parameters. We would present these calculations next and discuss their interpretations.

Which parameters have the biggest effect on the solutions?

In this section, we are interested to find the model parameters of two dis-similar competing plant species which when varied will have the biggest cumulative effect or biggest percentage change on the N_1 and N_2 solutions.

Without a detailed explanation on how to calculate the biggest cumulative effect, we shall present our results that relate directly to the question we want to tackle. These results are presented in the next section.

Main Results: 20 percent variation of model parameters

In this section, we want to find the biggest cumulative effect of 20 percent variation of model parameters on the solutions. Our results are presented in Table 4.1.

Norm of Solutions	20 Percent Variation of Model Parameters							
	a	b	c	d	e	f	sv1	sv2
1-norm	70.5	11.15	0.0094	1.23	0.09	0.00042853	6.7	20
2-norm	61.9	13.09	0.0087	1.43	0.166	0.00050077	5.8	20
∞ -norm	50.8	15.89	0.0073	2.43	0.5	0.00085677	5.1	20

Table 4.1: Sensitivity analysis of a 20 percent variation of model parameters

where *sv1* represents when only $N_1(0) = 0.04g/m^2$ is changing and *sv2* represents when only $N_2(0) = 0.045g/m^2$ is changing.

Therefore, when we vary the model parameters by 20 percent, the biggest cumulative effect on the solutions are observed for intrinsic growth rate a for species N_1 , the starting value when $N_1(0) = 0.04g/m^2$ is unchanged and $N_2(0) = 0.054g/m^2$, and the intraspecific or self interaction coefficient b irrespective of the norm being used to calculate the changes in the solutions.

Main Results: 10 percent variation of model parameters

Next, we consider the biggest cumulative effect of a 10 percent variation on the solutions. Our results are presented in Table 4.2.

Therefore, in this scenario, a 10 percent variation in model parameters will produce the biggest cumulative effect in the parameters a , b , and the starting values irrespective of the norm being used to calculate the changes in the solutions.

Norm of Solutions	10 Percent Variation of Model Parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	34.44	6.12	0.0047	0.61	0.045	0.000214	3.5	10
2-norm	30.88	7.24	0.0043	0.71	0.083	0.00025	3.04	10
∞ -norm	25.76	8.85	0.0036	1.21	0.25	0.000428	2.67	10

Table 4.2: Sensitivity analysis of a 10 percent variation of model parameters

Main Results: 5 percent variation of model parameters

Next, we would find the biggest cumulative effect of a 5 percent variation of parameters on the solutions. These results are briefly summarised in Table 4.3 below:

Norm of Solutions	5 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	16.93	3.07	0.0024	0.3	0.044	0.00012	1.79	5
2-norm	15.36	3.64	0.0022	0.35	0.075	0.00015	1.56	5
∞ -norm	12.9	4.46	0.0018	0.6	0.2	0.00025	1.37	5

Table 4.3: Sensitivity analysis of a 5 percent variation of model parameters

Therefore, in this scenario, our important model parameters are a , b , $sv2$.

Main Results: 2.5 percent variation of model parameters

In this section, we are interested to calculate the cumulative effect of varying the model parameters by 2.5 percent and study its impact on the solutions. Our results are briefly summarised and presented in Table 4.4.

Norm of Solutions	2.5 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	8.39	1.56	0.0012	0.15	0.01	0.0000535	0.909	2.5
2-norm	7.66	1.85	0.0011	0.17	0.02	0.0000625	0.79	2.5
∞ -norm	6.45	2.274	0.00091	0.3	0.06	0.000107	0.70	2.5

Table 4.4: Sensitivity analysis of a 2.5 percent variation of model parameters

In this scenario, our important model parameters are a , b , and $sv2$.

Main Results: 1.25 percent variation of model parameters

Finally, we would investigate the cumulative effect of varying the model parameters by 1.25 percent on the solutions. Our results are briefly summarised and presented in Table 4.5.

In this scenario, our important parameters are a , b , and $sv2$.

Norm of Solutions	1.25 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	4.2	0.788	0.0006	0.07	0.010	0.00003	0.45	1.25
2-norm	3.84	0.935	0.0005	0.08	0.020	0.00003	0.4	1.25
∞ -norm	3.22	1.15	0.00045	0.15	0.050	0.00006	0.35	1.25

Table 4.5: Sensitivity analysis of a 1.25 percent variation of model parameters

Main Results: 0.5 percent variation of model parameters

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 0.5 percent on the solutions. Our results are briefly summarised and presented in Table 4.6.

Norm of Solutions	0.5 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	94.96	51.3	0.0235	2.99	0.23	0.001	24.5	50
2-norm	94.72	64.2	0.0217	3.47	0.42	0.0013	21.8	50
∞ -norm	95.3	86.1	0.0182	5.82	1.25	0.002	19.2	50

Table 4.6: Sensitivity analysis of a 0.5 percent variation of model parameters

What do we learn? It is interesting to observe that if we vary parameter a by 0.5 percent, we shall obtain about 95 percent cumulative effect on the solutions. In this situation, if we vary each parameter by this much, we shall obtain a biggest effect on the solutions due to a variation of parameters a , b , and the starting values.

Main Results: 0.25 percent variation of model parameters

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 0.25 percent on the solutions. Our results are briefly summarised and presented in Table 4.7.

Norm of Solutions	0.25 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	99.6	114.87	0.0353	4.44	0.23	0.001	46.6	75
2-norm	99.4	151.7	0.0325	5.15	0.42	0.0013	42.5	75
∞ -norm	101.85	224.6	0.0273	8.6	1.25	0.002	37.35	75

Table 4.7: Sensitivity analysis of a 0.25 percent variation of model parameters

What do we learn? We learn that the less we vary parameters a , b , and the starting values, the bigger the cumulative effects on the solutions. In this case, our important model parameters are the intra-specific coefficient, the daily intrinsic growth rate for the first species and the starting values or biomasses.

Main Results: 0.125 percent variation of model parameters

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 0.125 percent on the solutions. Our results are briefly summarised and presented in Table 4.8.

Norm of Solutions	0.125 percent variation of model parameters							
	a	b	c	d	e	f	sv1	sv2
1-norm	100.07	182.78	0.0412	5.15	0.23	0.001	65.05	87.5
2-norm	99.78	254.2	0.0379	5.97	0.42	0.0013	60.7	87.5
∞ -norm	102.32	415.5	0.0319	9.97	1.25	0.002	53.48	87.5

Table 4.8: Sensitivity analysis of a 0.125 percent variation of model parameters

What do we learn? We learn that the less we vary parameters a , b , and the starting values, the bigger the cumulative effects on the solutions. In this scenario, our important model parameters are the intra-specific coefficient, the daily intrinsic growth rate for the first species and the starting values or biomasses.

4.4 Summary of our Sensitivity Analysis and Selection of Parameters for a Dis-Similar Competition Model

In summary, if we vary model parameters a , b , and the starting values a little, it produces biggest effect on the solutions. This is why we think that we have got the application of this powerful numerical method right in the case of two interacting dis-similar plant species. Therefore, these three important model parameters which we have used this numerical method to select are the daily intrinsic growth rate for the first plant species, the intra-specific coefficient for the first plant species, and the starting values for both the first and second plant species.

It would be a good idea to justify our conclusion for the case of the sensitivity analysis of varying model parameter a only for the purpose of clarity. Hence, we would present the following calculations which we have not seen elsewhere with a view to providing more insight about the application of our method of the norm of difference of two solutions over a long time interval.

Our results are presented in Table 4.9, Table 4.10, Table 4.11, and Table 4.12.

4.4.1 Sensitivity analysis for parameter a interval $[0.015, 0.053]$

In this section, we shall present our calculations for the sensitivity analysis of varying parameter a for the interval $[0.015, 0.053]$.

Parameter value	Calculation of sensitivity using 2-norm	
Parameter number	value of parameter a	2-norm sensitivity
1	0.015	99.84
2	0.017	99.83
3	0.019	99.80
4	0.021	99.78
5	0.023	99.76
6	0.025	99.74
7	0.027	99.71
8	0.029	99.68
9	0.031	99.64
10	0.033	99.61
11	0.035	99.56
12	0.037	99.52
13	0.039	99.46
14	0.041	99.41
15	0.043	99.34
16	0.045	99.27
17	0.047	99.20
18	0.049	99.11
19	0.051	99
20	0.053	98.90

Table 4.9: A detailed sensitivity analysis of varying parameter a on the solutions over a time interval for our chosen parameter interval

4.4.2 Sensitivity analysis for parameter a interval $[0.055, 0.093]$

In this section, we shall present our calculations for the sensitivity analysis of varying parameter a for the interval $[0.055, 0.093]$.

Parameter value	Calculation of sensitivity using 2-norm	
	Parameter number	value of parameter a
21	0.055	98.78
22	0.057	98.65
23	0.059	98.50
24	0.061	98.35
25	0.063	98.17
26	0.065	97.97
27	0.067	97.76
28	0.069	97.52
29	0.071	97.25
30	0.073	96.96
31	0.075	96.63
32	0.077	96.27
33	0.079	95.88
34	0.081	95.45
35	0.083	94.97
36	0.085	94.45
37	0.087	93.88
38	0.089	93.25
39	0.091	92.56
40	0.093	91.80

Table 4.10: A detailed sensitivity analysis of varying parameter a on the solutions over a time interval for our chosen parameter interval

4.4.3 Sensitivity analysis for parameter a interval $[0.095, 0.133]$

In this section, we shall present our calculations for the sensitivity analysis of varying parameter a for the interval $[0.095, 0.133]$.

Parameter value	Calculation of sensitivity using 2-norm	
	Parameter number	value of parameter a
41	0.095	90.99
42	0.097	96.105
43	0.099	89.14
44	0.101	88.09
45	0.103	86.95
46	0.105	85.72
47	0.107	84.40
48	0.109	82.98
49	0.111	81.47
50	0.113	79.84
51	0.115	78.12
52	0.117	76.27
53	0.119	74.30
54	0.121	72.27
55	0.123	70.10
56	0.125	67.80
57	0.127	65.40
58	0.129	62.98
59	0.131	60.40
60	0.133	57.70

Table 4.11: A detailed sensitivity analysis of varying parameter a on the solutions over a time interval for our chosen parameter interval

4.4.4 Sensitivity analysis for parameter a interval $[0.135, 0.181]$

In this section, we shall present our calculations for the sensitivity analysis of varying parameter a for the interval $[0.135, 0.181]$.

Parameter value Parameter number	Calculation of sensitivity using 2-norm	
	value of parameter a	2-norm sensitivity
61	0.135	54.94
62	0.137	52.07
63	0.139	49.13
64	0.141	46.10
65	0.143	43
66	0.145	39.83
67	0.147	36.60
68	0.149	33.30
69	0.151	29.96
70	0.153	26.57
71	0.155	23.14
72	0.157	19.66
73	0.159	16.15
74	0.161	12.60
75	0.163	9.04
76	0.165	5.44
77	0.167	1.82
78	0.169	1.826
79	0.171	5.45
80	0.173	9.13
81	0.175	12.82
82	0.177	16.46
83	0.179	20.14
84	0.181	23.84

Table 4.12: A detailed sensitivity analysis of varying parameter a on the solutions over a time interval for our chosen parameter interval

We can clearly observe that when we change parameter a by 8.9 percent (or when $a = 0.015$), we would get a change which is approximately equal to 100 percent in our N_1 and N_2 approximate solutions by using our 2-norm penalty function. In contrast, when we change parameter a by 107 percent (or when $a = 0.181$), we would get a change which is approximately equal to 24 percent in our N_1 and N_2 approximate solutions by the same method and starting values.

The key information we are getting from our sensitivity analysis for this example is that if we vary parameter a a little, the cumulative effect on the solutions would vary a lot. This is why we can conclude that parameter a is more sensitive and hence can be selected as an important model parameter.

We are aware that there is alternative numerical method for selecting model parameters. This method concerns the percentage change on the solutions using the changes in their steady states when each model parameter is varied.

We did not present our calculations on the application of this method because it gives similar conclusion as we have observed when we used the method of the norm of the difference of two solutions.

4.5 Model Equations of Competition: Similar Case

Based on some simplifying assumptions as mentioned in chapter three of this thesis, we present a possible model equations of competition between two similar interacting plant species:

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.0018N_2(t)) \quad (4.3)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.166 - 0.0015N_1(t) - 0.002N_2(t)) \quad (4.4)$$

with $N_1(0) = 0.04$ grams per area of grass cover and $N_2(0) = 0.045$ grams per area of grass cover.

In this section, we are interested to use the same method of the norm of the difference of two solutions to calculate the cumulative effects on the solutions due to a variation of parameters. We shall present our calculations by using the following examples.

4.5.1 Example 1: 0.125 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 0.125 percent on the solutions of a similar competition model. Our results are briefly summarised and presented in Table 4.13.

4.5.2 Example 2: 0.25 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 0.25 percent on the solutions of a similar competition model. Our following results are summarised and presented in Table 4.14.

Norm of Solutions	0.125 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	139	150.9	65.4	158.4	48	181	109.7	129.3
2-norm	110	186.9	66.7	123.5	45.8	222	85.9	99.5
∞-norm	157	424.3	117.2	197.6	81.3	490	114.5	154.6

Table 4.13: Sensitivity analysis of a 0.125 percent variation of model parameters

Norm of Solutions	0.25 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	138.5	105.4	55.9	157.7	41.3	124	84.7	104.5
2-norm	110.25	123	57.2	123	39.5	142.7	65.8	79.8
∞-norm	156.9	263.9	102	197	71	304.4	83.3	122

Table 4.14: Sensitivity analysis of a 0.25 percent variation of model parameters

4.5.3 Example 3: 0.5 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 0.5 percent on the solutions of a similar competition model. Our following results are summarised and presented in Table 4.15.

Norm of Solutions	0.5 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	134.2	52.3	36.9	152.3	27.7	61.2	44.9	65.4
2-norm	107.5	56.9	37.9	119.5	26.6	64.6	35	49.7
∞-norm	154	113.6	69.2	192.7	49.2	133.2	40.2	75.9

Table 4.15: Sensitivity analysis of a 0.5 percent variation of model parameters

4.5.4 Example 4: 1.0125 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 1.0125 percent on the solutions of a similar competition model. Our following results are summarised as presented in Table 4.16.

4.5.5 Example 5: 1.025 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 1.025 percent on the solutions of a similar competition model. Our results summarised as presented in Table 4.17.

Norm of Solutions	1.0125 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	8.7	0.88	0.88	8.9	0.69	1.02	12	9.9
2-norm	7	0.89	0.9	6.9	0.65	0.99	11.2	9.88
∞-norm	9.6	1.64	1.7	10.12	1.3	1.98	21.8	19.76

Table 4.16: Sensitivity analysis of a 1.0125 percent variation of model parameters

Norm of Solutions	1.025 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	17.7	1.75	1.75	18.4	1.38	2.03	13	9.9
2-norm	14.2	1.76	1.8	13.98	1.33	1.98	11.8	9.23
∞-norm	19.4	3.25	3.4	20.2	2.58	3.9	22.8	18.76

Table 4.17: Sensitivity analysis of a 1.025 percent variation of model parameters

4.5.6 Example 6: 1.05 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 1.05 percent on the solutions of a similar competition model. Our results are summarised as presented in Table 4.18.

Norm of Solutions	1.05 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	36.4	3.44	3.5	36.9	2.75	4	15.4	7.64
2-norm	29.14	3.47	3.6	28.3	2.66	3.89	13.1	8.01
∞-norm	39.2	6.36	6.8	40.2	5.17	7.67	24.8	16.8

Table 4.18: Sensitivity analysis of a 1.05 percent variation of model parameters

4.5.7 Example 7: 1.1 percent variation of model parameters for a similar competition model

In this section, we are interested to investigate the cumulative effect of varying the model parameters by 1.1 percent on the solutions of a similar competition model. Our results are presented in Table 4.19.

4.5.8 Summary of Results for the Similar Competition Model

In these seven examples of varying model parameters over a time interval, we can observe that the important parameters are the parameters which when varied a little produce biggest percentage cumulative effects on the solutions. The

Norm of Solutions	1.1 percent variation of model parameters							
Norm	a	b	c	d	e	f	sv1	sv2
1-norm	76.3	6.68	6.95	75.9	5.49	7.76	19.7	6.4
2-norm	60.6	6.7	7.11	57.6	5.3	7.5	15.8	6.1
∞ -norm	79.2	12.24	13.5	78.3	10.36	14.8	28.6	13

Table 4.19: Sensitivity analysis of a 1.1 percent variation of model parameters

intrinsic growth rates, the intra-specific coefficients, and the starting values can be categorised as important parameters in this context.

A few solution trajectories on which our novel method of the norm of the difference of two solutions are based are graphically presented in the appendix (Figure 8.4, Figure 8.5).

In the scenaria when the parameters are varied a bit more, these produce smallest percentage cumulative effects on the solutions and hence categorised as less important parameters.

4.6 Conclusion and Further Remarks

By a numerical simulation, we have used the technique of sensitivity analysis to select a few important model parameters for the competition between two interacting plant species.

These parameters are the intrinsic growth rate a for the first species N_1 , the intraspecific interaction coefficient b for the first species and the initial starting population sizes for our dis-similar competition model.

This is an important result which one has achieved in this chapter. Although the concept of sensitivity analysis is familiar, our method of selecting these sensitive parameters is a novel numerical approach.

Another interesting insight from our method is the fact that the sensitive parameters indirectly relate to the impact of temperature change on the growth of plant species. For example, plant ecologists have reported that temperature change does affect the growth of plant species. This impact can be reflected in our summer model only by changing the intrinsic growth rate for the first species and also by changing the intra-specific coefficient for the first species (or the carrying capacity of the first plant species).

For our dis-similar model, we observe that our important parameters relate more to the fast growing plant species because the second plant species reflects the characteristics of a slowly growing plant. We observe that a variation of the model parameters of a slowly growing plant may not produce any significant effect on the solutions.

The selection of these important model parameters is linked to the last two chapters of this thesis. In attempting to find the probability of extinction of each plant species, we would need to know whether it is more sensitive to a variation of the more sensitive model parameters which we have selected in this chapter. Instead of calculating the minimum biomass after each storm for all the parameters of our summer competition model, we would focus on computing the minimum biomass for only the important model parameters.

Similarly, we would also require the sensitive model parameters of our benign summer competition model which we derived in the previous chapter in order to find out the type of plant species interactions that we can obtain from a combination of our summer model and stochastic winter model qualitatively. This will be the subject of our next chapter.

Chapter 5

Simulation of Our Summer-Winter Model of Plant Species Interactions

5.1 Motivation

We know that most nonlinear systems of ordinary differential equations of first order which we cannot find a closed-form solution for can be analysed by coding these functions in a Matlab computer programming language.

Why do we choose to apply a simulation approach in this chapter? According to ([9]) and ([52]), experiments and analytical theory have been the two principal branches in the development of science. According to these authors, it is now generally accepted that computational science has become the third branch of the scientific endeavour of which simulation is an integral component.

Other important applications of modelling and simulation are in the study of cardiovascular and respiratory systems ([27]) and in immunology ([21]). The dynamics that explain vulnerability in human heart failure has been successfully defined, analysed, and discussed using a powerful technique of computational modelling and statistical analysis ([149]). A current successful application of a simulation of stochastic differential equations that describe a complex biophysical problem has been reported ([96]). There are several other applications of simulation approach which have been successfully conducted for biomedical problems as cited by these authors. Other applications of simulation technique in diverse industrial problems have been reported ([151]).

The computer approach to the study of complex competition interaction between two plant species is called ecological simulation. This means that the ordinary differential equations representing the dynamic characteristics between two competing plant species for a limited resource can be analysed simultaneously to produce time dependent approximate solutions which resemble the qualitative behaviour of the real system.

In effect, ecological simulation offers the following several advantages:

1. The qualitative behaviour of a competition interaction between two plant species for various summer-winter model parameters with the same start-

ing values can be obtained once a carefully written Matlab program has been constructed. The model parameters are usually changed merely by modifying and evaluating the two nonlinear interaction functions.

2. The prediction of the ways in which changes in the environment (for example, as a result of climate change) influence biodiversity is of particular concern. This initiative is the focus of several important research studies as cited in chapter 1 of this thesis. Nevertheless, one major difficulty in research in this field is that, in delicate ecosystems, the presence of research scientists may itself be a major influence on the environment and indeed on the results obtained. It would therefore be attractive to develop a mathematical model that would simulate the interactions and thereby reduce the need for actual experimentation.
3. An ecological simulation can be operated as a component in an actual ecological harsh environment. This has a cost effective advantage because the environmental impact of large numbers of scientists visiting the arctic to collect specimens can be significant as cited in chapter 1 of this thesis. One observed reason for variation in inter-specific interactions is the disturbance of the environment. Hence, in this situation, there can be significant environmental and cost advantages of a computational and mathematical modelling approach.
4. An ecological simulation can be time-scaled so that the response from the simulation is very fast compared with the response of the actual system which is being simulated. In this way, many example trajectories instead of exact solutions can be obtained in a short time.
5. The use of repetitive operation on the computer is advantageous in studying the effect of varying model parameters on the qualitative behaviour of solutions over time.

5.2 Introduction

In this chapter, we shall consider the numerical solution of summer competition model equations. The following nonlinear coupled ordinary differential equations of first order have been derived in chapter 3 of this thesis.

$$\frac{dN_1}{dt} = N_1(0.168 - 0.0020339N_1 - 0.0005N_2) \quad (5.1)$$

$$\frac{dN_2}{dt} = N_2(0.002 - 0.00002N_1 - 0.000015N_2) \quad (5.2)$$

where

$$N_1(0) = 0.04 > 0 \quad (5.3)$$

$$N_2(0) = 0.045 > 0 \quad (5.4)$$

Similarly, the unit of starting biomasses would be in grams per area of grass cover.

These model equations describe the interaction between two dis-similar competing plant species for single limited resources such as nutrients, light, water,

space and so on. The first species N_1 is a fast growing plant compared to a slowly growing species N_2 . We have assumed in this study a temperate type of weather conditions.

The above model equations describe the growth of two plant species over time. In the absence of interspecific competition coefficients, the two plant species will take the form of Malthusian exponential growth. In the presence of interspecific interaction coefficients, the plant species will grow instead of decaying or oscillating.

We have also done the basic simulation analysis to confirm that the two plant species grow better when interacting in isolation of each other than when interacting together. This result shows the evidence of competition factor taking place between these plant species. Our conclusion which will be defined and discussed in detail in chapter six is consistent with ecological insight ([13]).

According to these authors, when these two plant species grow in isolation, they usually have relative greater access to the same limited resources because they are not in competition. But when they are in competition for the same limited resources in the ecosystem, each plant species tends to outgrow the other.

In our case, the two dis-similar plant species have two different interspecific competition coefficients because the two plant species compete for the same limited resources. In this case, plant species N_1 will have bigger advantage over plant species N_2 in their struggle for limited resource within the ecosystem.

Assuming two plants grow in a garden and resources are plentiful, if the summer growing season is lengthened, the first start of a severe winter storm will have a more severe effect on taller plants than on shorter plants.

In this chapter, we are interested to simulate our summer competition model and winter model of plant species interactions.

5.3 Aims of this Chapter

In this chapter, we will use our numerical simulation Matlab program to analyse and answer the following questions

1. How do we approximate the number of storms?
2. For each storm, how do we approximate the intensity of the storm?
3. For each storm, how do we approximate how much biomass remains at the end of the storm?
4. Decide on a method for calculating the minimum biomass for each plant species over the 10 year period of one trajectory.
5. Write a program to simulate 1000 ten year periods with the starting values and calculate experimental probabilities of extinction of each species.
6. How do we upgrade our program to reflect the concepts of shortened winter and lengthening summer and use these to calculate experimental probabilities of extinction of each species?
7. Can we use our summer-winter model to produce a situation in which mutualism can be observed based on a summer competition model with winter storms?

5.4 Summer Model

In this chapter, we shall merge the usual seasons of spring, autumn, and summer into one growing season called the summer model. In order to analyse this model subsequently, we shall make the following realistic assumptions:

1. In a summer season which is characterised by a mild climate, we assume a continuous growth of two plant species.
2. We assume the possibility of two plant species N_1 and N_2 that live together and compete with each other for the same limited resource.
3. We assume that each population of plant species is inhibited not only by members of its own species but also by those of the other population.
4. We assume linear growth rates and intra-specific parameters are the logistic parameters for species N_1 and N_2 if they were living alone.
5. Our deterministic summer model rests on the assumption that the environmental parameters involved with our model system are all constants irrespective to time and environmental fluctuations.

5.5 Stochastic Winter Model

The winter season is characterised by an occasional frequency of storms which does not promote the growth of plant species. According to the analysis of arctic climatology, the number of storms varies within the arctic region ([12]). The occurrence of 2 or 3 storms every three months presupposes that we would expect to have an annual mean number of storms to be between 6 storms and 9 storms. Since the environment is so uncertain, we might consider figures below this range in our further analysis.

5.5.1 Poisson Distribution

We are motivated to use the Poisson distribution because it is an important discrete distribution frequently used in engineering to evaluate the risk of damage.

By assuming that all possible number of storms in the winter model occur only one at a time, that all such events occur independently, and that the probability of a storm occurring is constant per unit time, we can describe our winter model as a Poisson process, where the mean number of storms is distributed exponentially ([141], [142]).

Hence, a discrete Poisson probability density function (pdf) is defined by

$$f(x) = e^{-\lambda} \frac{\lambda^x}{x!} \quad (5.5)$$

for $x = 0, 1, 2, \dots$ where $E(x) = \lambda$, $Var(x) = \lambda$.

5.5.2 Gamma Distribution

Another concern is that of measuring the intensity of each storm on the biomass at the start of a winter season. In this chapter, we propose to use the gamma

distribution to determine the intensity of storm under some chosen shape and scale parameters ([141], [142]). The gamma distribution is an extension of the exponential distribution which is characterised by a scale parameter which describes the spread of the exponential distribution.

Hence, a gamma distribution is a two-parameter family of continuous probability distributions characterized by a scale parameter and a shape parameter.

There are several applications of gamma distribution in several books of mathematical statistics.

The probability density function of a gamma distribution is defined by

$$f(x) = \begin{cases} \frac{\lambda}{(r-1)!} (\lambda x)^{r-1} e^{-\lambda x} & x > 0 \\ 0 & \text{elsewhere} \end{cases} \quad (5.6)$$

According to [152], the structure of a plant is characterised by its shape and size. We know that two plant species can take several shapes such as spherical, square, rectangular, triangular and so on. For example, if the shape of a plant is spherical, it has a base and the effect of any external force on the plant can be studied as the impact of this force is distributed in terms of its shape and base or scale.

The gamma distribution model is defined in terms of several values of the shape and scale parameters. But the shape and scale parameters that could fairly model the physical structure of a plant species do not have precise values. Since the geometries of plant species differ ([152]), we have followed the idea in our paper to choose the values of $r = 5$ and $\lambda = 1$ ([69]).

Why do we propose to use a probability distribution? Having mentioned in chapter 1 of this thesis that actual experimentation in a harsh climate is more costly, the simple relations between the mean number of storms and its frequency of occurrence may not be realised. In this situation, we would think that the best description we can provide to model the occurrence of occasional storms in a harsh climate is in terms of a probability distribution.

5.6 Buckling

Buckling of a column occurs when the Euler critical load is exceeded ([187], [198]). The Euler load is defined by the formula

$$P_E = \frac{\pi^2 EI}{L^2}. \quad (5.7)$$

where P_E is the Euler buckling load, E is the Young's modulus for the material, I is the least second moment of area of cross section, L is the length of the strut between the pinned ends.

The Young's modulus is a measure of the amount of stress that a plant species can take before buckling. We assume that one end of a plant species structure is fixed in the direction of wind and the above ground section is free. Let the length of plant stem above soil surface be L units and effective length be $2L$ units.

According to ([152]), the Euler buckling load for the plant stem for the case $L = 2L$ in a wind direction can be similarly defined by

$$P_E = \frac{\pi^2 EI}{4L^2}. \quad (5.8)$$

A detailed mathematical analysis and proof of Euler Bukling formula can be found in the works of ([187], [198]).

Other researchers have examined the mechanical effect of wind on the growth of plants ([22], [11]). We are interested to tackle the effect of storm on the ecology of plant species in a severe arctic region where growth of plants is not a common process.

Next, we will explain how the Euler buckling load will be used with wind speed in the model to determine how much biomass is destroyed in a storm.

Assume that the force at the base of a plant of height H caused by wind speed V is proportional to $V^2 H^3$, that is, $F = cV^2 H^3$. Any force acting on a material can be described as producing a stress. The unit for stress is the pascal (Pa), which is the force per unit area. For the above ground plant species, assume that $P_E = F$. Then

$$\frac{\pi^2 EI}{4L^2} = cV^2 H^3 \quad (5.9)$$

From this equation, we can simply solve for c to obtain

$$c = \frac{\pi^2 E_{plantstem} I}{4V^2 H^3 L^2} \quad (5.10)$$

In the theory of elasticity ([187]), the Young's modulus is defined mathematically as the slope of the stress-strain relationship

$$E = \frac{\sigma}{\epsilon} \quad (5.11)$$

where the symbol σ represents the stress in the material while the symbol ϵ represents the strain in the material.

The amount of stress E that a plant species can take before buckling can be determined by dividing the stress exacted on the plant by any change in the dimension of the plant component ([205], [152]).

For example, if the force exerted on the biomass due to increasing storm intensity is 2 Newtons in a patch of plant species of a $10m$ by $10m$ dimension, then the stress $\sigma = \frac{2}{100} N/m^2$ which is $0.02 N/m^2$. We know that the strain is a dimensionless quantity.

Since the value of the strain does not have a precise value in the work of Zebrowski (1991), let us consider a situation when the strain $\epsilon = 0.0474$.

Consider when the length of the plant species before winter storm is $\ell_1 = 2m$. What do we want to find? We want to define and discuss how to calculate the amount of stress that a plant species can take before buckling.

The effect of storm on the length of the stem is modelled by $\frac{\ell_1 - \ell_2}{\ell_1}$. Since, the strain is modelled by dividing the change in the length of the stem by the original length before the winter storms, in this case

$$\frac{\ell_1 - \ell_2}{\ell_1} = 0.0474. \quad (5.12)$$

From this equation, we know that

$$\ell_1 - \ell_2 = 0.0948. \quad (5.13)$$

By substituting for the value of ℓ_1 , $\ell_2 = 2 - 0.0948 = 1.9052$. Therefore, the amount of stress E that a plant species can take before buckling

$$E = \frac{0.02}{0.0474} = 0.4219N/m^2. \quad (5.14)$$

What are we trying to find out? We want to find if a variation of the Young's modulus for the grass species would have any impact on our later calculation of the minimum biomass after each storm and its implication for approximating the experimental probability of extinction of each plant species.

Similarly, since the height of a plant is approximated by $H = B^{\frac{1}{3}}$, $H^2 = B^{\frac{2}{3}}$ and $H^3 = B$. Assume that $L = H$, then $L^2 = H^2$ and $4L^2 = 4B^{\frac{2}{3}}$. By substituting for these expressions in the above formula, we would obtain

$$c = \frac{\pi^2 EI}{4V^2 B^{\frac{5}{3}}} \quad (5.15)$$

For a given calculated wind speed and a calculated value for biomass, we can use the above formula to measure the effect of fierce storm on the biomass or the effect of storm intensity on the biomass.

In summary, since the Young's modulus is defined in terms of the stress and strain, strain is dimensionless (extension of material divided by the original length of material) and stress is defined as load per unit area, we would expect the sectional area to vary from one grass species to another. Therefore the stress is more likely to vary and so one can expect the Young modulus E to vary also.

5.7 Analysis of Stochastic Winter Model

In this section, our task is to attempt to analyse a few important questions about the stochastic winter model.

5.7.1 Assumptions leading to stochastic winter model

From the literature, taller plant species are generally subjected to greater mechanical stress because wind speed is said to increase with height above the ground surface ([140]). Hence, the relationship between wind speed or velocity V and height of plant's biomass H can be defined by

$$V = \beta H^2 \quad (5.16)$$

where β is a positive constant.

In order to construct a meaningful winter model, we shall assume that

1. Force at base of plant of height H caused by wind of velocity is proportional to $(V^2 H^3)$.
2. The impact of this force on the old biomass (or biomass at the start of winter) causes some parts of the old biomass to be destroyed.

3. In the winter season there will be no further growth and the plant populations will instead be subjected to various weather events (storms etc.) which lead to destruction of some or all of the biomass ([69]).

5.7.2 Old Biomass and New Biomass

The relationship between new biomass and old biomass is defined by New biomass = (1-Proportion destroyed)times Old biomass where the proportion of plant species destroyed is directly proportional to the force at base of plant of height H, that is, the proportion destroyed, denoted by P_d , is

$$P_d = cV^2H^3 \quad (5.17)$$

where c is a positive constant that depends on a range of wind speeds, range of plant heights, strength of stem, buckling effect, etc in such a way that the quantity $P_d < 1$ with $H^3 = B$ where B represents the quantity of biomass.

If the value of force at base of plant per unit area is 1 Pascal and a positive constant ϵ is assumed to control the error of computing the values of c , by using

$$F = cV^2H^3 \quad (5.18)$$

we shall obtain

$$c_1 = \frac{1}{V^2H_1^3 + \epsilon} \quad (5.19)$$

for species 1 and

$$c_2 = \frac{1}{V^2H_2^3 + \epsilon} \quad (5.20)$$

for species 2

Here the parameter V measures the effect of fierce storm on the biomass, c_1 measures the individual intensity of storm on species 1, c_2 measures the individual intensity of storm on species 2, H_1^3 measures the maximum biomass at the start of winter for plant species 1 and H_2^3 measures the maximum biomass at the start of winter for plant species 2. The two values of c are only calculated once.

We have used a numerical method of fourth order Runge-Kutta to simulate the summer only model from which the maximum biomass at the start of winter can be calculated.

Under the winter model, we are interested to tackle three important questions:

1. How do we approximate the number of storms?
2. For each storm, how do we approximate the intensity of the storm?
3. For each storm, how do we approximate how much "grass" species remains at the end of the storm?

5.7.3 How do we approximate the number of storms?

Ecologists are interested about how to determine the number of storms experimentally. But mathematicians approximate the number of storms.

Having mentioned that the mean number of storms can be determined using the Poisson distribution, we shall focus on illustrating this idea with a simple example.

For a 10 year ecological simulation, each simulation run will produce a sample of 10 data points representing a random list of mean number of storms in the arctic.

For example, a possible Matlab random sample if mean number of storms is 2 is 4, 2, 3, 3, 2, 2, 0, 3, 2. What these data mean is that in year 1, we would expect to have 4 storms, followed by 2 storms in year 2, then 3 storms in year 3 and so on. Then we will have no storm in year 8 and 2 storms in year 10. The number of storms varies for a 10 year simulation.

5.7.4 For each storm, how do we approximate the intensity of the storm?

We have used the gamma distribution to simulate the intensity of 1000 storms on the biomass during a ten year simulation period of one trajectory.

Given that the other parameters are positive constants with varying storm intensity on the biomass and the size of the biomass before the start of winter, the storm intensity in our analysis can be determined by using the formula

$$c = \frac{\pi^2 E_{plantstem} I}{4V^2 B^{\frac{5}{3}} + \epsilon} \quad (5.21)$$

where the parameter V measures the wind speed, B measures the biomass, and ϵ is a small positive constant that takes account of the error in the calculation. By substituting for parameters $E_{plantstem}$ and I as 0.4219 Pa and 1.2586, we would obtain

$$c_1 = \frac{1.311253146}{V^2 B^{\frac{5}{3}} + \epsilon} \quad (5.22)$$

$$c_2 = \frac{1.311253146}{V^2 B^{\frac{5}{3}} + \epsilon} \quad (5.23)$$

The square of the storm speed constitutes a huge set of data in 1000 storm simulations. We have used a Matlab function to order the data generated by this simulation in terms of their fierceness. The topmost value in this sequence of the square of the wind speed for 1000 storms represents how fierce the storm would be on the biomass at the start of winter during a period of ten years. The next values in the list after the worst effect of storm represent the individual intensity of each storm on each plant species.

5.7.5 How do we approximate how much plant species remains at the end of each storm?

Both analytically and computationally, we used the following formula to approximate how much plant species remains at the end of each storm:

$$NB = (1 - P_d)OB \quad (5.24)$$

where NB , P_d and OB represent new biomass, proportion of old biomass that is destroyed and old biomass. In a combined summer-winter model, the detail of our numerical approach is briefly defined:

1. Use the most popular version of fourth order Runge-Kutter method to simulate the summer only model with the chosen starting values
2. Next, from this simulation, we calculated the maximum biomass for each species at start of winter

For the start of first year winter, our summer model is simulated only once with which the maximum biomass for each species before the impact of storm is calculated.

At the end of first year winter season, the biomass that remains becomes the starting values to run the summer model for the second year from which we calculated the maximum biomass for each plant species at start of winter for the second year. This procedure is repeated for the ten year period.

5.7.6 Example: Determining how much biomass is destroyed in a storm by an analytical method

Under a different starting value of our summer competition model, the species biomass before the start of winter are 79.7979 grams and 0.0541 grams for species N_1 and N_2 . We choose the force at base of height of biomass to be 1 pascal whereas $V = 227.5616$ metres per second is the worst storm effect in a 1000 simulations. We used the Poisson distribution to determine the number of storms for a period of 10 years which gave us a random sample of 4 storms in the first year, 1 storm in the second year, no storms in the third and fourth years, 2 storms in the fifth year, 3 storms in the sixth year, 3 storms in the seventh year, 2 storms in the eighth year, 2 storms in the ninth year, and 2 storms in the tenth year. We used the gamma distribution to simulate 1000 storms subject to scale and shape parameters and observed a sample of a fierce storm having a speed of $227.5616m/s$, followed by the next levels of the velocity of storm with $196.0322m/s$, $162.9354m/s$, $156.715m/s$, and $151.2619m/s$.

To calculate the effect of storm on species 1 for the first year, the value of c_1 can be calculated using the formula

$$c_1 = \frac{1}{(227.5616)(79.7979) + 0.2} \quad (5.25)$$

When this formula is simplified, $c_1 = 0.00005506869385 < 1$ which measures the effect of storm intensity on species 1. The old biomass OB for species 1 is 79.7979 grammes. After storm 1, the proportion of species 1 destroyed P_d can be calculated using the formula

$$P_d = 196.0322c_1OB \quad (5.26)$$

Hence, $P_d = 0.861437259 < 1$.

The new biomass NB after storm 1 can be calculated from the formula

$$NB = OB(1 - P_d) \quad (5.27)$$

By substituting for the old biomass OB and the proportion destroyed P_d , the calculated new biomass NB is 11.057 grams. After the end of the first storm, the old biomass for the start of storm 2 is 11.057 grams. Similarly, after storm 2,

$$P_d = 162.9354c_1(11.057) \quad (5.28)$$

Hence, $P_d = 0.099210476 < 1$. Our new biomass NB is

$$NB = OB(1 - P_d) \quad (5.29)$$

where $OB = 11.057$ grams. In this case, the new biomass NB is 9.96 grams. After storm 2, the old biomass is now 9.96 grams for the start of storm 3.

Next, after storm 3,

$$P_d = 156.715c_1OB \quad (5.30)$$

where $OB = 9.96$ grams and $P_d = 0.085955699 < 1$. Our new biomass NB is equal to $9.96(1 - P_d)$ which is approximately 9.10388 grams. At the end of storm 3, the old biomass before the start of storm 4 is 9.10388 grams.

Our Poisson random sample of the number of storms when the mean number of storms per year is 2 specifies that the number of storms for the first year is 4. That means, we would stop our first year calculation after storm 4. In this scenario,

$$P_d = 151.2619c_1OB \quad (5.31)$$

where $OB = 9.10388$ grams and $P_d = 0.075833456 < 1$. Our calculated new biomass NB is 8.4135 approximately. Hence, at the end of storm 4, the old biomass before the start of the second year winter season is 8.4135 grams.

This example illustrates how we have calculated the minimum biomass at the end of storm 4 in the first year for the first species which has a starting biomass of 79.7979 grams per m^2 before the start of first year winter.

When the starting values are $N_1(0) = 0.04g/m^2$ and $N_2(0) = 0.045g/m^2$, our calculated biomasses without winter storms are $N_1 = 83.1887g/m^2$ and $N_2 = 0.0533g/m^2$ when the two plant species are interacting together whereas our calculated biomasses without winter storms are $N_{1i} = 83.2013g/m^2$ and $N_2 = 0.0787g/m^2$ when the two plant species are interacting separately.

By using the Poisson distribution to obtain a sequence of storms for a period of 10 years when the annual number of storms is 6, we would obtain (4, 10, 9, 9, 4, 4, 7, 5, 7, 9). That is, we would expect to have 4 storms in the first year and 9 storms in the tenth year. We also use the gamma distribution to measure the extent of the fierceness of winter storm for a simulation of 1000 storms.

The first five cases of storm intensity are (179.6793, 174.8924, 167.9871, 153.7375, 141.5542). The next five cases of storm intensity are (135.5836, 129.0163, 126.8739, 124.3238, 123.7429).

In this example, we would simply present our final calculations for the minimum biomass for the first year winter season in Table 5.1.

plant species	Analytical Calculation				
	start of winter	after st1	after st2	after st3	after st4
N_1	83.1887	2.21734	2.162085	2.11400585	2.071684
N_2	0.0533	0.00248	0.002374352	0.002285	0.002209

Table 5.1: Calculations of the minimum biomass for the first year winter season

where $st(i)$ denotes storm i . For the second year winter, the starting biomasses will be $2.0717g/m^2$ for the first plant species and $0.002209g/m^2$ for the second plant species.

To avoid lengthy algebraic calculations which may incur approximation errors, we propose to simulate our summer-winter model in order to calculate the minimum biomass after each storm. In our numerical simulation, we propose to use a fourth order Runge-Kutta numerical method to simulate our combination of a summer model and a winter model in only one Matlab program and hence calculate the minimum biomass.

5.8 Main Results

We shall only consider the simulation application of our summer-winter model in this section. It is worth mentioning that no closed-form solutions of nonlinear model equations of competition interaction between two dis-similar plant species have been found. The behaviour of solutions over a ten year period is better understood only in terms of example trajectories instead of exact solutions.

5.8.1 Calculation of the minimum biomass: variation of the mean number of storms

In this section, we are interested to calculate the minimum biomass after the effect of storm on each plant species. To achieve this, it is important to first derive the nonlinear interaction equations on which this present analysis is based. We have done this prior to this chapter.

The mean number of storms is deduced from arctic data. Hence, it is imperative to investigate the effect of varying winter parameters on the calculation of minimum biomass and experimental probability of extinction of each plant species.

In this section, we shall present our results on a method of calculating the minimum biomass for each plant species over the 10 year period of one trajectory.

We present these results which we have not seen elsewhere with the hope of providing further insight into this complex ecological simulation of two competing dis-similar plant species model in a harsh climate.

We present our simulation result when the mean number of storms is 6. We shall start this investigation with a five year simulation and use the figures we

would obtain to calculate the minimum biomass for each plant species over the 5 year period of one trajectory.

Our model parameters which are estimated (in chapter three) using the 2-norm are $a = 0.168$, $b = 0.0020339$, $c = 0.0005$, $d = 0.002$, $e = 0.00002$, and $f = 0.000015$ with starting values of $N_1(0) = 0.04$ grams/ m^2 and $N_2(0) = 0.045$ grams/ m^2 .

What do we want to find out? We want to work out the minimum biomass over the 5 year period of one trajectory and with the same starting values calculate our experimental probability of extinction of each species.

Our estimated value of the Young's modulus E for plant stem is 0.4219 N/m^2 , the second moment of area is 1.2586 m^4 , and the value of π^2 is 9.87755102 . By using these figures, the estimated intensity of storm on the biomass can be calculated by using the formula

$$c = \frac{1.311253146}{V^2 B^{\frac{5}{3}} + \epsilon} \quad (5.32)$$

where V specifies the magnitude of the storm intensity determined by the gamma distribution and B specifies the biomass in grams/ m^2 before the start of each storm.

We have used this formula, the fourth order Runge-Kutta scheme, the Poisson discrete distribution to develop a Matlab program for a fixed mean number of storms to determine the minimum biomass over a 5 year period of one trajectory.

Before the start of winter, the biomasses for the two plant species are $N_1 = 82.5878$, $N_2 = 0.0535$, $N_{1i} = 82.5999$, and $N_{2i} = 0.0787$ grams per area of grass cover when the initial conditions are $N_1 = 0.04$ grams/ m^2 and $N_2 = 0.045$ grams/ m^2 . These numbers show that the plant species tend to grow effectively separately than together which indicates competition between the two interacting plant species.

In Table 5.2, the following notations are used:

1. mbN_1 represents the minimum biomass that remains after each storm for plant species N_1 .
2. Pd_{N_1} represents the proportion of species N_1 that is destroyed by storm in percentage.
3. HN_1 represents the height that is related to the minimum biomass N_1 that remains after storm.
4. mbN_2 represents the minimum biomass that remains after each storm for plant species N_2 .
5. Pd_{N_2} represents the proportion of species N_2 that is destroyed by storm in percentage.
6. HN_2 represents the height that is related to the minimum biomass N_2 that remains after storm.

It is worth mentioning how we have calculated these variables. The minimum biomasses are calculated by using our Matlab program which we have

written. The proportion of plant species that is destroyed can simply be calculated analytically or by hand.

The height being referred to above is not the height of the biomass. It is a constant that is related to the biomass by the formula $H = (B)^{\frac{1}{3}}$ which can also be calculated by hand.

Before the start of winter season, the value of H_1 is the cube root of the biomass of plant species $N_1 = 82.5878$ grams/ m^2 which is 4.355. whereas the value of H_2 is the cube root of the biomass of plant species $N_2 = 0.0535$ grams/ m^2 which is 0.3768. We obtain the biomasses by simulating these two dis-similar interaction functions

$$f(N_1, N_2) = 0.168N_1 - 0.0020339N_1N_1 - 0.0005N_1N_2 \quad (5.33)$$

$$g(N_1, N_2) = 0.002N_2 - 0.000015N_2N_2 - 0.00002N_1N_2 \quad (5.34)$$

with starting population sizes of $N_1(0) = 0.04$ grams/ m^2 and $N_2(0) = 0.045$ grams/ m^2 .

To calculate our experimental probability of extinction for each plant species over a period of one trajectory, we simply count the number of cases of this simulation that hit extinction and divide this number by the number of simulation runs.

5.8.2 Example 1

In this section, we are interested to calculate the minimum biomass when the mean number of storms is 6 over a 5 year period of one trajectory. Our calculations are presented in Table 5.2.

Simulation Run	Calculation of the minimum biomass					
	mbN_1	Pd_{N_1}	HN_1	mbN_2	Pd_{N_2}	HN_2
1	0.04	99.95	0.342	0.007565	85.8	0.196
2	0.04	99.95	0.342	0.00496	90.7	0.171
3	0.04	99.95	0.342	0.004587	91.4	0.166
4	0.04	99.95	0.342	0.006118	88.5	0.183
5	0.04	99.95	0.342	0.010159	80.9	0.217

Table 5.2: Calculation of the minimum biomass if the number of storms is 6

What do we learn from these numbers in Table 5.2? We observe that our experimental probability of extinction for plant species N_1 is 1 because the number of cases of the minimum biomass that hit extinction is 5 if we consider a 5 year period of one trajectory. In contrast, our experimental probability of extinction for plant species N_2 is 0 because the number of cases of the minimum biomass that hit extinction is 0 for the same 5 year period of one trajectory.

5.8.3 Example 2

In this example, we would like to calculate the minimum biomass of each plant species if the mean number of storms is 8 over a 5 year period of one trajectory? Our calculations are presented in Table 5.3

Simulation Run	Calculation of the minimum biomass					
	n	mbN_1	Pd_{N_1}	HN_1	mbN_2	Pd_{N_2}
1	0.04	99.95	0.342	0.0063	88.2	0.18
2	0.04	99.95	0.342	0.0069	87.1	0.19
3	0.04	99.95	0.342	0.0072	86.5	0.193
4	0.04	99.95	0.342	0.0075	85.9	0.195
5	0.04	99.95	0.342	0.008	85	0.2

Table 5.3: Calculation of the minimum biomass if the number of storms is 8

In this scenario, the minimum biomass for species N_1 all hit extinction, that is, our experimental probability of extinction for species N_1 is 1. For species N_2 , our experimental probability of extinction is 0.

5.8.4 Summary of results

We have similarly calculated the minimum biomass of each plant species for other variations of the mean number of storms over a period of 5 years and 10 years of one trajectory.

Our experimental probabilities of extinction of each species are presented in Table 5.4.

Example	Summary			
	ns	ys	$psp1$	$psp2$
1	6	5	1	0
2	8	5	1	0
3	10	5	1	0
4	6	10	1	0
5	8	10	1	0
6	10	10	1	0.1
7	15	10	1	0.5

Table 5.4: Calculation of the minimum biomass for other variations of the number of storms

where

1. ns represents the mean number of storms.
2. ys represents the year of simulation of one trajectory.
3. $psp1$ represents the experimental probability of extinction of species N_1 .
4. $psp2$ represents the experimental probability of extinction of species N_2 .

We learn from Table 5.4 that a variation of the mean number of storms does not change the experimental probability of extinction of species N_1 as its value is 1 irrespective of the period of one trajectory. However, our experimental probability of extinction of species N_2 when the mean number of storms is 10

is 0.1. That is, we would expect to have 1 case out of 10 cases to hit extinction. In contrast, our experimental probability of extinction of species N_2 when the mean number of storms is 15 is 0.5. This calculation implies that 5 cases out of 10 cases to hit extinction.

In summary, we observe by our present calculations that species N_1 will not survive for the chosen year of simulation irrespective of a variation of the number of storms. We observe that species N_2 will survive for the chosen year of simulation irrespective of a variation of the number of storms.

5.8.5 Experimental probability of extinction for $a = 0.2016$

In chapter three of this thesis, we have selected three important model parameters of which one of these is our intrinsic growth rate parameter a .

How sensitive would the value of the experimental probability be if any of these important parameters is slightly changed when the annual mean number of storms is 10.

What do we want to find out? We want to find out how sensitive is the experimental probability of extinction when $a = 0.2016$ if the annual mean number of storms is 10 over a 10 year period of one trajectory. We would do this for 10 different cases to find out systematically the extent of the experimental probability of extinction of each plant species.

From our experimental analysis, we also know that the experimental probability of extinction of species N_1 is 1 if $a = 0.2016$. For this reason, we would focus to tackle the problem in this section only for the second species.

For this level of analysis, we recalculated the biomasses before the start of the winter season if $a = 0.2016$. If $a = 0.2016$, the new biomasses before the start of the winter season are $N_{1max} = 99.1079$ grams/ m^2 and $N_{2max} = 0.0488$ grams/ m^2 . The values of the other model parameters remain the same. Our calculations are presented in Table 5.5.

Data Points n(different years)	Different sample numbers for each year						
	mbN_2	Pd_{N_2}	HN_2	n	mbN_2	Pd_{N_2}	HN_2
1	0.002372	95.13	0.1334	6	0.002174	95.5	0.1295
2	0.002365	95.15	0.1332	7	0.002358	95.16	0.1331
3	0.001856	96.2	0.1229	8	0.002459	94.96	0.135
4	0.001894	96	0.1237	9	0.002298	95.3	0.132
5	0.00295	93.9	0.1434	10	0.00246	94.96	0.135

Table 5.5: Calculation of our experimental probability of extinction if the number of storms is 10

In order to provide a clearer interpretation of these numbers, we shall assume that a 95 percent of species N_2 is destroyed. In this scenario, we use the formula that defines the new biomass in terms of old biomass and the proportion of the old biomass that is destroyed by storm. By our assumption, the new biomass will be

$$NB = (1 - 0.95)0.0488 \quad (5.35)$$

Hence, our new biomass under this scenario is 0.00244 grams per area of grass. Therefore, if $NB \leq 0.00244$ then extinction of the second plant species will occur. Whereas if the value of our new biomass is bigger than 0.00244, then our second plant species will survive.

Hence, if $a = 0.2016$, our calculated experimental probability of extinction of the second species is 0.7 for a 10 year period of one trajectory.

In comparison, if $a = 0.168$, our calculated experimental probability of extinction of the second species is 0.1 for a 10 year period of one trajectory. On the basis of these numbers, we observe that our experimental probability of extinction is more sensitive when the annual mean number of storms is 10 over a 10 year period of one trajectory if $a = 0.2016$. This conclusion could be by chance.

Hence we propose a systematic method of tackling this problem for ten different cases. Since our experimental probability of extinction of the first species is 1 irrespective of the number of simulation runs, we shall only focus on studying the sensitivity behaviour of the experimental probability of extinction of the second species for a 10 year period of one trajectory if $a = 0.2016$ for a few repeated simulations.

We would simply present a brief overview which summarises our observations for the second species in Table 5.6 and Table 5.7 by using a similar calculation method as we have done in the previous sections.

The notation $mb1N_2$ stands for the minimum biomass of our second plant species over a 10 year period of one trajectory in simulation 1 whereas the notation $mb2N_2$ stands for the minimum biomass of our second plant species over a 10 year period of one trajectory in simulation 2.

Data Points n(different years)	Different sample numbers for each year				
	$mb1N_2$	$mb2N_2$	$mb3N_2$	$mb4N_2$	$mb5N_2$
1	0.002372	0.00281	0.001971	0.003239	0.003112
2	0.002365	0.002548	0.002855	0.004284	0.003444
3	0.001856	0.002305	0.002561	0.003718	0.002684
4	0.001894	0.002688	0.002643	0.003496	0.003703
5	0.00295	0.002409	0.002565	0.003471	0.00336
6	0.002174	0.002782	0.002779	0.00357	0.002915
7	0.002358	0.00281	0.002747	0.002741	0.003071
8	0.002459	0.00289	0.002795	0.002849	0.003688
9	0.002298	0.002504	0.002989	0.00328	0.00278
10	0.00246	0.0027	0.002448	0.003055	0.002585

Table 5.6: Another calculation of our experimental probability of extinction if the number of storms is 10

By using our 95 percent assumption that our second plant species is destroyed, our calculated probabilities of extinction for the first five columns over a 10 year period of our second plant species are $(\frac{7}{10}, \frac{2}{10}, \frac{1}{10}, \frac{0}{10}, \frac{0}{10})$.

In a similar manner, our calculated probabilities of extinction for the next five columns over a 10 year period of our second plant species are $(\frac{3}{10}, \frac{5}{10}, \frac{8}{10}, \frac{7}{10}, \frac{2}{10})$.

Hence, out of 100 data points, only 35 data points will hit extinction for our second plant species. Therefore, in this scenario, our experimental proba-

Data Points n(different years)	Different sample numbers for each year				
	$mb6N_2$	$mb7N_2$	$mb8N_2$	$mb9N_2$	$mb10N_2$
1	0.002721	0.002756	0.00212	0.002137	0.002539
2	0.002771	0.002539	0.002386	0.002387	0.002525
3	0.002408	0.002341	0.00286	0.001739	0.002344
4	0.002775	0.002745	0.002163	0.001833	0.002471
5	0.00242	0.002305	0.00218	0.002659	0.002567
6	0.002822	0.002158	0.00222	0.003001	0.002468
7	0.00261	0.002824	0.003531	0.002	0.002395
8	0.003012	0.002596	0.002362	0.001124	0.00293
9	0.002269	0.002317	0.002307	0.002107	0.002644
10	0.002689	0.002289	0.00241	0.002463	0.002558

Table 5.7: A similar calculation of our experimental probability of extinction if the number of storms is 10

bility of extinction for our second plant species is 0.35 whereas our experimental probability of extinction for our first plant species is 1.

In summary, we learn from this scenario that our second plant species has a good chance of surviving (with a probability of survival which is calculated as 0.65) than our first plant species which its probability of survival is zero.

Let us consider another scenario if $a = 0.2016$ in a 20 year period of one trajectory when the annual mean number of storms is 10. We have also calculated that our experimental probability of extinction of the first species will be 1 irrespective of the period of simulation. That is, about 99.96 percent of the first species will be destroyed after each storm. This result is consistent with our previous results.

Next, we shall discuss the situation when $a = 0.2016$ in a 20 year period of one trajectory when the annual mean number of storms is 10.

Due to lack of space and the fact that a further set of different sample numbers is not likely to change our expected pattern in the sensitivity of our experimental probability of extinction for the second plant species, we would simply present our results for only twenty different samples of numbers as displayed in Table 5.8.

In this scenario, our calculated experimental probability of extinction for our second plant species is $\frac{7}{20}$ over 20 repeated simulations.

In summary, if $a = 0.2016$ in a 20 year period of one trajectory when the annual mean number of storms is 10, we learn from these numbers in Table 5.8 that our experimental probability of extinction for the second species is simply 0.35. That is, 7 cases out of 20 cases hit extinction.

But in another 20 year period of one trajectory for $a = 0.2016$ when the number of storms is 20, we found that our experimental probability of extinction for the second species is 1. Our corresponding calculations are presented in Table 5.9. The second set of our 10 simulated minimum biomass for the second species are displayed under the third column.

In this scenario, we observe that 20 cases out of 20 cases of remaining biomass hit extinction for our second plant species.

In summary, our experimental probability of extinction of species N_2 varies

Data Points n(different years)	Different sample numbers			
	$mb1N_2$	$P_d(N_2)$	$mb1N_2$	$P_d(N_2)$
1	0.002353	95.17	0.002718	94.4
2	0.00261	94.64	0.00268	94.5
3	0.002291	95.3	0.002752	94.3
4	0.002667	94.52	0.002619	94.6
5	0.0022	95.48	0.002432	95
6	0.002693	94.47	0.002764	94.3
7	0.002318	95.24	0.003096	93.64
8	0.002526	94.8	0.002778	94.29
9	0.002677	94.5	0.002701	94.45
10	0.002402	95.07	0.002385	95.1

Table 5.8: Another calculation of our experimental probability of extinction if the number of storms is 10

Data Points n(different years)	Different sample numbers			
	$mb1N_2$	$P_d(N_2)$	$mb1N_2$	$P_d(N_2)$
1	0.001792	96.3	0.002034	95.8
2	0.001988	95.9	0.002138	95.6
3	0.002302	95.27	0.001897	96.1
4	0.002403	95.1	0.002045	95.8
5	0.002249	95.4	0.002039	95.81
6	0.002029	95.83	0.001896	96.1
7	0.002108	95.67	0.00224	95.4
8	0.001878	96.14	0.002376	95.12
9	0.001829	96.24	0.002141	95.6
10	0.00221	95.46	0.002144	95.59

Table 5.9: Another calculation of our experimental probability of extinction if the number of storms is 20

when the number of storms varies for the case $a = 0.2016$. We observe that increasing the number of storms would increase the chance of complete extinction for both plant species.

But we are yet to calculate our experimental probability of extinction for the plant species growing separately. This calculation would be necessary in order to deduce if we can obtain mutualism from a combination of our summer competition model and our stochastic winter storms.

5.8.6 Example 3

So far, we have considered only the repeated simulated trajectories when the two dis-similar plant species are interacting together. Next, we would like to consider also when the two species are growing in isolation or separately. For a complete understanding of this problem, we have applied the same technique to calculate the minimum biomass of each plant species (the detailed calculations are not

presented in this chapter) and hence calculated our experimental probabilities of extinction of plant species.

We shall present our final calculations in Table 5.10 which would be discussed qualitatively.

Parameter Value	Extinction Probabilities					
	ns	ys	pN_1	pN_{1i}	pN_2	pN_{2i}
a=0.084	8	5	1	1	0	0
a=0.084	10	5	1	1	0	0
a=0.084	10	10	1	1	0	0
a=0.084	15	10	1	1	0.6	0.8
a=0.084	20	10	1	1	1	1
a=0.0924	20	10	1	1	1	0.9
a=0.0924	20	10	1	1	0.8	0.9
a=0.1008	20	10	1	1	0	1
a=0.1008	20	10	1	1	0.4	0
a=0.1008	20	10	1	1	0.5	0

Table 5.10: A different calculation of our experimental probability of extinction

In summary, for these changes in our parameter a , we observe that our experimental probabilities of extinction of species N_1 and N_{1i} are each 1 irrespective of the number of storms and the number of our repeated simulations.

Under these scenarios, we would expect our experimental probability of extinction and survival for our second plant species to vary.

But over 20 repeated simulations with different starting biomasses, we are interested to find out if the behaviour of our experimental probability of extinction under a different set of starting values would either change or stay the same as we observed above.

5.8.7 Example 4

One of the ways to tackle the problem observed in the last section is to consider a different set of starting values. In this scenario, we shall consider $N_1(0) = 12.48$ grams/ m^2 , $N_2(0) = 24$ grams/ m^2 and $a = 0.2016$. The starting values before the start of a winter season for a period of 70 days are

1. $N_1 = 93.4572$ grams/ m^2 .
2. $N_{1i} = 99.1199$ grams/ m^2 .
3. $N_2 = 24.3357$ grams/ m^2 .
4. $N_{2i} = 37.0044$ grams/ m^2 .

Another important observation is that the plant species tend to grow effectively separately than together which indicates competition.

To illustrate the effect of using these new starting values if the mean number of storms is 20, we have used our summer-winter model to calculate the minimum biomasses of each plant species over a 10 year period of one trajectory. Over another 20 repeated simulations, we present our calculations in Table 5.11.

For example, when our experimental probability of extinction for any of the species is 0, it means that particular species will survive for that simulation. When our experimental probability of extinction for any of the species is 1, it means that species has reached a zero biomass for that simulation. If our simulation produces 2 cases out of 10 cases for a particular species, then its experimental probability of extinction is 0.2 compared with its probability of survival which in this case is 0.8.

Simulation Runs n(different years)	experimental probability of extinction								
	N_1	N_{1i}	N_2	N_{2i}	n	N_1	N_{1i}	N_2	N_{2i}
1	0.1	0.2	0.2	0.4	11	0	1	0	1
2	0.2	0.3	0.3	0.4	12	0	1	0	1
3	0.1	0.2	0	1	13	0.2	1	0.3	0.3
4	0.1	0.1	1	1	14	0.1	1	1	0.8
5	0	0	0	1	15	0	1	0.3	0.4
6	0	0.5	0	1	16	1	1	0	0.1
7	0	0.1	0	1	17	1	1	0	0
8	0.2	0	0.1	1	18	1	1	0	0
9	0.1	0	0	1	19	1	1	0.5	0.8
10	0	0	0	1	20	0	1	0	0

Table 5.11: A different calculation of our experimental probability of extinction for a different set of starting values

What can we learn from these numbers? In order to provide a clear interpretation of these numbers, we would break down these information into categories such as

1. complete survival of the plant species where the value of our probability of species survival is 1, that is, 10 cases out of 10 cases will survive in a 10 year period of one trajectory.
2. higher probability of survival where the value of our probability of species survival is between 0.7 and 0.9, that is, 7 or 9 cases out of 10 cases will survive in a 10 year period of one trajectory.
3. moderate probability of survival where the value of our probability of species survival is 0.6, that is, 6 cases out of 10 cases will survive in a 10 year period of one trajectory.
4. even probability of survival where the value of our probability of species survival is 0.5, that is, 5 cases out of 10 cases will survive in a 10 year period of one trajectory.
5. lower or weak probability of survival where the value of our probability of species survival is less than 0.5.
6. complete extinction of the plant species where the value of our probability of species survival is 0, that is, minimum biomass reach zero biomass.

In summary, we have used our summer-winter prototype model to obtain the following results which we can now report with the expectation of providing a further insight into our complex ecological problem.

Over 20 repeated simulation runs, species N_1 would have 8 runs of complete survival out of 20 runs, 8 runs of higher probability of survival out of 20 runs, and reached a zero biomass on 4 runs out of 20 runs.

Over 20 such runs, species N_{1i} would have 4 runs of complete survival out of 20 runs, 5 runs of higher probability of survival out of 20 runs, 1 run of even chance of species survival out of 20 runs, and reached a zero biomass on 10 runs out of 20 runs.

Over 20 such runs, species N_2 would have 12 runs of complete survival out of 20 runs, 5 runs of higher probability of survival out of 20 runs, 1 run of even chance of species survival out of 20 runs, and reached a zero biomass on 2 runs out of 20 runs.

Over 20 such runs, species N_{2i} would have 3 runs of complete survival out of 20 runs, 2 runs of higher probability of survival out of 20 runs, 3 runs of moderate chance of species survival out of 20 runs, 2 runs of lower or weak chance of species survival and reached a zero biomass on 10 runs out of 20 runs.

Therefore, we observe from our numerical simulation analysis that the two plant species grow more effectively together than separately. In this scenario, our summer-winter model has produced a situation in which mutualism can be observed from a combination of our summer competition model and our stochastic winter model. This result is consistent with the stress gradient hypothesis as defined and discussed in chapter 1 of this thesis.

This is one of the important results of this chapter which is also consistent with the dominant ecological viewpoint which we have defined and discussed in chapter one of this thesis.

5.9 Effect of varying the length of our summer growing season

Having examined the effects of changing one of our important parameters on the calculation of the minimum biomass and its implication for estimating our experimental probability of extinction of each species, we would progress to find out the effects of varying the length of summer on the minimum biomass and its implication for the experimental probability of extinction of each plant species.

In this scenario, we shall consider $N_1(0) = 4$ grams/ m^2 , $N_2(0) = 10$ grams/ m^2 and $a = 0.168$. The starting values before the start of a winter season for a period of 10 days are

1. $N_1 = 77.8478$ grams/ m^2 .
2. $N_{1i} = 80.6783$ grams/ m^2 .
3. $N_2 = 10.3973$ grams/ m^2 .
4. $N_{2i} = 10.7651$ grams/ m^2 .

Under these new starting values, we shall consider when the mean number of storms is 20. Another important observation is that the plant species grow effectively separately than together which indicates competition.

Over 20 repeated simulations, the calculations of our experimental probability of extinction of each plant species are presented in Table 5.12.

Simulation Runs n(different years)	experimental probability of extinction								
	N_1	N_{1i}	N_2	N_{2i}	\mathbf{n}	N_1	N_{1i}	N_2	N_{2i}
1	1	1	1	1	11	1	1	1	0
2	1	1	1	0.1	12	1	1	1	0
3	1	1	1	0	13	1	1	1	0.8
4	1	1	0.9	0	14	1	1	1	0
5	1	1	0.8	0.1	15	1	1	0.6	0
6	1	1	0.9	0.1	16	1	1	0	0.1
7	1	1	0.9	0	17	1	1	1	0
8	0.9	0.3	1	0.7	18	1	1	1	0.1
9	1	1	1	0.9	19	1	1	0.9	0
10	1	1	0.7	0.2	20	1	1	0.8	0.8

Table 5.12: A different calculation of our experimental probability of extinction for a different set of starting values when the number of storms is 20

In this scenario, we observe that in 20 different repeated simulations, in 20 cases out of 20 cases, species N_1 will go extinct whereas for species N_{1i} , in 19 cases out of 20 cases, it will go extinct and will survive in 1 case out of 20 cases where its experimental probability of survival is 0.7.

However, over similar repeated simulations, we observe that species N_{2i} has a better chance of surviving than species N_2 .

Next, we shall consider $N_1(0) = 4$ grams/ m^2 and $N_2(0) = 10$ grams/ m^2 . We shall assume that the mean number of storms is 20. The starting values before the start of a winter season for a period of 100 days are

1. $N_1 = 80.0188$ grams/ m^2 .
2. $N_{1i} = 82.5999$ grams/ m^2 .
3. $N_2 = 11.3315$ grams/ m^2 .
4. $N_{2i} = 20.3725$ grams/ m^2 .

An important observation is that the plant species tend to grow effectively separately than together which indicates competition.

Our calculations of the experimental probability of extinction of each plant species are presented in Table 5.13.

Simulation Runs n(different years)	experimental probability of extinction								
	N_1	N_{1i}	N_2	N_{2i}	n	N_1	N_{1i}	N_2	N_{2i}
1	1	1	1	0.2	11	1	1	1	0
2	1	1	1	0.1	12	1	1	1	0
3	1	1	1	0	13	1	1	1	0.8
4	1	1	0.9	0	14	1	1	1	0
5	1	1	0.8	0.1	15	1	1	0.6	0
6	1	1	0.9	0.1	16	1	1	0	0.1
7	1	1	0.9	0	17	1	1	1	0
8	0.9	0.3	1	0.7	18	1	1	1	0.1
9	1	1	1	0.9	19	1	1	0.9	0
10	1	1	1	0.2	20	1	1	0.8	0.8

Table 5.13: A different calculation of our experimental probability of extinction for a different set of starting biomasses

In this scenario, we observe that both species N_1 and N_{1i} have a greater risk of suffering from the ecological risk of extinction. Similarly, species N_{2i} has a better chance of surviving than species N_2 .

By our present analysis, increasing the length of summer season indicates that the second plant species grow effectively separately than together under these starting conditions. We would expect this pattern to change if we consider a small interval for the number of storms. We propose to investigate this problem further in chapter six in order to find out the extent of obtaining other types of species interactions due to a variation of the length of summer season.

5.10 Conclusion and Further Remarks

In this chapter, we have achieved the following

- We have used a Poisson distribution to approximate the number of storms.
- We have used the gamma distribution to approximate the intensity of the storm.
- For each storm, we have approximated both analytically and numerically how much biomass remains at the end of the storm.
- We have constructed a sound methodology with which to calculate the minimum biomass for each plant species over a 10 year period of one trajectory and illustrated this idea with a few examples.
- Under appropriate variation of summer and winter parameters, we have calculated experimental probabilities of extinction of each plant species and used these figures to study the sensitivity of our calculated experimental probabilities of extinction.
- By using the same summer-winter model and modifying our starting biomasses, we can now draw the conclusion from our numerical experiments that the species grow more effectively together than separately.
- Therefore, our summer-winter model has produced a situation in which mutualism can be observed from a combination of our summer model and stochastic winter model.
- Similarly, by a variation of the length of our summer growing season, our model can predict mutualism qualitatively from a combination of our summer model and our stochastic winter model (see section 5.8). Those results are consistent with the dominant ecological viewpoint which we have defined and discussed in chapter one of this thesis.

In chapters two and three, we have studied the dynamics of two competing plant species under some simplifying assumptions and analysed the corresponding model equations mathematically. In chapter four, we have developed a numerical methodology for finding the sensitivity of each model parameter over a time interval and on the basis of this approach selected the model parameters that have the biggest effect on the solutions of our deterministic competition

model equations. It is interesting to see the link between this chapter and the first four chapters of this thesis.

In chapter six, we would further investigate the extent of obtaining mutualism for more variations of summer and winter model parameters from a combination of our summer competition model and our stochastic winter model.

Chapter 6

Numerical Simulation of Changes in Qualitative Interactions of Plant Species

6.1 Motivation

The classical experimental approach is to determine competition and mutualistic interactions between two plant species. The primary motivation of this important chapter is to find out if we can obtain a mutualistic interaction from a combination of our summer competition model and our stochastic winter model due to a variation of some summer and winter parameters which is consistent with the early ecological viewpoint which we cited in chapter one of this thesis.

Our test model equations are based on the interaction between two dissimilar competing plant species which we derived in chapter three of this thesis. But the question of obtaining mutualism from a combination of our summer competition model and our stochastic winter model on a single simulation run would not be satisfactorily answered because the observation from only one ecological simulation may have emerged by chance.

In order to provide a clearer explanation about the extent of obtaining mutualism from a combination of our summer competition model and our stochastic winter model due to a variation of summer-winter model parameters, we would like to carry out a systematic ecological simulation of our summer-winter model over a ten year period of one trajectory in which we can observe the pattern of plant species interaction over ten repeated simulations.

6.2 Introduction

In this chapter, we would like to investigate the qualitative behaviour of obtaining mutualism from a combination of our deterministic summer competition model and our stochastic winter model. In chapter one, we have already cited

the relevant ecological references on positive interactions in a harsh climate and negative interaction in a benign climate.

In this chapter, we consider the following nonlinear coupled model of ordinary differential equations of first order which we have constructed in chapter three by using our 2-norm penalty function fitting method. This system of model equations of competition is

$$\frac{dN_1(t)}{dt} = N_1(t)(0.168 - 0.0020339N_1(t) - 0.0005N_2(t)) \quad (6.1)$$

$$\frac{dN_2(t)}{dt} = N_2(t)(0.002 - 0.00002N_1(t) - 0.000015N_2(t)) \quad (6.2)$$

with $N_1(0) = 0.04g/m^2$ and $N_2(0) = 0.045g/m^2$.

We do not intend to analyse these model equations in this chapter because we have done that in chapter three of this thesis.

6.3 What is the main aim of this chapter?

Our main objective in this important chapter is to attempt to investigate the possibility and extent of obtaining mutualism and facilitation qualitatively from a combination of our summer model and our stochastic winter model which is consistent with the dominant/mainstream ecological viewpoint.

6.4 How does the mid-year value of each plant species behave in the presence or absence of the other?

For two interacting dis-similar plant species for limited resources, first we shall attempt to look for cases where the limiting values are higher in the absence of another species than in the presence of another species due to a variation of the number of storms, storm intensity and the length of summer growing season. This idea if achieved would be an indication of obtaining competition qualitatively from our numerical simulation.

Next, we shall similarly attempt to look for cases where the limiting values are higher in the presence of another species than in the absence of another species due to a variation of the number of storms, storm intensity and the length of summer growing season. This idea if achieved would be an indication of obtaining mutualism qualitatively from our numerical simulation.

6.4.1 The limit of the sequence of mid-year values

In a sequence of mid-year plant growth data over ten years, it is the limit of the sequence of mid-year values of plant growth at the tenth year which determines the type of plant species interaction observed over a period of ten years when compared between plant species interacting together and plant species growing in isolation. What ecologists do experimentally is to grow two plant species. They come back every mid-year of a growing season to measure the new biomasses of the two plant species. In this situation, all the nine mid-year

values do not tell us which type of interaction has emerged over the period of ten years. It is the tenth limiting mid-year values over 10 years that tell us which type of species interaction has emerged. This is the well established classic experimental method.

In this chapter, we shall use a numerical simulation to find out if we can obtain mutualism from a combination of a summer competition model and a stochastic winter model.

6.4.2 A simple method of interpretation: how do we go about it?

For each simulation and each year, the outcome of our numerical simulation experiment consists of four limiting numbers namely the mid-year values when species 1 and 2 are interacting together along with their corresponding mid-year values when the species are interacting in isolation. If we think in this way, we would obtain a set of four limiting mid-year values such as $S = (N_1, N_{1i}, N_2, N_{2i})$. We would expect to have four types of species interactions which are:

1. If $S = (N_{1i} > N_1, N_{2i} > N_2)$, we will have a $(-, -)$ interaction whether a winter parameter or a summer parameter is considered.
2. If $S = (N_1 > N_{1i}, N_2 > N_{2i})$, we will have a $(+, +)$ interaction whether a winter parameter or a summer parameter is considered.
3. If $S = (N_1 > N_{1i}, N_2 = N_{2i})$, we will have a $(+, 0)$ interaction whether a winter parameter or a summer parameter is considered.
4. If $S = (N_1 > N_{1i}, N_{2i} > N_2)$, we will have a $(+, -)$ interaction whether a winter parameter or a summer parameter is considered.

In this chapter, the unit of our biomass is in grams per metre squared.

We would use this method to make sense of our time series data points. We would think that this simple method would provide better insight into how we can obtain patterns of species interactions from the outcome of our numerical simulation indexed by time.

6.5 Important ecological insights from our numerical simulations

In this section, we shall present some important results that this thesis has achieved. We have not seen these results elsewhere. By using our mathematical model and a sound numerical simulation, it is possible for the first time to obtain mutualism from an ecological competition between two interacting dis-similar plant species from a combination of our summer model and a stochastic winter model in a harsh climate.

Our results are consistent with the dominant/mainstream perspective in the ecological literature. It is our expectation that these results would provide an insight about this complex ecological problem.

In this chapter, we would consider a few examples with which to illustrate their ecological implications.

6.5.1 Illustrating how to obtain mutualism from competition due to a variation of winter storms

In this section, we would discuss what would happen if the number of storms is 6. Can we tell which outcome of our numerical simulation would be competition, mutualism, commensalism or parasitism? We do not know the outcome in advance, otherwise there would be no need of this detailed systematic investigation using this method and data to establish facts and reach new conclusions that are more consistent with experimental finding.

In this case, all the model parameters as well as the storm intensity and the length of summer growing season are not changing. We consider a summer growing season of 70 days.

6.5.2 Example: Can we obtain mutualism from competition when there is no storms?

First, we shall consider the case when there is no storm, that is, the summer growing season only. What would happen in this instance? Our two species growth data are presented in Table 6.1. Our analysis is based on the assumption that the two plant species grow better in isolation than when growing together ([13]).

Example n (year)	mid-year growth data				Type of Interaction
	N_1	N_{1i}	N_2	N_{2i}	
1	11.3588	11.3669	0.0481	0.0482	(-, -)
2	83.1844	83.1968	0.0503	0.0554	(-, -)
3	83.1886	83.2013	0.0514	0.0637	(-, -)
4	83.1883	83.2013	0.0527	0.0731	(-, -)
5	83.1879	83.2013	0.0539	0.0840	(-, -)
6	83.1876	83.2013	0.0552	0.0966	(-, -)
7	83.1873	83.2013	0.0565	0.1110	(-, -)
8	83.1870	83.2013	0.0578	0.1275	(-, -)
9	83.1866	83.2013	0.0592	0.1465	(-, -)
10	83.1863	83.2013	0.0606	0.1683	(-, -)

Table 6.1: Obtaining competition only in the absence of winter storms

What do we learn from Table 6.1? The first line of this table shows the mid-year growth data for two interacting plant species for the first year. As we can see, the plants grow better in isolation of the other than when interacting together. This means that the factor of competition is acting to reduce the growth of plants when interacting together. Our conclusion is consistent for the entire ten year growth data when there is no winter storms in the environment.

By our calculations which we cannot present in this chapter because they predict competition only, we remark that we have observed the occurrence of competition interaction when there is no winter storms for other variations of summer and winter parameters.

Our result is consistent with the plant competition theory which we have defined and discussed in chapter one of this thesis. Our result is also consistent

with one of the dominant/mainstream plant ecological perspective ([13]).

Next, this pattern of competition interaction is more likely to change due to increasing number of storms.

6.6 Key Achievements of this Research

In this section, we would present our novel key achievements which we have not seen elsewhere with a view to contributing further insights on the possibility and extent of obtaining mutualism from a combination of our summer model and our stochastic model which are consistent with the dominant/mainstream ecological perspective.

6.6.1 Variation of the Number of Storms

First, what is the more likely impact of increasing the number of storms in a harsh climate on mutualism?

1. By simulating our summer-winter model when the number of storms is 6, our model predicts one case of mutualism, one case of commensalism, one case of parasitism, and seven cases of competition qualitatively over a ten year period of one trajectory.
2. By simulating our summer-winter model when the number of storms is 6.25, our model predicts two cases of mutualism, one case of commensalism, one case of parasitism, and six cases of competition qualitatively over a ten year period of one trajectory.
3. By simulating our summer-winter model when the number of storms is 6.5, our model model predicts three cases of mutualism, one case of commensalism, one case of parasitism, and five cases of competition qualitatively over a ten year period of one trajectory.
4. By simulating our summer-winter model when the number of storms is 6.75, our model predicts four cases of mutualism, one case of commensalism, one case of parasitism, and four cases of competition qualitatively over a ten year period of one trajectory.
5. When the number of storms is 7, our summer-winter model predicts five cases of mutualism, one case of commensalism, one case of parasitism, and three cases of competition qualitatively over a ten year period of one trajectory.
6. When the number of storms is 7.25, our summer-winter model predicts six cases of mutualism, one case of commensalism, one case of parasitism, and two cases of competition qualitatively over a ten year period of one trajectory.
7. When the number of stor is 7.50, our summer-winter model predicts seven cases of mutualism, one case of commensalism, one case of parasitism, and one case of competition qualitatively over a ten year period of one trajectory.

In summary, increasing the number of storms in a harsh climate is more likely to increase the incidence of mutualism and decrease the incidence of competition (see the graphs in the appendix).

This result suggests that the plant species interaction of mutualism could be more important than competition. Hence, by using our numerical simulation, we can obtain instances of mutualism from a combination of our summer model and our stochastic winter model which are consistent with the dominant/mainstream ecological perspective.

6.6.2 Variation of storm intensity

From our chapter five of this thesis, we know that c_1 and c_2 correspond to the constants which determine the damage produced by a storm based on the gamma distribution. If storms become more intense, this phenomenon can be modelled by increasing c_1 and c_2 slightly.

The cases of mutualism which we have obtained from a combination of our summer model and our stochastic model due to a variation of storm intensity have been presented in the appendix of this thesis.

In summary, increasing the number of storm intensity in a harsh climate is more likely to increase the incidence of mutualism and decrease the incidence of competition making the process of mutualism to be more important than competition over a 10 year period of one trajectory.

6.6.3 Variation of the Young's Modulus

From our chapter five of this thesis, we know that Young's modulus corresponds to the constants which determine the damage of plant species due to a variation of the strength of the plant species before buckling. The concept of buckling can be modelled by increasing Young's modulus slightly.

The cases of mutualism which we have obtained from a combination of our summer model and our stochastic model due to a variation of Young's modulus have been presented in the appendix of this thesis.

We remark that a variation in the number of the Young's modulus in a harsh climate is more likely to increase the incidence of mutualism and decrease the incidence of competition over a ten year period of one trajectory.

In summary, a variation of our winter model parameter is more likely to predict more cases of mutualism qualitatively from a combination of our summer model and our stochastic winter model than any other type of plant species interactions in a harsh climate. According to plant ecologists as we have mentioned in chapter one of this thesis, the impact of abiotic stress leads more to mutualism and facilitation. We would expect this pattern to change due to changes in the environment.

From both the dominant/mainstream ecological perspective and our mathematical modelling/numerical simulation, mutualism and facilitation are more likely to favour biodiversity while competition is more associated with decreasing the size of biomass which may enhance the loss of biodiversity. Hence, the process of competition could be regarded as a mechanism responsible for the loss of biodiversity.

At the present analysis, our results indicate a good link between ecological theory, mathematical modelling, and our qualitative numerical simulation

predictions.

6.6.4 Variation of the length of summer growing season

We know that a variation of the length of summer season is characterised by a more likely chance of obtaining competition than mutualism. To understand the impact of the length of summer, we would both lengthen and shorten the length of summer and investigate the extent of obtaining mutualism from a combination of our summer model and our winter model. We have obtained another result which is consistent with the dominant/mainstream ecological perspective which is presented in the appendix of this thesis.

By using our numerical simulation, we have found that an increase in the length of summer growing season increases the incidence of competition and decreases the incidence of mutualism. This result is consistent with facts about the arctic climate: in the summer season growing conditions are reasonably favourable and species will compete for resources ([169], [69]). This makes the process of ecological competition to be more important than mutualism in this scenario.

6.6.5 Variation of important model parameters

In our sensitivity analysis chapter, we have used our novel numerical method to select four important parameters which are the intrinsic growth rate of species N_1 , the intra-specific interaction coefficient of species N_1 , and the starting biomasses for the two interacting plant species.

By using our numerical simulation, we have found that a variation of each of these important model parameters leads to an increase in the volume of competition and a decrease in the volume of mutualism making competition to be an important process than mutualism. These results are presented in the appendix of this thesis.

6.6.6 Conclusion of Chapter Six

In chapter six of this thesis, we have achieved the following results which we have obtained from the combination of our summer competition model and our stochastic winter model over a 10 year period of one trajectory:

1. We have obtained only the evidence of competition in the absence of winter storms irrespective of a variation of our summer competition model and stochastic winter model parameters.
2. If the number of storms is varied, our model predicts that the volume of mutualism is more likely to rise while the volume of competition is more likely to fall.
3. If the number of storm intensity is slightly increased, our model predicts that the volume of mutualism is more likely to rise while the volume of competition is more likely to fall.
4. If the number of the Young's modulus (or the amount of stress that a plant species can take before buckling) is varied, our model predicts that the

volume of mutualism is more likely to rise while the volume of competition is more likely to fall.

5. If the number of the length of our summer growing season is varied, our model predicts that the volume of mutualism is more likely to fall while the volume of competition is more likely to rise.
6. If the number of our daily intrinsic growth rate of the first plant species is slightly varied, our model predicts that the volume of mutualism is more likely to fall while the volume of competition is more likely to rise.
7. If the number of our intra-specific or self interaction coefficient and our inter-specific coefficient of the first plant species are slightly varied, our model predicts that the volume of mutualism is more likely to fall while the volume of competition is more likely to rise.
8. Similarly, if the number of our starting values for the two plant species are slightly varied, our model predicts that the volume of mutualism is more likely to fall while the volume of competition is more likely to rise.

We have conducted similar analyses to obtain instances of facilitation over a 10 year period and 20 year period of one trajectory. Our results are graphically summarised in the appendix of this thesis. All these results are consistent with the dominant/mainstream ecological perspective.

In summary, we would think that the patterns of plant species interactions which our model has predicted in this thesis are likely to change due to a changing environment and global warming.

We would think that our analysis in this thesis has opened up an aspect of research which is not considered in this thesis. For example, we know that when plant species grow and compete for limited resources, they tend to spread out. But the construction and simulation of these complex models with spatial dimension would require a well over five years of dedicated research in order to fully tackle this problem satisfactorily.

We also know that as global temperatures rise, the positive interactions which we have observed in this thesis would at some point cease and begin to compete in which case the loss of facilitation can lead to the loss of biodiversity.

Chapter 7

Conclusions and Ideas for Further Research

Concluding Remarks: Key Achievements

In this dissertation, we conducted some numerical simulations on plant species interactions in a harsh climate over a 10 year and a 20 year periods of one trajectory. For the first time, these specific contributions are the following:

1. A variation in the number of the winter storms, the storm intensity, and the Young's modulus in a harsh climate due to global warming predicts mutualism qualitatively from a combination of our summer model and our stochastic winter model. By manipulating the length of our summer growing season and the number of our daily intrinsic growth rate (reflecting the impact of temperature change on the growth of the biomass) for the first plant species in a benign climate, both mutualism and facilitation are more likely to change to competition.
2. A variation in the number of the winter storms, the storm intensity, and the Young's modulus in a harsh climate due to global warming predicts mutualism qualitatively from a combination of our summer model and our stochastic winter model. By manipulating the number of our intra-specific coefficient for the first plant species, our starting biomasses, and our inter-specific coefficient for the first plant species in a benign climate, both mutualism and facilitation are more likely to change to competition.
3. Another numerical experimental simulation is a variation in the number of winter storms only in a harsh climate due to global warming which predicts mutualism and facilitation qualitatively from a combination of our summer model and our stochastic winter model. By manipulating the length of our summer growing season only in a benign climate, both mutualism and facilitation are more likely to change to competition over a 20 year period of one trajectory.
4. In some scenarios, a variation in the number of the winter storms only in a harsh climate over a 10 year period of one trajectory predicts instances

of competition and parasitism qualitatively from a combination of our summer model and our stochastic winter model. By manipulating the length of our summer growing season only in a benign climate, competition is more likely to be preserved while parasitism is more likely to change to competition.

These results have been graphically summarised in Figure 8.6, Figure 8.7, Figure 8.8, Figure 8.9, Figure 8.10, and so forth (see the appendix).

These results from our numerical simulation are consistent with the dominant/mainstream plant ecological viewpoints which suggest that the loss of mutualism and facilitation can have an impact on the biodiversity.

Mathematical modelling of plant species in the arctic presents major attractions: conventional research based on substantial data collection is very expensive and arctic climates are inhospitable. Further, as we have remarked in chapter one of this study, changes happen slowly under arctic conditions and therefore it is not possible to collect large amounts of data.

In addition, the environmental impact of large numbers of scientists visiting the arctic to collect specimens can be significant: one observed reason for variation in inter-specific interactions is the disturbance of the environment. Thus in this situation, there can be significant environmental and cost advantages of mathematical modelling.

We hope that these novel contributions would provide some useful insights pending some policies of handling ecological problems.

It is our expectation that a combination of our experimental numerical simulation results and the dominant/mainstream ecological viewpoints would contribute to the progress of knowledge in this area of interdisciplinary research.

Limitations of this Thesis

In this thesis, one has worked with a single source of data which is sufficient to achieve the primary objective of this thesis. The use of a single source of data in another intra-disciplinary study has been conducted. A numerical simulation of plant species interactions in a harsh climate is no exception. An example of developing an ordinary differential equation growth model to tackle the problem of determinate plant growth ([203]) in which estimated parameter values for total biomass of a maize plant were provided by ([118]) is an example in this context. In the study conducted and reported by ([203]), a new methodology was applied to an old data (see, [118]). Hence, we have proposed and applied a new theory and a novel numerical methodology to analyse old data in this thesis.

Uptil now, other researchers have not provided a method of analysing our provided data. So the application of our novel method of analysing these data has produced a satisfactory research outcome.

What this thesis has achieved is that it has produced important useful ecological insights which we have not seen elsewhere with the expectation of contributing to the progress of knowledge in this complex interdisciplinary study.

Other related data

One could extend our similar approach to analyse other data which are related to our present analysis such as

1. Current yearly growth rates of plant species ([2]) from which daily intrinsic growth rate can be determined.
2. If each data point of the data provided by ([35]) is driven by a noise intensity, we can obtain huge data sets.

Due to paucity of data, we conducted similar analyses using data provided by Voisin([191]). These data were also cited by ([175]) in pages 17 and 18. The work of Linehan ([126]) on which a similar analysis was conducted was also cited by ([191]) and ([175]).

Another similar data are due to Alder ([2]). We found a similar variation in patterns of obtaining mutualism from a combination of our summer competition model and our stochastic model indicating some results which are consistent with the dominant/mainstream plant ecological perspective.

Suggestions for further research

We suggest possible directions of investigation for other scholars who might be interested

1. The models which we have developed in this study will, if successful, be an attractive basis for further work with data gathered from a less delicate ecosystem (the Dee estuary) that nevertheless displays the same types of plant interaction that are of major interest in (for example) the arctic. This would take a longer period of dedicated research.
2. We propose to extend our numerical simulation approach to analysing other related data which assumed exponential, expolinear, and other forms of growth functions under some simplifying assumptions.
3. We propose to use the stochastic numerical bifurcation method to study and discuss the various implications of some parts of the analyses which are reported in this thesis. This would take a longer period of dedicated research.
4. We propose to investigate the numerical simulation of our summer logistic model when spatial variations in the population are taken into account on the understanding that plant species tend to grow and spread.

Chapter 8

Appendix

8.1 Fitting Biomass Data with Logistic Model Parameters

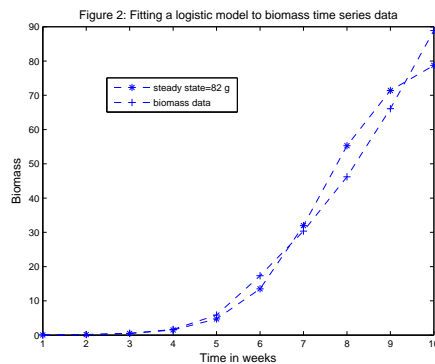
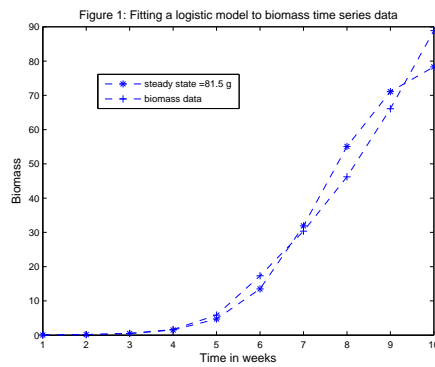


Figure 8.1: Data used when steady states are 81.5 grams (left plot) and 82 grams (right plot)

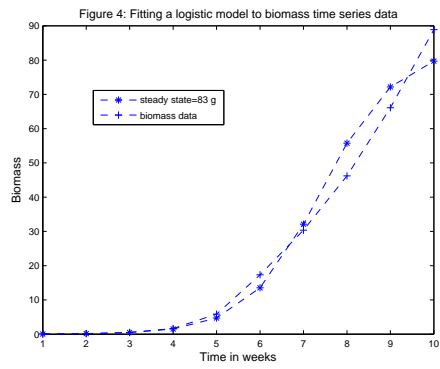
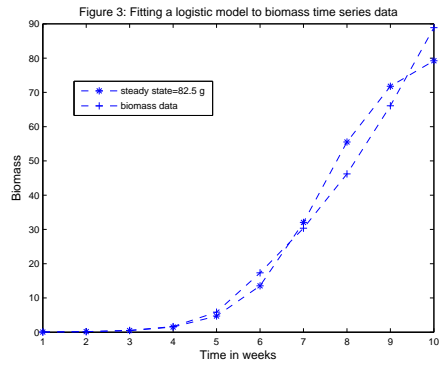


Figure 8.2: Data used when steady states are 82.5 grams (left plot) and 83 grams (right plot)

8.2 Sequence of Our 2-Norm Penalty Function for a given Steady State

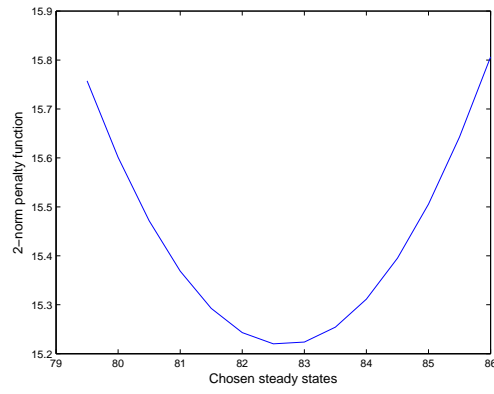


Figure 8.3: Minimum 2-norm penalty function

8.3 Solution Trajectories of Original Solution and Modified Solution: Examples

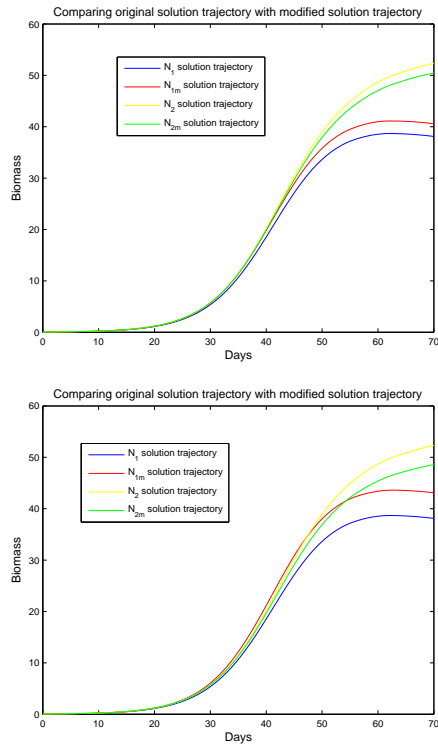


Figure 8.4: Solution of competition model over 70 days for $a = 0.1701$ (left plot) and for $a = 0.1722$ (right plot)

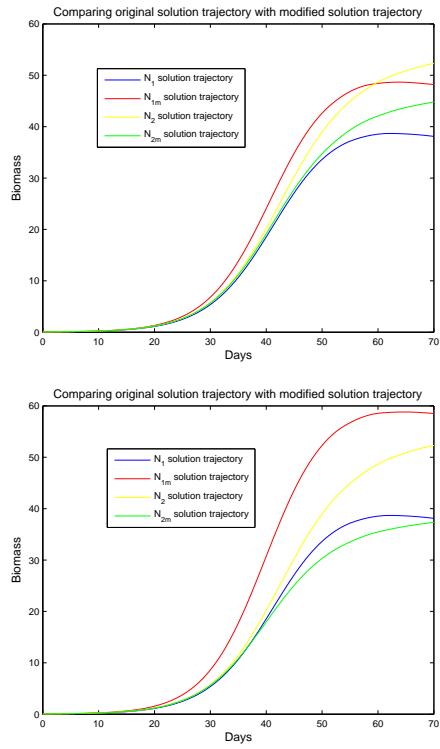


Figure 8.5: Solution of competition model over 70 days for $a = 0.1764$ (left plot) and for $a = 0.1848$ (right plot)

8.4 Qualitative prediction of mutualism from a variation of winter storms and changes in the positive interaction behaviour: ecological insights

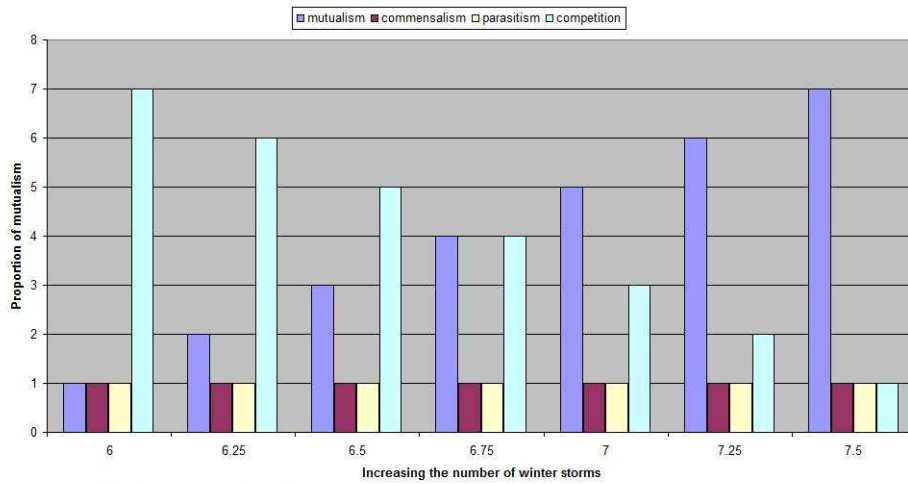


Figure 8.6 Variation of the number of winter storms: mutualism from a combination of our summer model and stochastic winter model in a harsh climate

Figure 8.6: Variation of the number of winter storms: mutualism from a combination of our summer model and stochastic winter model in a harsh climate

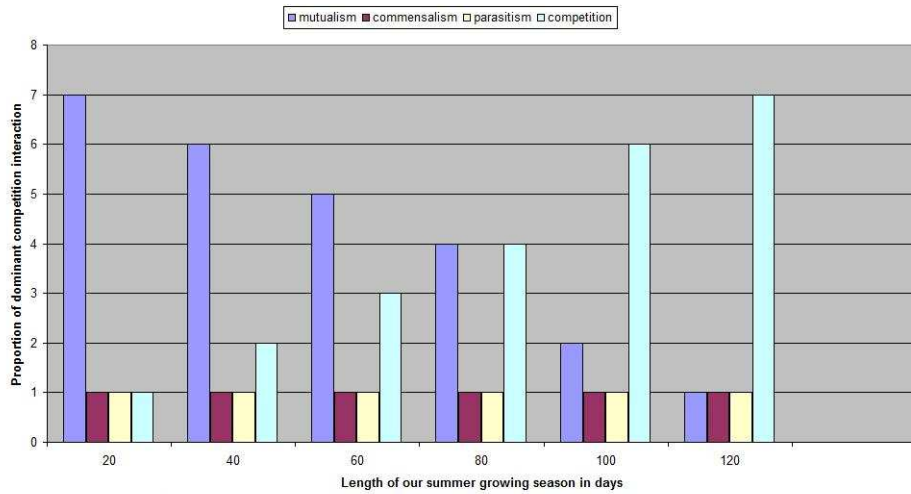


Figure 8.7 Variation of the length of our summer growing season: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

Figure 8.7: Variation of the length of our summer growing season: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

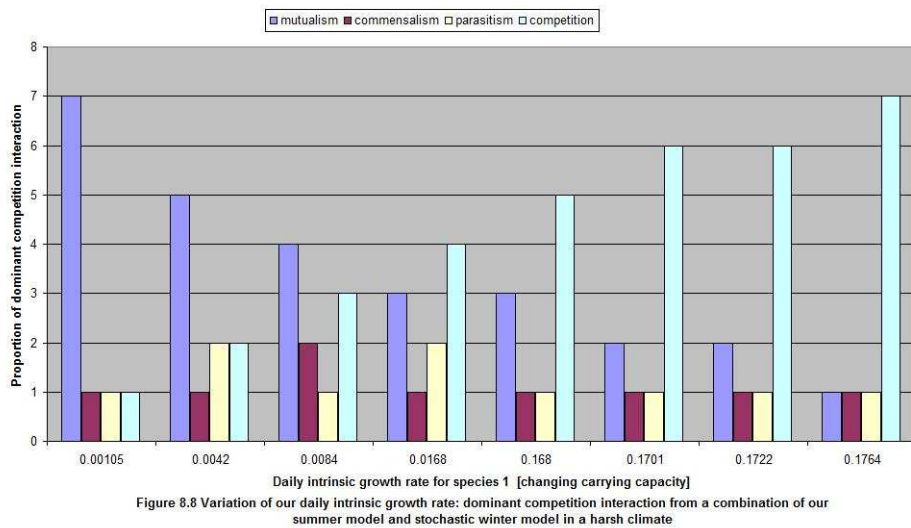


Figure 8.8: Variation of the number of our daily intrinsic growth rate for species 1 or changes in our carrying capacity for species 1 reflecting temperature changes: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

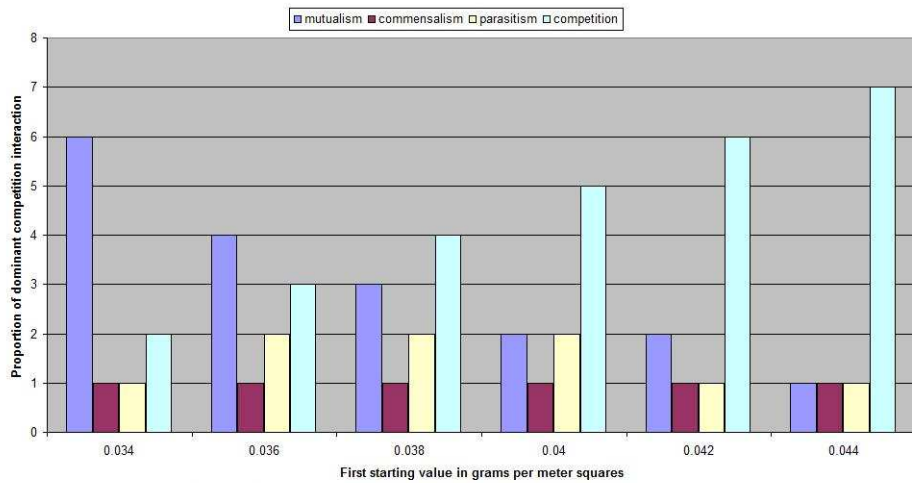


Figure 8.9 Variation of the number of our first starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

Figure 8.9: Variation of the number of our first starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

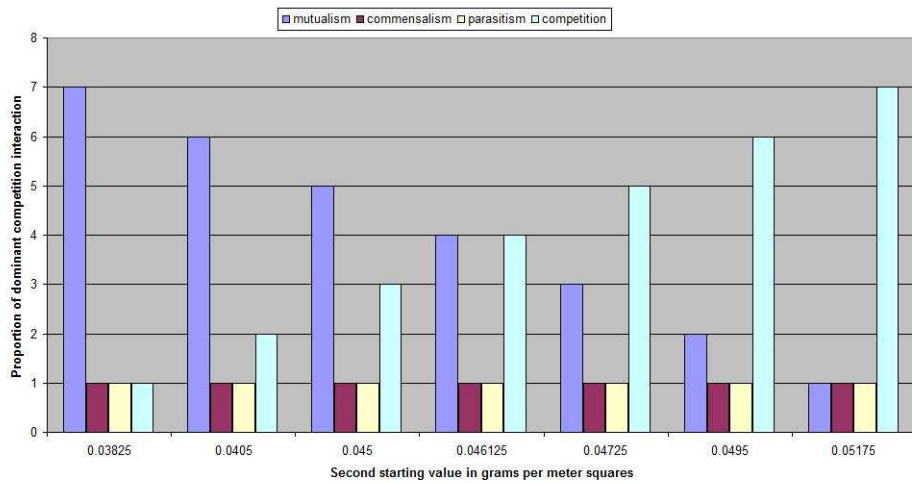


Figure 8.10 Variation of the number of our second starting value: dominant competition interaction from our summer model and stochastic winter model in a benign climate

Figure 8.10: Variation of the number of our second starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

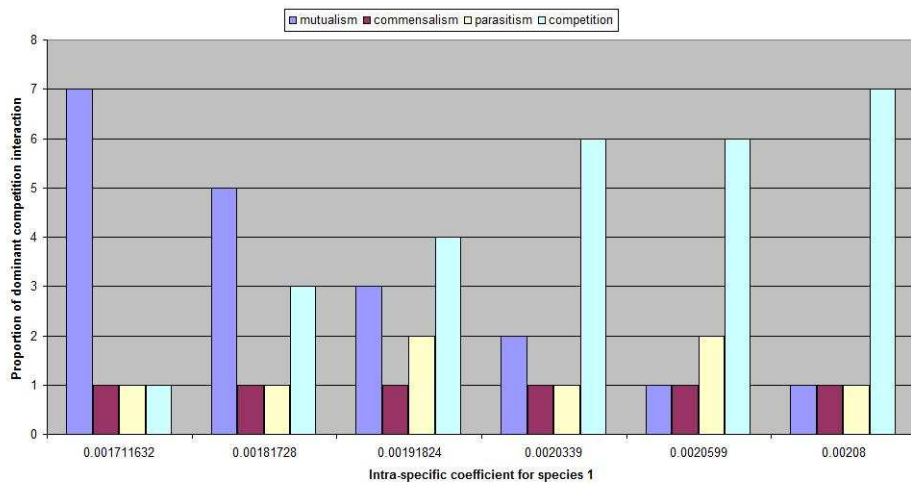


Figure 8.11 Variation of the number of our intra-specific coefficient: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

Figure 8.11: Variation of the number of our intra-specific coefficient or carrying capacity 1 reflecting the impact of temperature changes: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

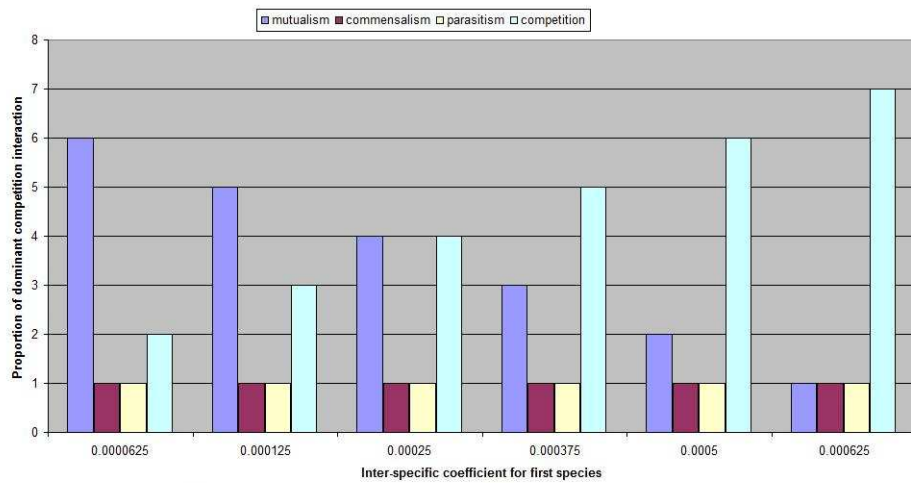


Figure 8.12 Variation of the number of our inter-specific coefficient: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

Figure 8.12: Variation of the number of our inter-specific coefficient for species 1 reflecting the inhibiting effect of warmer summers: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

8.5 Qualitative prediction of mutualism from a variation of storm intensity

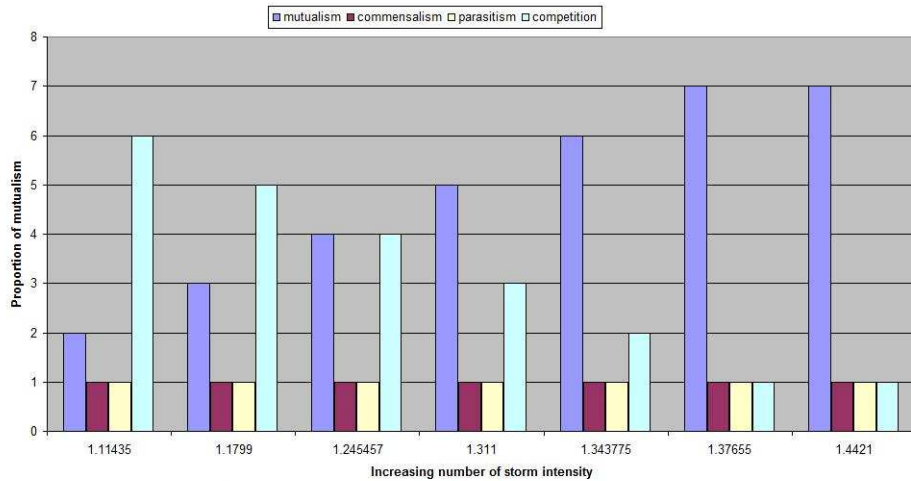


Figure 8.13 Variation of the number of storm intensity: mutualism from a combination of our summer model and our stochastic winter model in a harsh climate

Figure 8.13: Variation of the number of our storm intensity: mutualism from a combination of our summer model and stochastic winter model in a harsh climate

The changes in our summer model which can contribute to the changes in this positive interaction behaviour when our storm intensity is varied are graphically summarised above in Figure 8.7, Figure 8.8, Figure 8.9, Figure 8.10, Figure 8.11, and Figure 8.12.

8.6 Qualitative prediction of mutualism from a variation of our Young's modulus

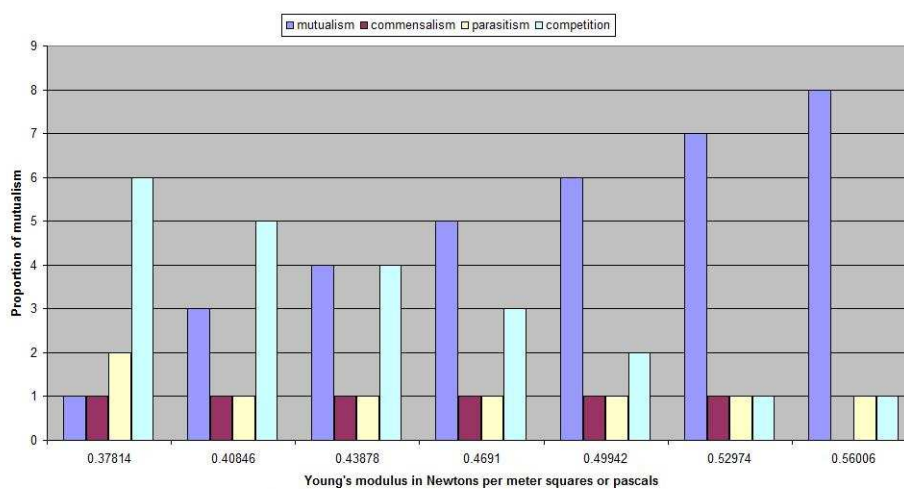


Figure 8.14 Variation of the number of our Young's modulus: mutualism from a combination of our summer model and stochastic winter model in a harsh climate

Figure 8.14: Variation of the number of our Young's modulus: mutualism from a combination of our summer model and stochastic winter model in a harsh climate

Similarly, the changes in our summer model which can contribute to the changes in this positive interaction behaviour when our Young's modulus is varied are graphically summarised above in Figure 8.7, Figure 8.8, Figure 8.9, Figure 8.10, Figure 8.11, and Figure 8.12.

8.7 Qualitative prediction of facilitation from a variation of our winter storms: ecological insight 1

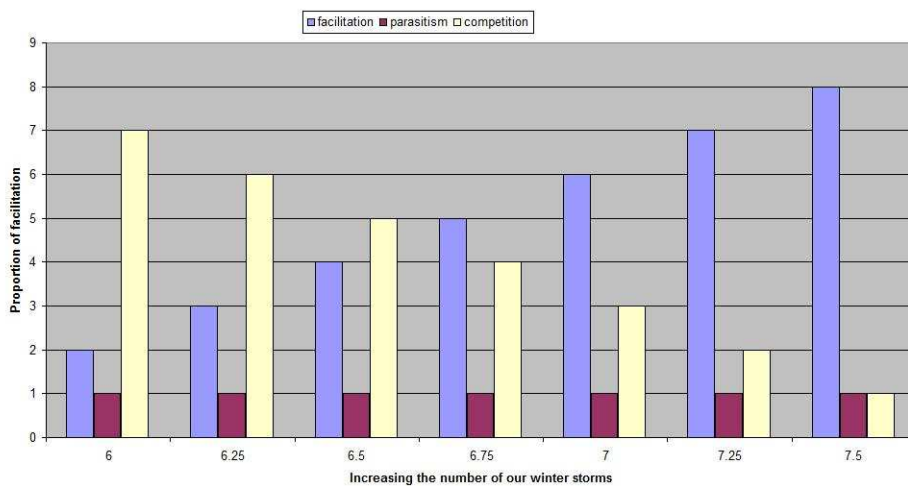


Figure 8.15 Variation of the number of our winter storms: facilitation from a combination of our summer model and stochastic winter model in a harsh climate

Figure 8.15: Variation of the number of our winter storms: facilitation from a combination of our summer model and stochastic winter model in a harsh climate extracted from Figure 8.6

8.8 Qualitative prediction of facilitation from a variation of our storm intensity: ecological insight 2

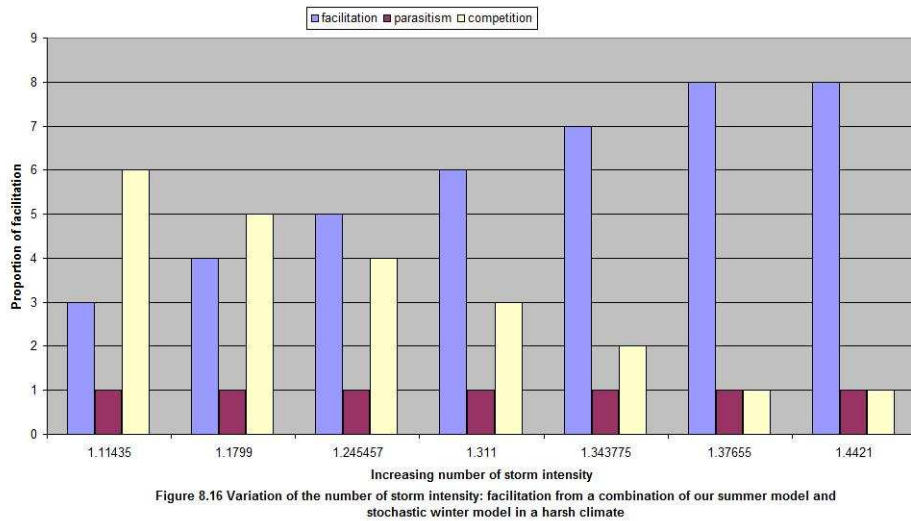


Figure 8.16: Variation of the number of our storm intensity: facilitation from a combination of our summer model and stochastic winter model in a harsh climate extracted from Figure 8.13

8.9 Qualitative prediction of a dominant competition interaction from a variation of our growing season: ecological insight 3

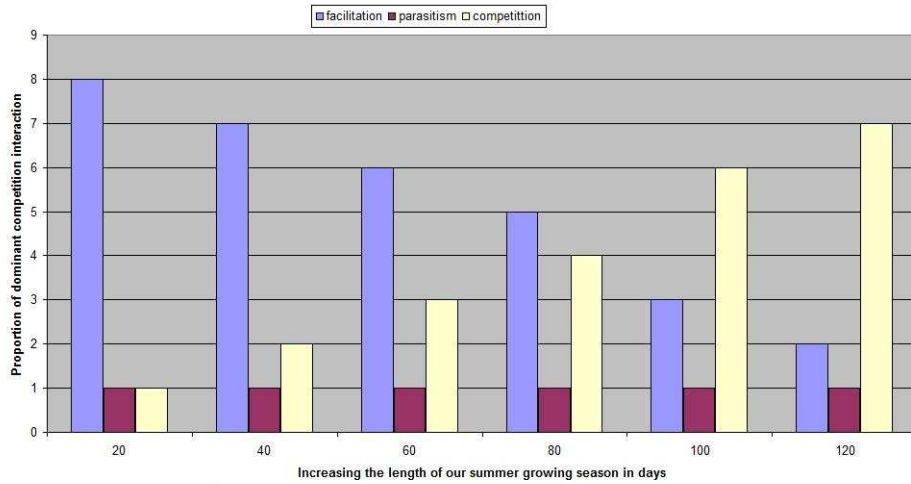


Figure 8.17 Variation of the number of our length of summer growing season: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate

Figure 8.17: Variation of the length of our growing season: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate extracted from Figure 8.7

8.10 Qualitative prediction of a dominant competition from a variation of our winter storms: ecological insight 4

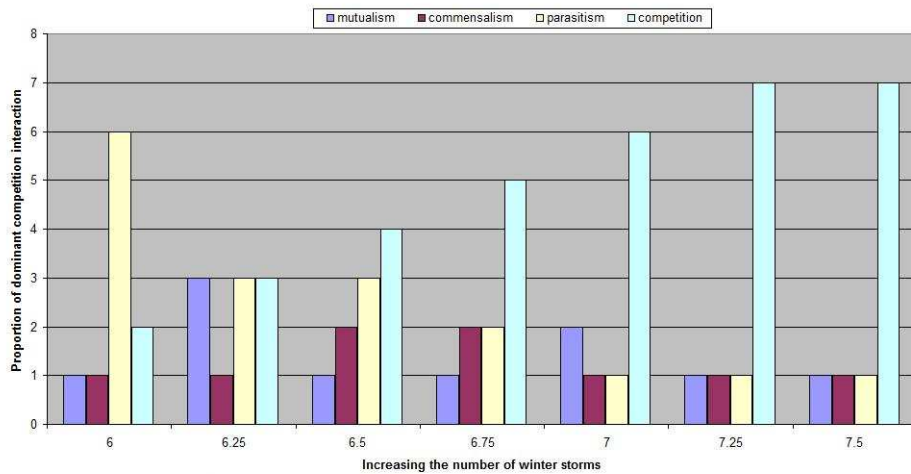


Figure 8.18 Variation of the number of our winter storms: dominant competition interaction from a combination of our summer model and stochastic winter model in a harsh climate over a 10 year period of one trajectory

Figure 8.18: Variation of our winter storms: dominant competition interaction from a combination of our summer model and stochastic winter model in a harsh climate

8.11 Qualitative prediction of a dominant parasitism from a variation of our winter storms: ecological insight 5

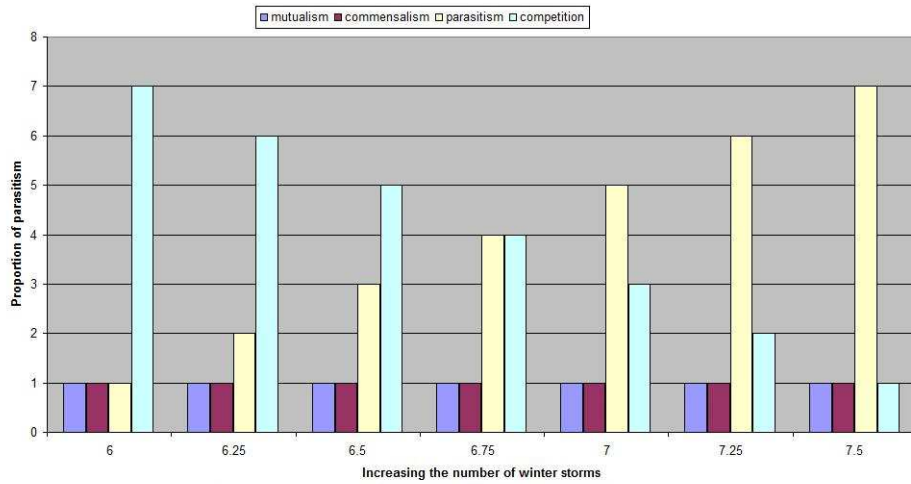


Figure 8.19 Variation of the number of our winter storms: dominant parasitism from a combination of our summer model and stochastic winter model in a harsh climate over a 10 year period of one trajectory

Figure 8.19: Variation of our winter storms: dominant parasitism from a combination of our summer model and stochastic winter model in a harsh climate

Our numerical simulation suggests that the changes in the parasitic interaction behaviour can occur if the length of our growing season is varied as displayed above.

8.12 Qualitative prediction of a dominant facilitation from a variation of winter storms over a 20 year period of one trajectory: ecological insight 6

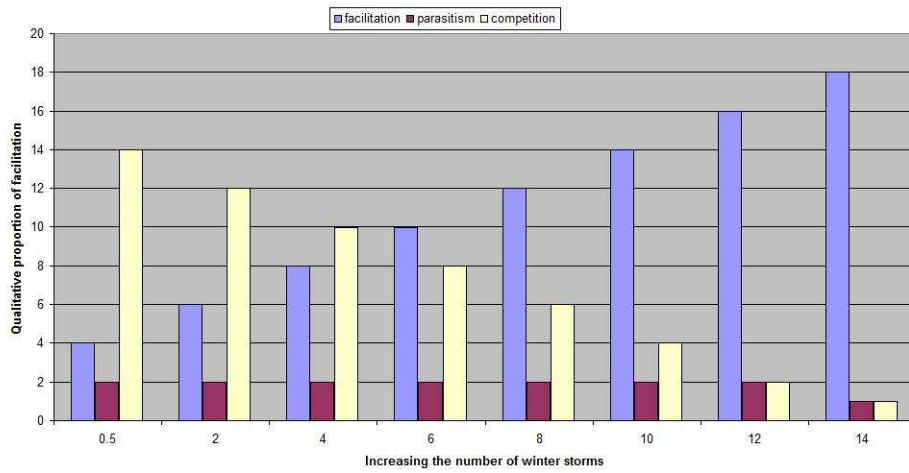


Figure 8.20 Variation of the number of winter storms: obtaining facilitation from a combination of our summer competition model and our stochastic winter model in a harsh climate over a 20 year period of one trajectory

Figure 8.20: Variation of winter storms: dominant facilitation from a combination of our summer model and stochastic winter model in a harsh climate over a 20 year period of one trajectory

8.13 Qualitative prediction of a dominant competition interaction from a variation of the summer season over a 20 year period of one trajectory: ecological insight 7

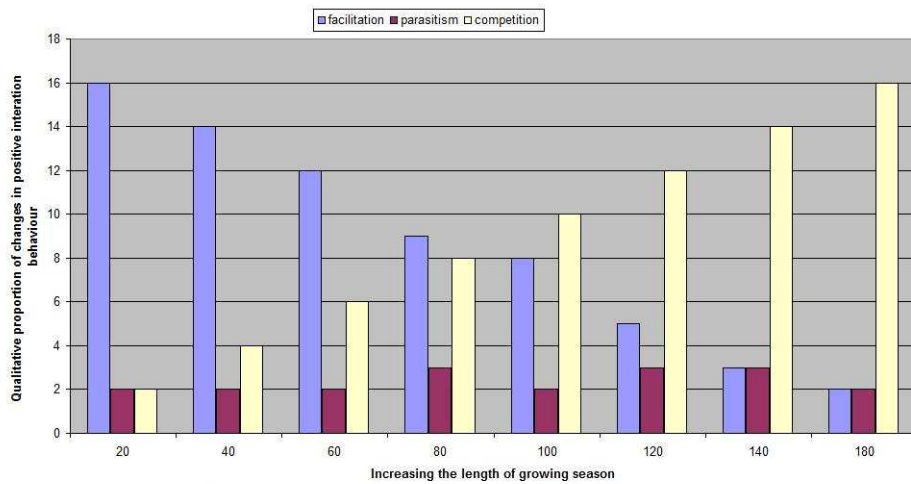


Figure 8.21 Variation of the length of growing season: obtaining facilitation from a combination of our summer model and our stochastic winter model in a benign climate over a 20 year period of one trajectory

Figure 8.21: Variation of our length of summer growing season: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

Source: <http://www.climatehotmap.org/references.html> [sub-title: Arctic and Antarctic warming-69 Barrow, Alaska] Quote: Summer days without snow have increased from fewer than 80 in the 1950's to more than 100 in the 1990's.

8.14 Qualitative prediction of a dominant competition interaction from a variation of our first starting value over a 20 year period of one trajectory: ecological insight 8

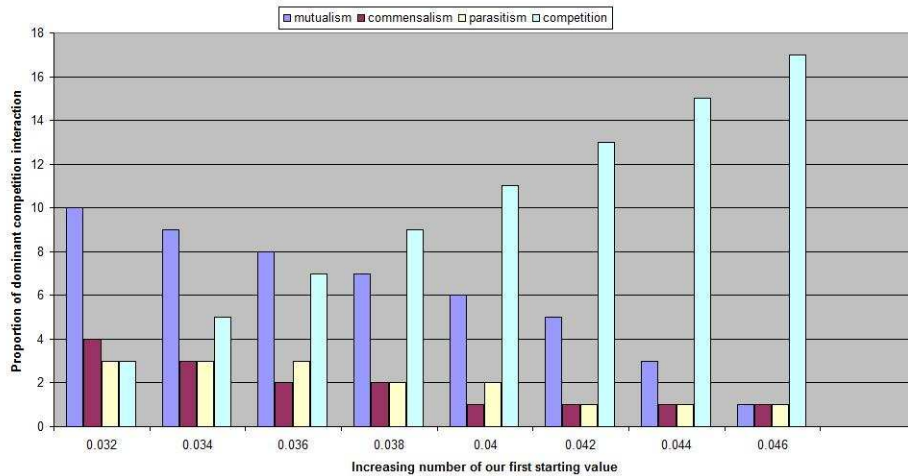


Figure 8.22 Variation of our first starting value: dominant competition interaction from a combination of our summer model and stochastic winter model over a 20 year period of one trajectory in a benign environment

Figure 8.22: Variation of our first starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

8.15 Qualitative prediction of a dominant competition interaction from a variation of our first starting value over a 20 year period of one trajectory: another ecological insight

9

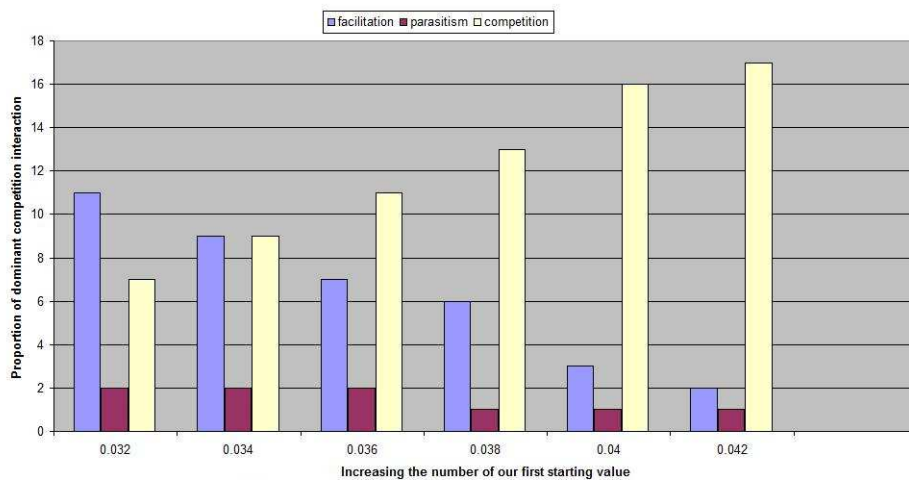


Figure 8.23 Variation of our first starting value: dominant competition interaction from a combination of our summer model and stochastic winter model over a 20 year period of one trajectory in a benign environment

Figure 8.23: Variation of our first starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

8.16 Qualitative prediction of a dominant competition interaction from a variation of our second starting value over a 20 year period of one trajectory: ecological insight 10

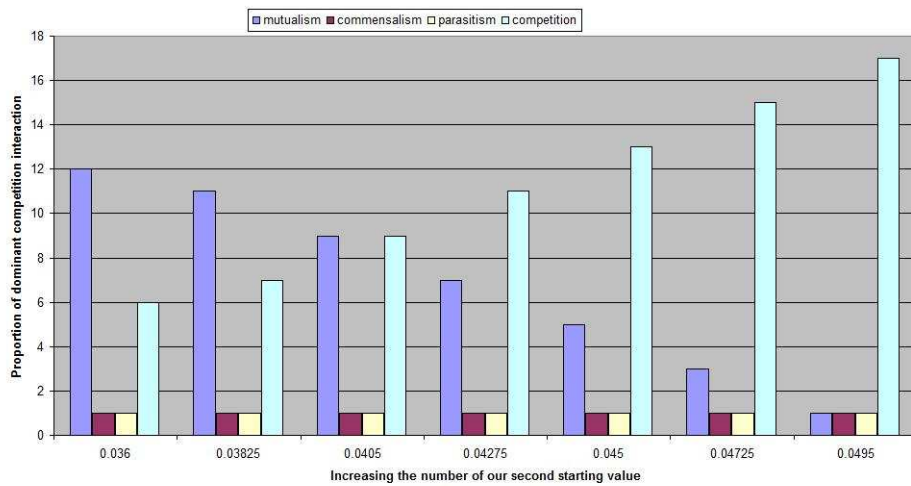


Figure 8.24 Variation of our second starting value: dominant competition interaction from a combination of our summer model and stochastic winter model over a 20 year period of one trajectory in a benign environment

Figure 8.24: Variation of our second starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

8.17 Qualitative prediction of a dominant competition interaction from a variation of our second starting value over a 20 year period of one trajectory: another ecological insight 11

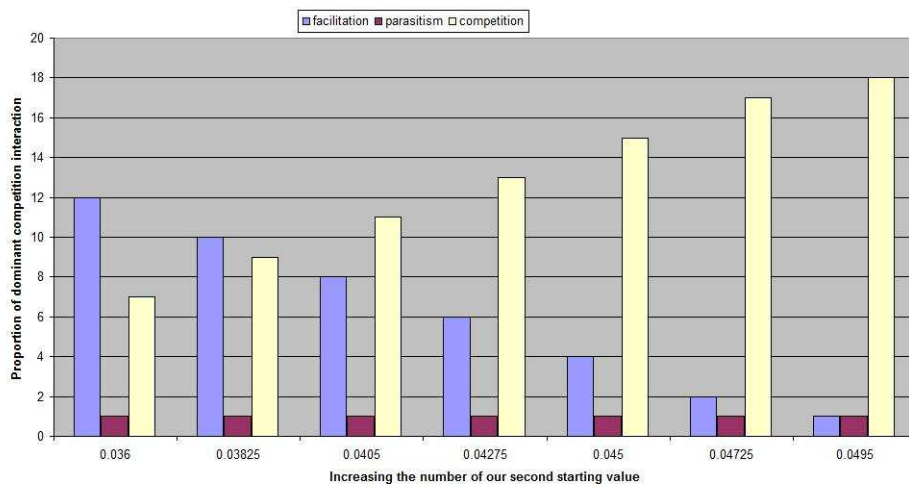


Figure 8.25 Variation of our second starting value: dominant competition interaction from a combination of our summer model and stochastic winter model over a 20 year period of one trajectory in a benign environment

Figure 8.25: Variation of our second starting value: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

8.18 Qualitative prediction of a dominant competition interaction from a variation of our daily intrinsic growth rate over a 20 year period of one trajectory: another ecological insight 12

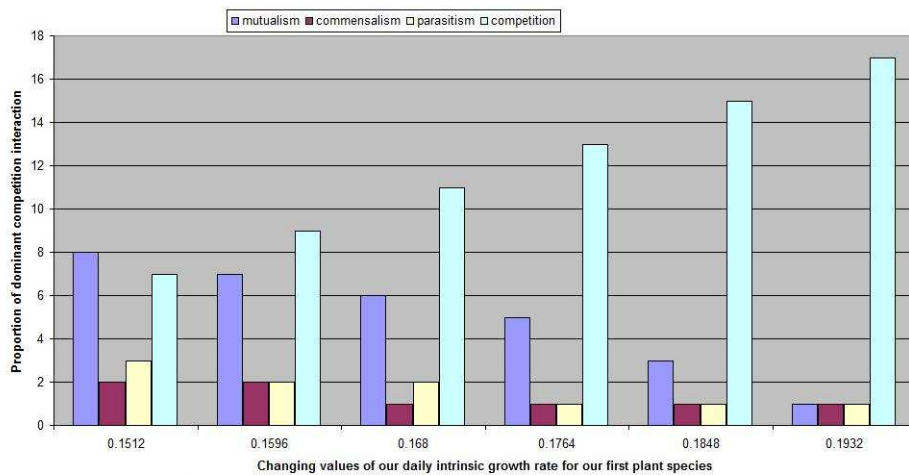


Figure 8.26 Variation of our daily intrinsic growth rate for our first plant species: dominant competition interaction from a combination of our summer model and stochastic winter model over a 20 year period of one trajectory in a benign environment

Figure 8.26: Variation of our daily intrinsic growth rate for our first plant species: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

8.19 Qualitative prediction of a dominant competition interaction from a variation of our daily intrinsic growth rate over a 20 year period of one trajectory: another ecological insight 13 extracted from Figure 8.26

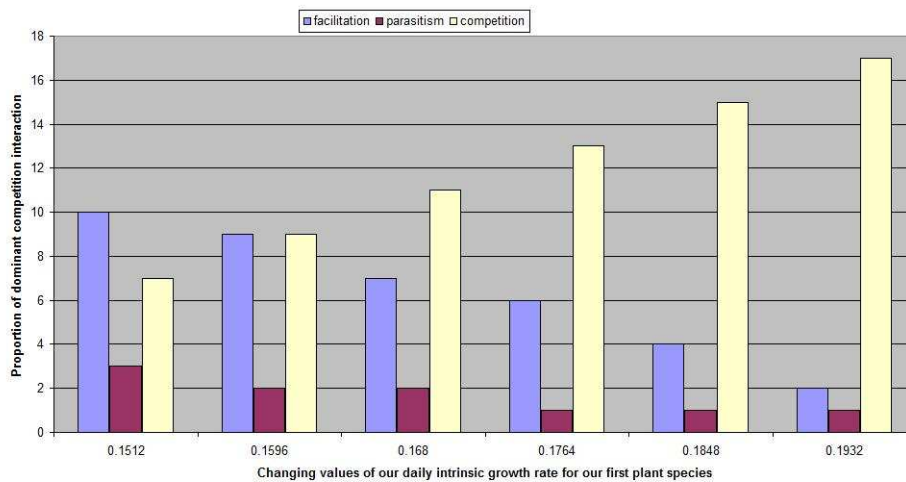


Figure 8.27 Variation of our daily intrinsic growth rate for our first plant species: dominant competition interaction from a combination of our summer model and stochastic winter model over a 20 year period of one trajectory in a benign environment

Figure 8.27: Variation of our daily intrinsic growth rate for our first plant species: dominant competition interaction from a combination of our summer model and stochastic winter model in a benign climate over a 20 year period of one trajectory

8.20 Calculation of Our Penalty Functions: Why we did not Use 1-Norm and Infinity Norm to Select Our Best Fit Parameters

1. The letter M stand for the measured data.
2. The letter S_i stand for our simulated data ranging from $i = 1$ to $i = 20$.
3. The letter V_i stand for the difference between the measured data and our simulated data.

p -Norm	calculation of penalty functions				
Type	V_1	V_2	V_3	V_4	V_5
1-norm	30.3	30.5	30.7	31	31.2
2-norm	15.75	15.6	15.48	15.36	15.3
∞ - norm	12.46	12	11.5	10.94	10.57

Table 8.1: Calculation of our penalty functions

p -Norm	calculation of penalty functions				
Type	V_6	V_7	V_8	V_9	V_{10}
1-norm	31.33	31.52	31.72	31.92	32.13
2-norm	15.25	15.2144	15.22	15.26	15.31
∞ - norm	10.15	9.66	9.55	9.78	10

Table 8.2: Calculation of our penalty functions

p -Norm	calculation of penalty functions				
Type	V_{11}	V_{12}	V_{13}	V_{14}	V_{15}
1-norm	32.33	32.53	32.73	32.93	33.16
2-norm	15.4	15.51	15.64	15.81	16
∞ - norm	10.23	10.45	10.66	10.9	11.1

Table 8.3: Calculation of our penalty functions

8.20.1 Remark

We did not use our 1-norm penalty function to select our best fit parameters because our calculated sequence of errors between the measured data and our simulated data do satisfy a monotonic property but the local minimum of 1-norm penalty function is 30.3.

Although, our infinity-norm between the measured data and our simulated data do satisfy a monotonic property using our infinity norm, our local minimum of infinity-norm penalty function is 9.55. A further gridding provides a best fit

p -Norm	calculation of penalty functions				
Type	V_{16}	V_{17}	V_{18}	V_{19}	V_{20}
1-norm	33.47	33.64	33.99	34.02	34.17
2-norm	16.25	16.45	16.9	16.95	17.17
∞ - norm	11.35	11.55	11.95	11.98	12.15

Table 8.4: Calculation of our penalty functions

intra-specific coefficient of 0.0020302. Using either the 2-norm penalty function best fit model parameters or the infinity-norm penalty function best fit model parameters would provide similar patterns of ecological conclusions.

8.20.2 Plant Growth Data

These 10 plant growth data points are the average dry weights or biomass in grams of an annual plant provided by Blackman ([35]). These data are displayed below.

1. The average biomass for the beginning of the first week which starts on day 1 is 0.0454 grams.
2. The average biomass for the beginning of the second week which starts on day 8 is 0.147 grams.
3. The average biomass for the beginning of the third week which starts on day 15 is 0.508 grams.
4. The average biomass for the beginning of the fourth week which starts on day 22 is 1.653 grams.
5. The average biomass for the beginning of the fifth week which starts on day 29 is 5.868 grams.
6. The average biomass for the beginning of the sixth week which starts on day 36 is 17.33 grams.
7. The average biomass for the beginning of the seventh week which starts on day 43 is 30.35 grams.
8. The average biomass for the beginning of the eighth week which starts on day 50 is 46.2 grams.
9. The average biomass for the beginning of the ninth week which starts on day 57 is 66.1 grams.
10. The average biomass for the beginning of the tenth week which starts on day 64 is 88.9 grams.

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