

UNIVERSITY OF MINES AND TECHNOLOGY (UMaT)

TARKWA

FACULTY OF ENGINEERING

DEPARTMENT OF MATHEMATICAL SCIENCES

A THESIS REPORT ENTITLED

**MATHEMATICAL MODELLING OF FOREST GROWTH,
SPREAD AND VEGETATION PATTERN FORMATION**

**SUBMITTED IN FULFILMENT OF THE REQUIREMENT FOR THE
AWARD OF THE DEGREE OF DOCTOR OF PHILOSOPHY IN
MATHEMATICS**

BY

PETER KWESI NYARKO

TARKWA, GHANA

FEBRUARY, 2019

UNIVERSITY OF MINES AND TECHNOLOGY (UMaT)

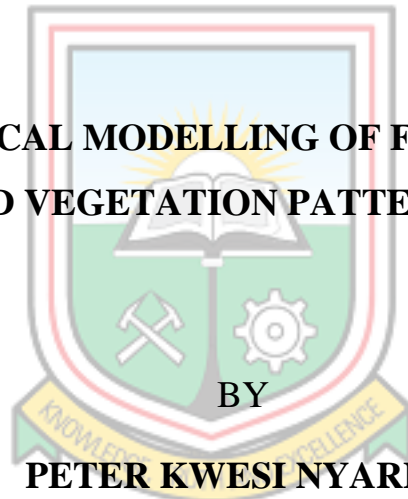
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DECLARATION

I declare that this thesis is my own work. It is being submitted for the degree of Doctor of Philosophy (PhD) in Mathematics at the University of Mines and Technology (UMaT), Tarkwa. It has not been submitted for any degree or examination in any other University.

.....

(Signature of Candidate)

..... day of (year)



ABSTRACT

The mechanism for growth, spread and vegetation pattern formation is largely unknown and poorly understood. To improve understanding of this mechanism, two mathematical models each consisting of three nonlinear partial differential equations for surface water balance (W), soil water balance (N) and plant biomass density variable (P) to investigate the dynamics of forest growth and vegetation pattern formation were developed. The models have a parameter β that accounts for the influence of the interactions among multiple resources such as light, water, temperature and nutrients on the growth, spread and vegetation pattern formation. The methods used include Michaelis-Menten Kinetics for the rate of nutrients uptake by a cell or organism for growth; Continuous-Time Markov (CTM) method as a standardised methodology that describes plant metabolism responses to multiple resource inputs and the Taylor Series Expansion method used to linearise the nonlinear models formulated in order to explain the dynamics of the growth, spread and vegetation pattern formation of the forest. The linear stability analysis of homogeneous steady-state solutions provided a reliable predictor of the onset and nature of pattern formation in the reaction-diffusion systems. The results revealed that, stability conditions needed for pattern formation is possible provided that $aN_0/[aN_0 + m(rN_0 + l)] \rightarrow 0$, as $a \rightarrow 0$. Thus, the homogeneous plant equilibrium decreases with decreasing rainfall until plant become extinct. Based on this condition, the trace and determinant criteria for stability were obtained as $-(m+u)$ and mu respectively. Thus, as N_0 increases or decreases, $aN_0/[aN_0 + m(rN_0 + l)]$ also increases or decreases respectively irrespective of the values of the other parameters; where $0 \leq N_0 < \infty$. This suggests that N_0 which is a surrogate for dimensionless infiltration capacity prohibits pattern formation at high levels. In the non-trivial case, the linear stability analysis of the study shows that the conditions needed for pattern formation to be satisfied is that $rmu < a - lw_s$ and $w_s > gu$. Thus, ecologically feasible region of the parameter space that gives rise to Turing regimes in which vegetation patterns continuously evolve in space is such that $gu < w_s < (a - rmu)/l$. Finally, numerical simulations of system of partial differential equation models were carried out based on different fertility levels under different water conditions. The simulation results show that, regardless of the parameter space, and the level of

precipitation, the shift of the vegetation cover from uniform to gaps, labyrinths, spots, and into bare soil or almost bare soil is possible. The proposed model derived in the study could be applied to any vegetation type. The model could be used to further analyse the conditions for the development of dynamic patterns and their occurrence in different biological systems.



DEDICATION

This work is dedicated firstly to the Almighty God for his kindness and mercies. Again, to my dear wife, Dr (Mrs) Christiana C. Nyarko and to my children: Victoria Nyarko, Doreen Essuon Panyin Nyarko, Gloria Efua Essuon Nyarko, Mary Saman-Pa Nyarko, Peter Saadade Nyarko and Adelaide Boatemaa Nyarko. My nephew Richford Mensah and many other relations whose names I cannot mention all, for their support and encouragement. I also dedicate this work to my parents: Mr. Peter Kwame Nyarko and Mrs. Elizabeth Nyarko for their fervent prayer towards this achievement.



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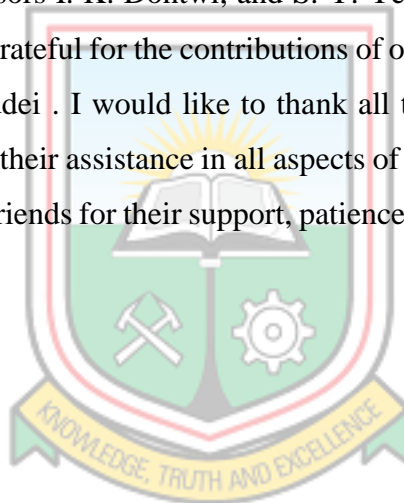


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CHAPTER 1

INTRODUCTION

1.1 Preamble

Mathematics is notably known as the Queen of sciences and permeates every discipline as well as every area of our lives. Mathematics as a discipline has two broad divisions which provide one with the skills or tools one needs to shape the world around us. This starts from simple arithmetic computations in business transactions to complex functions. This field is the practical side of mathematics and permeates also into forestry and ecology.

1.2 Ecological Background

Forests are long-lived dynamic biological systems that are continuously changing. The study of forest dynamics which is concerned with the changes in forest structure and composition over time, including its behaviour in response to anthropogenic and natural destructions is therefore crucial. Tree growth and forest destructions are primary evidence of forest dynamics. They are determined by resources (such as radiation, water, nutrients supply) and environmental conditions (such as temperature, soil acidity, air pollution and human activities). It is therefore often necessary to project these changes in order to obtain relevant information for sound decision making. Forest management decisions are made based on information about both current and future resource conditions. Inventories taken at one instant in time provide information on current wood volumes and related statistics. Growth and yield models describe forest dynamics (that is, the growth, mortality, reproduction and associated changes in the stand) over time. These models have been widely used in forest management because of their ability to update inventories, predict future yields, and to explore management alternatives and silvicultural options, thus providing information for decision-making (Vanclay, 1994).

Human activities affect forest growth in many diverse ways. To begin with, human activities influence the composition, cover, age and density of the vegetation. The landscapes for these forests systems are altered by human activities. Thus, changing the kinds of stands present and their spatial arrangement, which influences the movement of wind, water, animals and soils. At the regional level, humans introduce by-products into the air that may fertilize or kill forests. At the global scale, human consumption of fossil

fuels has increased atmospheric carbon dioxide levels and changed the way that carbon is distributed in vegetation, soils and the atmosphere, with implications on global climate. The worldwide demand for forests products has stimulated not only the transfer of processed wood products from one country to another, but also the introduction of non-native tree species, along with associated pests, that threaten native forests and fauna. While the management of forested lands is becoming increasingly important, it is also becoming more contentious because less forested land is available for an increasing range of demands.

The 1985 Tropical Forestry Action Plan of the FAO contends that 7.5 million hectares of closed forest and 3.8 million hectares of open forest are cleared in the tropics each year. Globally, the major cause of deforestation is shifting cultivation by landless farmers (not traditional forest dwellers) who account for nearly half the deforestation. The second is the clearing of forest for permanent agriculture and settlement programmes. The next most important cause is gathering of wood as a source of fuel, whilst commercial timber harvesting ranks fourth. The pressure to extract more resources from a dwindling base is leading to a number of challenging questions. These include whether there are any or no environmental, economic and social values of the forest. If there are, has there been enough research on the growth processes of the forest and the timescale to replenish the forest resource once it is devastated?

1.2.1 Environmental and Economic Values of the Forest

It is becoming increasingly clear that, forests that are managed in a sustainable manner are able to produce both high quality wood products and other ecological goods and services such as water purification, wildlife habitat and carbon sequestration. Forest management practices that protect aquatic systems, minimise soil disturbance and erosion, and promote rapid forest regeneration are all components of sustainable forestry. When forests are managed in a sustainable manner, the environmental values can be explained along the following lines of action:

- (i) the forests play an important role in our water cycle by pumping water from the soil back into the atmosphere through transpiration. This process also helps to cool the surrounding environment;
- (ii) the forests stabilise soil and reduce erosion and sedimentation into aquatic systems thereby help maintain water quality; and

- (iii) the forests remove airborne particles and ozone from our air and improve air quality.

In similar manner, forests have natural economic values that are often overlooked by society. When forests are degraded, there is a financial cost incurred by society to replace the lost ecological goods and services through the following:

- (i) increased water treatment cost;
- (ii) increased illness and health care costs due to decreased water and air quality;
- (iii) decreased property value due to degraded aesthetic qualities; and
- (iv) decreased revenues from tourism and other non-timber commercial activities associated with healthy ecosystems.

It is therefore worth noting that “the contribution of forests to the country’s economy, environment and social well-being is significant. Our forests therefore form an important part of our roots as a nation and a big part of our future. Taking care of them and ensuring their ongoing health, is a key priority”.

Despite these numerous benefits of our forest to the country’s economy, environment and social well-being, the level of degradation of the forest reserves is high. Studies on the forests therefore cannot be over emphasized due to its economic, environmental and health importance to the society. Although, a large fraction of forestland has been converted to agricultural and urban uses, humans remain dependent on that remaining for the production of paper products, lumber and fuel wood. In addition to wood products, forested lands serve as a cover for the production of freshwater from mountain watersheds, cleans the air of many pollutants, offer habitat for wildlife and domestic grazing animals, and provide recreational opportunity (Keto *et al.*, 1990). With projected increases in human population and rising standards of living, the importance of the world’s remaining forests will likely continue to increase, and along with it, the challenge to manage and sustain this critical resource.

However, sustainability depends on management policies applied to the forest. Information about forest composition which is often inferred through modelling studies is fundamental for understanding rainforest resilience and dynamics.

1.3 Statement of the Problem

The forest stand consists of trees with different diameters and heights which depend on a lot of unsearchable genetic and environmental factors. Its dynamics is affected by many processes and varies among stands (Temesgen and Gadow, 2004). Over the years, an extensive amount of research has been conducted by several researchers in various parts of the world.

The early studies on forests growth were basically on continuous population dynamics and the original research on growth models was attributed to Thomas Malthus (1798). He was therefore considered as the originator of growth models and asserted that, every population is considered to grow in size when the birth rate exceeds the death rate and proposed a model given by $dN/dt = rN$ where N is the population after some time t . dN/dt is the rate of change in population with respect to time while r is the intrinsic growth rate. Forty years later, Verhulst (1838), in his research on growth models, indicated that growth in general must be limited by over-consumption of resources and therefore, exponential growth for population size as indicated by Malthus is unrealistic over a long period. The works of Smith (1963), Pearl and Reed (1920), Turner *et al.* (1969, 1976), Nelder (1961) and Pearl (1920) are few examples of research works associated with continuous population dynamics.

In the early 1960s, there was a paradigm shift and studies on forest growth were more into the modelling of nutrient uptake as a key component for plant growth. Bouldin (1961) and Olsen *et al.*, (1962) proposed mathematical models to simulate diffusion of solutes through soils, which were used to explain phosphate movement and uptake. Nye and Spiers (1964) subsequently developed the partial differential equations used to describe simultaneous mass flow and diffusion for nutrient uptake by a unit length of root. Nye and Marriot (1969) defined boundary conditions for the equations and solved them numerically, while Baldwin *et al.* (1973), on the other hand, solved the equations analytically with steady state approximations. Their work became the foundation for mechanistic nutrient uptake models. Building on this, Claassen and Barber (1976), Nye and Tinker (1977), Barber and Cushman (1981), Claassen *et al.* (1986), Smethurst and Comerford (1993), Yanai (1994), Smethurst *et al.* (2004), and Comerford *et al.* (2006) proposed model revisions to cover the major sub-processes of nutrient uptake and to accommodate a variety of additional conditions. Other

researchers such as Wu *et al.* (1985), Wu *et al.* (1994) and Sharpe *et al.* (1985) modelled the physical growth of the forest by considering the influence of stem, crown and roots. Others just considered the effect of either one of the following: availability of light, surface water or nutrients to the growth of the tree and subsequently to the growth of the forest.

Rangel (1993) indicated that, two general models, empirical and mechanistic have been developed for such a study. The empirical model is based mainly on regression as well as statistical means, often for practical use (Classen and Steingrobe, 1999). The mechanistic model on the other hand, requires an understanding of the mechanisms and a quantitative description of the phenomena (Rengel, 1993). Mechanistic models were therefore considered useful to test the correctness of one's knowledge of the phenomena (Claassen and Steingrobe, 1999). Extrapolation of a verified mechanistic model was thus more reliable than that of an empirical model (Claassen and Steingrobe, 1999). The typical mechanistic nutrient uptake model describes the supply of nutrients from bulk soil to root surfaces, root growth and morphology, and root uptake kinetics (Barber, 1995).

In recent times, almost all vegetation modelling studies have been redirected to pattern formation. It is assumed that pattern formation, is from a starting point of uniform vegetation, as a response to a decrease in mean annual rainfall and human activities. Many authors have additionally investigated the subsequent transitions between different patterned states when environmental conditions such as rainfall are varied (Meron, 2012; Gowda *et al.*, 2014). Studies on the vegetation is now concentrated on pattern formation. Vegetation patterns are examples of ecosystem-scale and self-organisation. In addition to this, they are very important and serve as a potential early warning signals of climate change and imminent regime shifts (Bentil and Murray, 1993; Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007; Corrado *et al.*, 2014). Therefore, they have been the subject of intensive study over the last decade.

Vegetation patterns occur in many semi-arid regions of the world, including Africa (Deblauwe *et al.*, 2012; Müller, 2013), Australia (Berg and Dunkerley, 2004; Moreno-delas Heras *et al.*, 2012), North America (Pelletier *et al.*, 2012; Penny *et al.*, 2013), the Middle East (Buis *et al.*, 2009; Sheffer *et al.*, 2013), and Asia (Yizhaq *et al.*, 2014). Such patterns consist of vegetated regions separated by bare ground. They are usually labyrinthine or spotted on flat terrain, but on slopes the typical form is stripes running parallel to the

contours, known as “banded vegetation” or “tiger bush” (Deblauwe *et al.*, 2008, 2011; Meron, 2012). Most authors attributed the underlying cause of vegetation pattern formation to competition for water and positive feedback between vegetation and water availability. Some of the researchers in this field include (Bel *et al.*, 2012). They investigated the formation and spread of isolated regions of patterned vegetation within an unvegetated background state, on flat terrain in semi-arid environment. Deblauwe *et al.*, (2012) and Dralle *et al.*, (2014), in their studies asserted that, slope can have a major effect on processes governed by water redistribution, due to the downhill flow of water both on the surface and within the soil. Available literature on the subject indicates that, in all these afore mentioned works on forest growth, and pattern formation the researchers never considered the effect of interactions among these multiple resources on the growth, spread and vegetation pattern formation.

This research seeks to model the dynamics of the forest by determining the influence of the interactions among multiple resources such as light, water, temperature and nutrients on the growth, spread and vegetation pattern formation using Continuous Time Markov Chain. These and many other factors have therefore necessitated the study into the modelling of the dynamics of pattern formation of the vegetation in Ghana by means of a system of nonlinear partial differential equation models.

1.4 Objectives of the Study

The objectives of this research are to:

- (i) formulate a mathematical model for the growth, spread and vegetation pattern formation.
- (ii) investigate the homogeneous and heterogeneous dynamics of the forest reserves.
- (iii) simulate the dynamics of the forest reserves using model designed in (i) above.

1.5 Methods Used for the Study

The methods used to achieve the desired objectives included Literature Survey from journals, textbooks and from internet sources; Taylor Series expansion method for the linearization of the nonlinear partial differential equations; Michaelis-Menten method was

used to determine the rate of nutrients uptake by a cell or organism; Continuous-time Markov (CTM) method for synthesising the four resources (light, water and nutrients together with temperature) and Finite Difference Method for discretisation schemes.

1.6 Facilities Used for the Research

The facilities and resources used in this research include:

Computers, library and internet facilities at University of Mines and Technology, Tarkwa. GIS images of some selected forests in Western region of Ghana from Western Regional Library of the forestry Commission

1.7 Organisation of the Thesis

This thesis is divided into seven chapters. Chapter 1 provides the general overview and ecological background of the study, statement of the problem, the objectives of the study, the methods used to achieve the objectives and the facilities that were available for the development and writing of the thesis. The chapter also covers the expected outcomes and the organization of the thesis. Chapters 2 deals with theoretical background and some fundamental concepts. The chapter basically focusses on continuous-time Markov chain method, linearisation of nonlinear systems, and description of nutrient-cell plant growth, discretisation schemes and other fundamental definitions that are relevant to the study. Chapter 3 examines a number of literatures on forest growth, spread and vegetation pattern formation. Chapter 4 presents the mathematical model formulation of forest growth, spread and vegetation pattern formation and its dimensionless form to reduce the parameters associated with the original model. Analysis of the models were considered in chapter 5. Chapter 6 was dedicated to the simulation processes where computer simulations in Python were used, discussion and interpretation of the results obtained from the study. Chapter 7 is the summary of the work. In this chapter, the major findings from the study are summarised, the conclusions drawn and the recommendations provided for future research.

CHAPTER 2

LITERATURE REVIEW

2.1 Preamble

This Chapter presents review of a number of literatures on some previous works, components of growth, the framework of existing theories and review of some previously developed models on the dynamics of the forest growth, spread and vegetation pattern formation.

2.2 Forest Growth Models

The concept of modelling forest growth, dates as far back as 1798 when Thomas Malthus, in “An Essay on the Principle of Population”, used unchecked population growth to famously predict a global famine. Since then, studies on vegetation has graduated steadily from continuous population dynamics through to the early 1960s when there was a paradigm shift and studies on forest growth were more into the modelling of nutrient uptake as a key component for plant growth. In recent times, almost all vegetation modelling studies have been redirected to pattern-formation. Studies on the vegetation is now concentrated on pattern formation and are considered as examples of ecosystem-scale and self-organisation.

Models assist forest researchers and managers in many ways. Some important uses include the ability to predict future yields and to explore silvicultural options. They provide an efficient way to prepare resource forecasts, but a more important role may be their ability to explore management options and silvicultural alternatives. For example, foresters may wish to know the long-term effect on both the forest and on future harvest of a particular silvicultural decision, such as changing the cutting limits for harvesting. With a growth model, they can examine the likely outcomes, both with the intended and alternative cutting limits, and can make their decisions objectively. The process of developing a growth model may also offer interesting new insights into stand dynamics.

Many nonlinear theoretical models such as the Logistic, the Gompertz, the Bertalanffy-Richards and the Schnute rather than empirical models like the polynomial models have been used to model forest growth and yield and tree height-diameter relationships (Pienaar

and Turnbull, 1973; Payandeh, 1983; Huang *et al.*, 1992; Zeide, 1993; and Fang and Bailey, 1998) because theoretical models have an underlying hypothesis associated with cause or function of the phenomenon described by the response variable (Vanclay, 1994). However, empirical models such as polynomial equations were not considered as modeling nonlinear growth and yield in forestry because they are devoid of any biological interpretation and do not have meaningful parameters from forestry.

Growth studies in many branches of science have demonstrated that more complex nonlinear functions are justified and required if the range of the independent variable encompasses juvenile, adolescent, mature and senescent stages of growth (Philip, 1994). Thus, a function with a sigmoid form, ideally its origin at (0, 0), a point of inflection occurring early in the adolescent stage and either approaching a maximum value, an asymptote, or peaking and falling in the senescent stage, is justified. It is therefore prudent to begin the study with results of some previous works.

2.3 Some Previous Works

The study reviewed works associated with continuous population dynamics, environment factors and plant resource competition dynamics of the forest. Other works on extensions of logistic growth model were also considered and these include the works of Von Bertalanffy, Richard, Smith (1963), Blumberg (1968), Schnute (1981), Pearl and Reed (1920), Pearl (1920), Nelder (1961) and Turner *et al.*, (1950).

2.3.1 Continuous Population Dynamics

The early studies on forests growth were basically on continuous population dynamics and the original research on growth models was attributed to Thomas Malthus (1798). He was therefore considered as the originator of growth models. The works of Smith (1963), Nelder (1961), Pearl (1920) Pearl and Reed (1920), Turner *et al.* (1969; 1976), are few examples of research works associated with continuous population dynamics.

The Malthusian Growth Model

Thomas Malthus proposed an exponential growth model and assumed that, if $N(t)$ is the number of individuals in a population at time t , and let b and d be the average per capita

birth and death rates, respectively, then in a short time Δt , the number of births in the population is $b\Delta tN(t)$, and the number of deaths is $d\Delta tN(t)$. Thus, the change in population between the times t and $(t+\Delta t)$ is determined by the relation $N(t+\Delta t)-N(t)=\Delta t(b-d)N(t)$ which can be rearranged as $(N(t+\Delta t)-N(t))/\Delta t=(b-d)N(t)$. Now, the limit as $\Delta t \rightarrow 0$, this expression was obtained as Equation (3.1)

$$\frac{dN(t)}{dt} = rN(t) \quad (2.1)$$

with the integral form which proposes an exponentially growth as Equation (2.2)

$$N(t) = N_0 e^{rt} \quad (2.2)$$

where, N_0 is the initial population, $N(t)$ is the population after some time t and $r = b - d$ being the intrinsic growth rate.

The Logistic Growth Model

One of the two regulation models to the Malthus exponential growth model is the logistic growth model by Verhulst. Verhulst's findings in 1838 revealed that, Malthus exponential growth for population size is unrealistic over a long period since growth will eventually be checked by over-consumption of resources. He therefore proposed a model called the Logistic growth model which is of the form given by Equation (2.3)

$$\frac{dN}{dt} = rNF(N) \quad (2.3)$$

where $F(N)$ provides a model for environmental regulation. He indicated that, this function should satisfy $F(0) = 1$ when the population grows exponentially with growth rate r and N is small, $F(k) = 0$ indicating that the population stops growing at the carrying capacity, and $F(N) < 0$ when $N > k$ thus the population decays when it is larger than the carrying capacity. The simplest function, $F(N)$ satisfying these conditions is linear and was given by $F(N) = 1 - N/K$. The resulting model is the well-known logistic equation given as Equation (2.4)

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{k} \right) \quad (2.4)$$

where $(1 - N/k)$ represents the fractional deficiency of the current size from the saturation level, k . This is an important model for many processes besides bounded population growth.

Verhulst Logistic Growth Scaled by the 'Delaying' Factor $[1 + c(N/K)]^{-1}$

The other regulation model to the Malthus exponential growth model is by Smith (1963). Smith also reported that the Verhulst logistic growth equation did not fit experimental data satisfactorily due to problems associated with time lags. According to Smith, the major problem in applying the logistic growth equation to data concerns an accurate portrayal of the portion of the limiting factor as yet unutilized given by $1 - (N/k)$. He then argued that for a food-limited population, the term $1 - (N/k)$ should be replaced with a term representing the proportion of the rate of food supply currently unutilized by the population. Thus, if F is the rate at which a population of size N uses food and T is the corresponding rate at saturation level, then the model can best be represented as Equation (2.5)

$$\frac{dN}{dt} = rN \left(1 - \frac{F}{T} \right) \quad (2.5)$$

where $(F/T) > (N/K)$, since a growing population will use food faster than a saturated population. F must depend on N and dN/dt , and the simplest relationship was identified to be linear indicated as Equation (2.6)

$$F = aN + b \frac{dN}{dt}, \quad a > 0, \quad b > 0 \quad (2.6)$$

At saturation $F = T$, $N = k$, $\frac{dN}{dt} = 0$, hence $T = ak$ and as a result the modified Verhulst logistic growth equation is given as Equation (2.7)

$$\frac{dN}{dt} = rN \left(\frac{1 - \frac{N}{k}}{1 + c \frac{N}{k}} \right) \quad (2.7)$$

where $c = \frac{rb}{a}$.

2.3.2 Extensions of the Logistic Growth Model

In this section, some other well-known growth models that are extensions to the logistic growth model were considered. In addition, the existence of the sigmoidal feature that characterizes most growth curves was established. This is normally responsible for the existence of an inflection point, where present. Since the original work of Verhulst (1938) and Pearl and Reed (1920), there have been several contributions suggesting alternative functional forms $f(N)$ for growth whilst retaining the sigmoidal and asymptotic property of the Verhulst logistic curve. In plant sciences, Richards (1959) was the first to apply a growth equation developed by Von Bertalanffy (1938) to describe the growth of animals. Richard's growth curve was used for fitting experimental data by Nelder (1961) who introduced the term generalized logistic equation to describe the equation. Blumberg (1968) introduced the hyperlogistic equation as a generalization of Richard's equation. Turner *et al.* (1969; 1976) suggested a further generalization of the logistic growth and termed their equation the generic logistic equation. In a survey paper, Buis (1991) revisited several previous logistic growth derived functions that have been introduced and outlined some of their respective properties. The generalised logistic growth model was deduced based on the three postulates of the kinetic theory of growth. The three postulates are stated as follows:

P1: The rate of change of size is jointly proportional to a monotonically increasing function ϕ_1 of the distance between the origin and the size, and to a monotonically increasing function ϕ_2 of the distance between size and ultimate size. This is represented mathematically as Equation (2.8)

$$\frac{dN}{dt} \propto \phi_1[\delta_n(0, N)] \phi_2[\delta_n(N, k)] \quad (2.8)$$

P2: The monotonically increasing functions ϕ_1 and ϕ_2 are power functions where $\theta_1, \theta_2 > 0$. These are represented by Equations (2.9) and (2.10)

$$\phi_1[\delta_n(0, N)] = [\delta_n(0, N)]^{\theta_1} \quad (2.9)$$

$$\phi_2[\delta_n(N, k)] = [\delta_n(N, k)]^{\theta_2} \quad (2.10)$$

P3: The exponents θ_1 and θ_2 obey the constraints represented by Equations (2.11) and (2.12)

$$\theta_1 = 1 - np \quad (2.11)$$

$$\theta_2 = n + np \quad (2.12)$$

where $n > 0$, $-1 \leq p \leq 1/n$, $\theta_1 + \theta_2 > n + 1$

Based on these postulates of the kinetic theory of growth, the generalized logistic function is defined as Equation (2.13):

$$\frac{dN}{dt} = rN^\alpha \left[1 - \left(\frac{N}{k} \right)^\beta \right]^\gamma \quad (2.13)$$

where α , β and γ are positive real numbers. The emphasis is mostly on positive values for these parameters, as negative exponents do not always provide a biologically plausible model. Other growth models that follow come under extensions of generalised logistic growth model. Three main features that can be made out of the generalized logistic growth model are as follows:

- (i) $\lim_{t \rightarrow \infty} N(t) = k$, the population will ultimately reach its carrying capacity.
- (ii) the relative growth rate dN/Ndt attains its maximum value at N^* given by Equation (2.14)

$$N^* = \left(1 + \frac{\beta\gamma}{\alpha - 1} \right)^{-\left(\frac{1}{\beta}\right)} k \quad (2.14)$$

provided N^* is real and greater than N_0 , otherwise it declines non-linearly reaching its

minimum zero value at $N = k$. The maximum relative growth rate is given by Equation (2.15)

$$\left(\frac{1}{N} \frac{dN}{dt}\right)_{\max} = rk^{\alpha-1} \left(\frac{\alpha-1}{\alpha-1+\beta\gamma}\right)^{(\alpha-1)/\beta} \left(\frac{\beta\gamma}{\alpha-1+\beta\gamma}\right)^{\gamma} \quad (2.15)$$

Important limit values of N^* are

$$\lim_{\alpha \rightarrow 0} N^* = 0$$

$$\lim_{\beta \rightarrow 0} N^* = e^{\gamma/(1-\alpha)}$$

$$\lim_{\gamma \rightarrow 0} N^* = k$$

(iii) The population at the inflection point (where growth rate is maximum), is given by Equation (2.16)

$$N_{\text{inf}} = \left(1 + \frac{\beta\gamma}{\alpha}\right)^{-1/\beta} k > N^* \quad (2.16)$$

Few examples of growth equations that are derived from the generalised logistic growth model are considered below.

Von Bertalanffy's Growth Equation

Von Bertalanffy (1938) introduced his growth equation to model fish weight growth. Here the Verhulst logistic growth curve was modified to accommodate crude 'metabolic types' based upon physiological reasoning. He proposed the form given as Equation (2.17) which can be seen to be a special case of the Bernoulli differential equation

$$\frac{dN}{dt} = rN^{2/3} \left[1 - \left(\frac{N}{k}\right)^{1/3}\right] \quad (2.17)$$

which has the solution given as Equation (2.18)

$$N(t) = k \left[1 - \left[1 - \left(\frac{N_0}{k}\right)^{1/3}\right] e^{\left(\frac{r}{3k^{1/3}}\right)t}\right]^3 \quad (2.18)$$

Here, N_{inf} is given by Equation (2.19)

$$N_{\text{inf}} = \frac{8k}{27} \quad (2.19)$$

The time to inflection was found and represented as Equation (2.20)

$$t_{\text{inf}} = -\frac{3k^{1/3}}{r} \ln\left[\frac{1}{3}\right] + \frac{3k^{1/3}}{r} \ln\left[1 - \left(\frac{N_0}{k}\right)^{1/3}\right]$$

$$t_{\text{inf}} = \frac{3k^{1/3}}{r} \ln\left[3\left\{1 - \left(\frac{N_0}{k}\right)^{1/3}\right\}\right] \quad (2.20)$$

and the maximum growth rate was represented as Equation (2.21):

$$\left(\frac{dN}{dt}\right)_{\text{max}} = \frac{4}{27} rk^{2/3} \quad (2.21)$$

Richard's Growth Equation

Richard extended the growth equation developed by Von Bertalanffy to fit empirical plant data (Richards, 1959). In Richard's suggestion, he came up with Equation (3.22) which is also a special case of the Bernoulli differential equation:

$$\frac{dN}{dt} = rN\left[1 - \left(\frac{N}{k}\right)^\beta\right] \quad (2.22)$$

This has a solution given by Equation (2.23)

$$N(t) = \frac{kN_0}{\left[N_0^\beta + (k^\beta - N_0^\beta)e^{\beta rt}\right]^{1/\beta}} \quad (2.23)$$

Here, the inflection N_{inf} occurs at a value given by Equation (2.24)

$$N_{\text{inf}} = \left(\frac{1}{1+\beta}\right)^{1/\beta} k \quad (2.24)$$

Richard's form is readily deduced from generalised logistic function (2.13) with $\alpha = \gamma = 1$. For $\beta = 1$, Equation (2.22) trivially reduces to the Verhulst logistic growth equation (2.4) and similarly exhibits the same inflexible inflection point value.

Blumberg's Growth Equation

Blumberg (1968) introduced another growth equation based on a modification of the Verhulst logistic growth equation to model population dynamics of organ size evolution. He observed that the major limitation of the logistic curve was the inflexibility of the inflection point. He further observed that attempts to modify the constant intrinsic growth rate term r , treating this as a time-dependent polynomial to overcome this limitation, often led to under estimation of future values. Blumberg therefore introduced what he called the hyperlogistic function, given as Equation (2.25)

$$\frac{dN}{dt} = rN^\alpha \left(1 - \frac{N}{k}\right)^\gamma \quad (2.25)$$

Equation (2.25) was reformulated as the integral of the form given by Equation (2.26)

$$\int_{N_0/k}^{N(t)/k} x^\alpha (1-x) dx = rk^{\alpha-1} t \quad (2.26)$$

This does not always afford a closed form analytical solution for $\alpha < 1, \gamma < 1$. Blumberg therefore catalogued analytic expressions of the growth function $N(t)$ for various values of the parameters α and γ . The population at the inflection point, N_{inf} , was given by Equation (2.27)

$$N_{inf} = \frac{\alpha}{\alpha + \gamma} \quad (2.27)$$

This also coincides with that of the Verhulst logistic equation when $\alpha = \gamma = 1$. For $\alpha \gg \gamma$ the inflection occurs very near the carrying capacity, and for $\alpha \ll \gamma$, N_{inf} approaches 0 and inflection occurs only if $N_0 < N_{inf}$. Equation (2.25) is obtained by setting $\beta = 1$ in equation (2.13).

Schnute's Growth Equation

Schnute (1981), in his paper, suggested the use of the relative growth rate as the quantity of interest. Thus, if $z = (1/N)dN/dt$ is the relative growth rate, then $(1/Z)dZ/dt$ is the relative growth rate of the relative growth rate. Schnute's assumption was that $(1/Z)dZ/dt$ is a linear function of Z represented as Equation (2.28)

$$\frac{1}{Z} \frac{dZ}{dt} = -(a + bZ) \quad (2.28)$$

where a , b are positive, negative, or zero constants, and the minus sign on the right-hand side indicates that the growth rate typically decreases. For appropriate values of a , and b , some growth models can be derived from (2.28). In contrast, for the generalized logistic model (2.13), $(1/Z)dZ/dt$ has the following form given as Equation (2.29):

$$\frac{1}{Z} \frac{dZ}{dt} = Z \left[(\alpha + \beta\gamma - 1) - \beta\gamma r^{1/\gamma} N^{(\alpha-1)/\gamma} Z^{-(1/\gamma)} \right] \quad (2.29)$$

which clearly indicate that Equation (2.29) is not a linear function of Z , but rather of the form given as Equation (2.30)

$$\frac{1}{Z} \frac{dZ}{dt} = aZ + b(N)Z^c \quad (2.30)$$

where $a = \alpha + \beta\gamma - 1$ is a constant, b a function of N , and c a constant. From (2.29) with $\alpha = \beta = \gamma = 1$ one obtains the Verhulst logistic growth form given as Equation (2.31)

$$\frac{1}{Z} \frac{dZ}{dt} = Z \left(1 - \frac{r}{Z} \right) = Z - r \quad (2.31)$$

2.3.3 Environment Factors and Plant Resource Competition Dynamics

Another field of study under plant growth models in biology reviewed is associated with environment and plant resource competition. These run from the simple single-variable equation to the complex dynamic model which contain the form process of plant biomass. These models often pay more attention to the action of individual environment factors and plant competition for resources. Gates (1980) growth equation stressed the space interaction of the individual plants; McMartrie and Wolf (1983) considered the light use;

Walker *et al.* (1981) studied plant on the water use; Yin-ping *et al.* (2000) and Rui-hai *et al.* (2000) have studied the dynamic mechanism using the determined method. Olson (1985) and Sharpe *et al.* (1985) arose the Continuous-time Markov (CTM) approach in ecological view. These examples are few works associated with environment factors and plant resource dynamics.

In the early 1960s, there was a paradigm shift and studies on forest growth were more into the modelling of nutrient uptake as a key component for plant growth. Bouldin (1961) and Olsen *et al.* (1962), proposed mathematical models to simulate diffusion of solutes through soils, which were used to explain phosphate movement and uptake. Nye and Spiers (1964) subsequently developed the partial differential equations used to describe simultaneous mass flow and diffusion for nutrient uptake by a unit length of root. Nye and Marriot (1969) defined boundary conditions for the equations and solved them numerically, while Baldwin *et al.* (1973), on the other hand, solved the equations analytically with steady state approximations. Their work became the foundation for mechanistic nutrient uptake models. Building on this, Claassen and Barber (1976), Nye and Tinker (1977), Barber and Cushman (1981), Claassen *et al.* (1986), Smethurst and Comerford (1993), Yanai (1994), Smethurst *et al.* (2004), and Comerford *et al.* (2006) proposed model revisions to cover the major sub-processes of nutrient uptake and to accommodate a variety of additional conditions. Other researchers such as Wu *et al.* (1985), Wu *et al.* (1994) and Sharpe *et al.* (1985) modelled the physical growth of the forest by considering the influence of stem, crown and roots. Others just considered the effect of either one of the following: availability of light, surface water or nutrients to the growth of the tree and subsequently to the growth of the forest.

Rangel (1993) indicated that, two general models, empirical and mechanistic have been developed for such a study. The empirical model is based mainly on regression as well as statistical means, often for practical use (Classen and Steingrobe, 1999). The mechanistic model on the other hand, requires an understanding of the mechanisms and a quantitative description of the phenomena (Rengel, 1993). Mechanistic models were therefore considered useful to test the correctness of one's knowledge of the phenomena (Claassen and Steingrobe, 1999). Extrapolation of a verified mechanistic model was thus more reliable than that of an empirical model (Claassen and Steingrobe, 1999). The typical mechanistic nutrient uptake model describes the supply of nutrients from bulk soil to root surfaces, root growth and morphology, and root uptake kinetics (Barber, 1995).

In recent times, almost all vegetation modelling studies have been redirected to pattern formation. It is assumed that patterns form from a starting point of uniform vegetation, as a response to a decrease in mean annual rainfall and human activities. Many authors have additionally investigated the subsequent transitions between different patterned states when environmental conditions such as rainfall are varied (Meron, 2012; Gowda *et al.*, 2014). Studies on the vegetation is now concentrated on pattern formation. Vegetation patterns are examples of ecosystem-scale and self-organisation. In addition to this, they are very important and serve as a potential early warning signals of climate change and imminent regime shifts (Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007; Corrado *et al.*, 2014). Therefore, they have been the subject of intensive study over the last decade.

Vegetation patterns occur in many semi-arid regions of the world, including Africa (Deblauwe *et al.*, 2012; Müller, 2013), Australia (Berg and Dunkerley, 2004; Moreno-delas Heras *et al.*, 2012), North America (Pelletier *et al.*, 2012; Penny *et al.*, 2013), the Middle East (Buis *et al.*, 2009; Sheffer *et al.*, 2013), and Asia (Yizhaq *et al.*, 2014). Such patterns consist of vegetated regions separated by bare ground. They are usually labyrinthine or spotted on flat terrain, but on slopes the typical form is stripes running parallel to the contours, known as “banded vegetation” or “tiger bush” (Deblauwe *et al.*, 2008, 2011; Meron, 2012). Most authors also attributed the underlying cause of vegetation pattern formation to competition for water and positive feedback between vegetation and water availability. Some of the researchers in this field include Bel *et al.*, (2012). They investigated the formation and spread of isolated regions of patterned vegetation within an unvegetated background state, on flat terrain in semi-arid environment. Others including (Deblauwe *et al.*, 2012; Dralle *et al.*, 2014) in their study asserted that, slope can have a major effect on processes governed by water redistribution, due to the downhill flow of water both on the surface and within the soil.

In all, a number of hypotheses have been suggested about the origin of this vegetation pattern formation. Yet no consensus has been reached. For instance, Boaler and Hodge (1962), attributed the presence of vegetation stripes to the variation in texture of soil parent material. Belsky (1986), suggested that the initiation of the vegetation mosaics was caused by soil sodicity and salinity through differential leaching of salts from the sodic soils. Kellner and Bosch (1992), suggested that vegetation patterns in semi-arid grassland were created through selective grazing by herbivores. Thiery *et al.* (1995), demonstrated that

patterns such as those in tiger bush can be generated if plants are positively affected by lateral and downslope plants, but negatively affected by upslope plants. Jeltsch *et al.* (1997), related vegetation patterns to the interplay of factors such as competition, colonization and changes in the vegetation caused by fire and grazing. Similarly, Bromley *et al.* (1997), suggested that vegetation mosaics develop out of a complete cover of vegetation through the creation of patches by termites, grazing or fire. Lefever and Lejeune (1997), found vegetation mosaics resulting from the “interplay between short-range cooperative interactions controlling plants reproduction and long-range self-inhibitory interactions originating from plant competition for environmental resources.

2.4 The Primary Components of Growth

Growth results from the interaction of two opposing forces. The positive component, mostly manifested in expansion of an organism, represents the innate tendency towards exponential multiplication. This component is associated with biotic potential, photosynthetic activity, absorption of nutrients, constructive metabolism, anabolism and many others. The opposing component represents the restraints imposed by external (competition, limited resources, respiration and stress) and internal (self-regulatory mechanisms and aging) factors. Those factors that adversely affect growth have been referred to as environmental resistance, destructive metabolism, catabolism, respiration and so on.

Appropriately, laws or postulates of growth are often formulated in pairs that reflect both the multiplicative and limiting components. One of such is Hutchinson's (1978), two postulates of population growth stated as below:

- i. Every living organism has arisen from at least one parent in like kind (the postulate of parenthood);
- ii. In a finite space there is an upper limit to the number of finite beings that can occupy or utilize the space under consideration (the postulate of an upper limit). The relative growth rate is always decreasing (Minot's law).

The conflict between infinity implicit in multiplicative reproduction and the limit imposed by finite space is the chief source of all challenge in living being, including growth. This conflict is the driving force of evolution and is crucial to understanding virtually all

biological and social phenomena. Growth equations provide a succinct expression of this conflict and its resolution.

2.5 Review of Some Related Past Works

Theoretical studies have shown that, local interactions coupled by dispersal can cause non-uniform distributions of organisms to develop in the absence of underlying heterogeneity. Most of these studies have focused on interactions between animal populations, not on the interaction of plants and their abiotic resources. Klausmeier (1999), having observed a striking vegetation pattern of regular stripes on hillsides and irregular mosaic on flat ground developed a mathematical model of plant and water dynamics based on ecologically realistic assumptions and reasonable parameter values to study the conditions that led to such observations. He developed a model to investigate into the causes and effects. The developed model is given by Equation (2.32)

$$\left. \begin{aligned} \frac{\partial W}{\partial T} &= A - LW - RWN^2 + V \frac{\partial W}{\partial X} \\ \frac{\partial N}{\partial T} &= RJWN^2 - MN + D \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right) \end{aligned} \right\} \quad (2.32)$$

where T is the time coordinate, and (X, Y) represents the spatial domain. In order to narrow down to the causes and effects of his observations, the model Equation (2.32) was non-dimensionalised to obtain dimensionless model given by Equation (2.33)

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - w - wn^2 + v \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= wn^2 - mn + D \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \end{aligned} \right\} \quad (2.33)$$

The dimensionless model Equation (2.33) has only three parameters and these are: a , which controls water inputs, m , which measures plant losses; and v , which controls the rate at which water flows downhill. The two cases examined were hillside and flat ground. In his analysis it was found that, for given mortality rate m and water flow speed v , there is a critical value of water input a below which regular stripes form on the hillside. He further indicated that a potential explanation for the irregular mosaics is that slight topographic variation can lead to large variation in plant density. Thus, higher ground is left bare

whereas lower points support dense vegetation. Thus, the ecological dynamics amplify the underlying heterogeneity into a sharply differentiated mosaic. This hypothesis is supported by Belsky's observation that water flows from sparsely to densely vegetated patches in a grassland mosaic. It supports the verbal argument that water-plant dynamics can explain the formation and maintenance of striped vegetation patterns and suggests that irregular mosaics are most likely due to slight topographic variation. These results show that spatial pattern in ecological systems can result from both self-organization and amplification of underlying heterogeneity.

Rietkerk *et al.* (1997), by means of a bifurcation analysis of two mathematical models indicated how site specific properties determine the resilience of vegetation changes in semi-arid grazing systems. This concept of vegetation change came about as a result of more than a decade of thinking about resilience by Walker *et al.* (1981), and Noy-Meir (1982). Closely related to the definition of resilience, there has persisted the notion that grazing systems are intrinsically resilient because they have persisted for decades or more in Africa despite large and frequent environmental fluctuations (Ellis and Swift, 1988; Abel and Blaikie, 1989; Behnke and Scoones, 1992). To these authors, this meant that there is some sort of in-built resistance to land degradation to these systems and that vegetation change is mainly determined by rainfall variations and not by herbivory. This implies that when vegetation is drastically reduced as a result of intense herbivory during drought, it will nevertheless always recover if periods with higher rainfall follow. The two mathematical models that were presented by Rietkerk and his co-authors were water-limited model and nutrient-limited model. For the water-limited model, the rate of change of both plant density and soil water availability is presented by the system of differential Equation (2.34).

$$\left. \begin{aligned} \frac{dP}{dt} &= g(W)P - (d + b)P \\ \frac{dW}{dt} &= W_{in}(P) - c(W)P - r_w W \end{aligned} \right\} \quad (2.34)$$

where P and W denote plant density and soil water availability and $g(W)$ is specific plant growth as a function of soil water availability, d is specific plant loss due to mortality and b is specific plant loss due to herbivory. $W_{in}(P)$ describes water infiltration into the soil as a function of plant density. $c(W)$ is the specific soil water uptake by the plants as a

function of soil water availability and r_w is the specific soil water loss due to soil evaporation and deep percolation. In their presentation, they assumed that specific plant growth and specific soil water uptake are both saturation functions of soil water availability with Michaelis-Menten equation as an example of a saturation function. Thus, the specific plant growth was given by Equation (2.35)

$$g(W) = g_{\max} \frac{W}{W + k_1} \quad (2.35)$$

and the specific soil water uptake by plants was also given by Equation (2.36)

$$c(W) = c_{\max} \frac{W}{W + k_1} \quad (2.36)$$

where g_{\max} is the maximum specific plant growth, c_{\max} is the maximum specific soil water uptake by the plants and k_1 is a half saturation constant. The relationship between water infiltration into the soil and plant density was given by the authors based on (Walker *et al.*, 1981) by Equation (2.37)

$$W_{in}(P) = PPT \frac{P + k_2 W_0}{P + k_2} \quad (2.37)$$

where PPT stands for rainfall, W_0 is the minimum water infiltration in the absence of plant, and k_2 is a half saturation constant.

For the nutrient-limitation model, the rate of change of both plant density and soil nutrient availability is represented by the system of differential Equations (2.38).

$$\left. \begin{aligned} \frac{dP}{dt} &= g(N)P - (d + b)P \\ \frac{dN}{dt} &= N_{in} - c(N)P - r_N(P)N \end{aligned} \right\} \quad (2.38)$$

where P and N denote plant density and soil nutrient availability and $g(N)$ is specific plant growth as a function of soil nutrient availability, d is specific plant loss due to mortality and b is specific plant loss due to herbivory. N_{in} describes nutrient release from geochemical cycle which is considered independent of plant density. $c(N)$ is the net plant

specific soil nutrient loss as a function of soil nutrient availability and $r_N(P)$ is the specific soil nutrient loss due to water and wind erosion. Now in their presentation, they assumed that specific plant growth and specific nutrient release are both saturation functions of soil nutrient availability with Michaelis-Menten equation as an example of a saturation function. Thus, the specific plant growth as a function of soil nutrient availability was given by Equation (2.39)

$$g(N) = g_{\max} \frac{N}{N + k_1} \quad (2.39)$$

The parameter g_{\max} is the maximum specific plant growth, k_1 is a half saturation constant. $c(N)$ consists of two terms: the specific soil nutrient uptake by the plants as a Michaelis-Menten function of soil nutrient availability and the specific nutrient release from plant mortality. Specific plant growth increases linearly with increasing specific soil nutrient uptake and is at its maximum if the availability of soil nutrients permits maximum specific soil nutrient uptake. This can be written as Equation (2.40)

$$c(N) = c_{\max} \frac{N}{N + k_1} - d \frac{c_{\max}}{g_{\max}} \quad (2.40)$$

The parameter c_{\max} is the maximum specific soil water uptake by the plants. The factor $d \cdot c_{\max} / g_{\max}$ is the nutrient release as a consequence of plant mortality d whereby g_{\max} / c_{\max} is the C/N ratio of the plant material. The relationship between the specific soil nutrient loss due to water and wind erosion and plant density was given by the authors as Equation (2.41)

$$r_N(P) = r_{N,\max} \frac{k_2}{P + k_2} \quad (2.41)$$

where $r_{N,\max}(P)$ is the maximum specific soil nutrient loss when plant density is zero and k_2 is a half saturation constant. In their results by the water limitation model, it was indicated that the rate at which water infiltration increases with plant density (k_2), can be interpreted as the capacity of the vegetation to improve the structural and water-holding capacities of the soil. Clayey and sandy soils were two examples that were considered.

Their results indicate that herbivory is likely to trigger continuous and irreversible vegetation changes on soils with a low infiltration capacity. As a result, on clayey soil the vegetation will be neither resilient to herbivore impact nor to disturbances. Again, fluctuating rainfall may trigger discontinuous and irreversible changes in plant density if water infiltration in the absence of plant is relatively low. So under these conditions, the vegetation will not be resilient to fluctuating rainfall. In the case of nutrient limitation model, the rate at which specific nutrient loss decreases with plant density (k_2) can be interpreted as the nutrient retention capacity of the vegetation. Herbivory is likely to trigger continuous and irreversible vegetation changes in plant density on soils with a high erodibility. So on sandy soils, the vegetation will be neither resilient to herbivore impact nor to disturbances for certain ranges of herbivore action.

2.6 Summary of Review of Literature

Over the years, extensive research works have been conducted by several researchers in various parts of the world. The early studies on forests growth were basically on continuous population dynamics and the original research on growth models was attributed to Thomas Malthus (1798). He was therefore considered as the originator of growth models and asserted that, every population is considered to grow in size when the birth rate exceeds the death rate. He further proposed a model given by $dN/dt = rN$ where N is the population after some time t . dN/dt is the change in population with time and r is the intrinsic growth rate. Forty years later, Verhulst (1838), in his research on growth models, indicated that growth in general will be limited by over-consumption of resources and therefore, exponential growth for population size as indicated by Malthus is unrealistic over a long period. The works of Smith (1963), Pearl and Reed (1920), Turner *et al.* (1969; 1976), Nelder (1961) and Pearl (1920), are few examples of research works associated with continuous population dynamics.

Another field of study under plant growth models in biology is associated with environment and plant resource competition. These run from the simple single-variable equation to the complex dynamic model which contain the form process of plant biomass. These models often pay more attention to the action of individual environment factors and plant competition for resources. Gates (1980) growth equation stressed the space interaction of

the individual plants; McMartrie and Wolf *et al.* (1983), considered the light use; Walker *et al.* (1981), studied plant on the water use; Zhang Yin-ping *et al.* (2000) and Guo Rui-hai *et al.* (2000), also studied the dynamic mechanism using the determined method. Olson (1985) and Sharpe *et al.* (1985), used the Continuous-time Markov (CTM) approach in ecological view. These examples are few works associated with environment factors and plant resource dynamics.

This research however, seeks to model the dynamics of the forest by determining the influence of the interactions among these multiple resources such as light, water, temperature and nutrients on the growth, spread and vegetation pattern formation which had never been done in any of the literatures reviewed.



CHAPTER 3

THEORETICAL BACKGROUND AND SOME FUNDAMENTAL CONCEPTS

3.1 Preamble

This chapter discusses the definitions of some fundamental terms used in the thesis together with existing theories and methods. These include Markov process for synthesising multiple resource availability for growth, linearisation procedure based on the Taylor series expansion and on knowledge of nominal system trajectories and inputs. Others include Michaelis-Menten Kinetics used to model the rate of nutrients uptake by a cell of a plant and both local and global sensitivity analyses that emphasise how the behaviour of physical and chemical systems is affected by many parameters that characterise the system.

3.2 The Continuous-Time Markov Chain (CTMC)

A continuous-time Markov Chain $(X_t)_{t \geq 0}$ is defined by a finite or countable state space S , a transition matrix Q with dimensions equal to that of the state space for which the element q_{ij} for $i \neq j$ are non-negative and describe the rate of the process transitions from state i to state j . The elements q_{ii} are also chosen such that each row of the transition rate matrix sums to zero. A state j is said to be accessible from a state i (written $i \rightarrow j$) if it is possible to get to j from i , and this is indicated as Equation (3.1)

$$\Pr_i(X_t = j \text{ for some } t \geq 0) > 0 \quad (3.1)$$

These Markov chains are used to model interactions between components and therefore, many examples of dependencies among system components have been observed in practice and captured by Markov models. The interactions among the multiple resources such as light, water, temperature and nutrients were modelled by use of the Markov chains. They are considered as State-Space based models where the states represent various conditions of the system and the transitions between states indicate occurrences of events. An example of growth model in which continuous-time Markov chains has been used is “Dynamic model of crop growth system and numerical simulation of crop growth process under the multi-environment external force action” by Li *et al.* (2003).

CTMC is the type in which the time variable associated with the system evolution is continuous. It is characterised by state changes that can occur at any arbitrary time with a continuous index space. However, the state space is discrete valued. A CTMC can be completely described by an initial state probability vector for $X(t_0)$ given by Equation (3.2)

$$P(X(t_0)=k) \quad k=0,1,2,\dots \quad (3.2)$$

The transition probability functions (over an interval) are given by Equations (3.3) and (3.4)

$$P_{ij}(v,t) = P(X(t)=j | X(v)=i) \text{ for } 0 < v < t \text{ and } ij = 0,1,2,\dots \quad (3.3)$$

$$P_{ij}(t,t) = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{otherwise} \end{cases} \text{ and } \sum_{j \in I} P_{ij}(v,t) = 1 \quad \forall i; \quad 0 < v < t \quad (3.4)$$

3.2.1 The Transition Rate Matrix

A transition rate matrix (also known as an intensity matrix or infinitesimal generator matrix) is defined in probability theory as an array of numbers describing the rate a continuous time Markov chain moves between states. The elements of the transition rate matrix Q , given by q_{ij} for $i \neq j$ denotes the rate departing from state i and arriving in state j and the diagonal elements q_{ii} are defined as indicated by Equation (3.5)

$$q_{ii} = -\sum_{j \neq i} q_{ij} \quad (3.5)$$

and therefore the rows of the matrix sum to zero. This matrix is a fundamental quantity associated with the continuous-time Markov chain $\{X(t):t \geq 0\}$ and it is also called the infinitesimal generator, or simply generator, of the chain. Suppose g_{ij} denote the (i,j) th entry of generator matrix G , then the off-diagonal entries of G are represented by Equation (3.6)

$$g_{ij} = q_{ij} \text{ for } i \neq j \quad (3.6)$$

and the diagonal entries are represented by Equation (3.7)

$$g_{ii} = -v_i \quad (3.7)$$

The generator matrix G contains all the rate information for the chain and, even though its entries are not probabilities, it is the counterpart of the one-step transition probability matrix P for discrete time Markov chains. According to Kolmogorov's (1931) Backward equations, if one had conditioned on $X(t)$ instead of $X(h)$, one would have derived another set of differential equations called Kolmogorov's Forward equations, which in matrix form are given by Equation (3.8)

$$P'(t) = P(t)G \quad (3.8)$$

For both the backward and the forward equations, the common boundary condition used is given by Equation (3.9)

$$P(0) = I \quad (3.9)$$

where I is the $|S| \times |S|$ multiplicative identity matrix. For an identity matrix, if $i = j$ then the boundary condition satisfies the expression given in Equation (3.10)

$$P_{ii}(0) = P(X(0) = i | X(0) = i) = 1 \quad (3.10)$$

and, for $i \neq j$, it is given as in Equation (3.11)

$$P_{ij}(0) = P(X(0) = j | X(0) = i) = 0 \quad (3.11)$$

3.2.2 Properties of Continuous-Time Markov Chains

Though the backward and forward equations are two different sets of differential equations, with the above boundary condition given by Equation (3.9), they have the same solution, given by Equation (3.12)

$$P(t) = e^{tG} = \sum_{n=0}^{\infty} \frac{(tG)^n}{n!} \quad (3.12)$$

where n is an integer.

The expanded form of Equation (3.12) is given by Equation (3.13) where I is the multiplicative identity matrix.

$$P(t) = I + tG + \frac{(tG)^2}{2!} + \frac{(tG)^3}{3!} + \frac{(tG)^4}{4!} + \dots + \dots \quad (3.13)$$

It must be noted that the notation e^{tG} is meaningless except as shorthand notation for the infinite sum above. To see that the above satisfies the backward equations one will simply plug it into the differential equations and check that it solves them. Differentiating with respect to t , one get Equation (3.14)

$$P'(t) = \frac{d}{dt} e^{tG} = \frac{d}{dt} \sum_{n=0}^{\infty} \frac{(tG)^n}{n!} \quad (3.14)$$

In its expanded form, Equation (3.14) leads to Equation (3.15)

$$\begin{aligned} P'(t) &= G + tG^2 + \frac{t^2G^3}{2!} + \frac{t^3G^4}{3!} + \frac{t^4G^5}{4!} + \dots + \dots \\ &= G \left[I + tG + \frac{t^2}{2!}G^2 + \frac{t^3}{3!}G^3 + \dots + \dots \right] \\ &= GP(t) \end{aligned} \quad (3.15)$$

and, $P(0) = I$ is clearly satisfied. Moreover, one could also have written the expanded form as Equation (3.16)

$$\begin{aligned} P'(t) &= \left[I + tG + \frac{(tG)^2}{2!} + \frac{(tG)^3}{3!} + \dots + \dots \right] G \\ &= P(t)G \end{aligned} \quad (3.16)$$

Thus, even though one cannot normally obtain $P(t)$ in an explicit closed form, the infinite sum representation e^{tG} is general, and can be used to obtain numerical approximations to $P(t)$ if $|S|$ is finite, by truncating the infinite sum to a finite sum. In some text, the notation R is used for the generator matrix, presumably to stand for the Rate matrix. However, in this thesis, the notation G which is more common will be adopted, and the terminology “generator matrix” or “infinitesimal generator matrix” as standard.

The solution $P(t) = e^{tG}$ shows how basic the generator matrix G is to the properties of a continuous-time Markov chain. It can be shown that the generator matrix G is also the key quantity for determining the stationary distribution of the chain. First, one can define what is meant by a stationary distribution for a continuous-time Markov chain.

3.2.3 Stationary Distributions

Let $\{X(t) : t \geq 0\}$ be a continuous-time Markov chain with state space S , generator matrix G , and matrix transition probability function $P(t)$. An $|S|$ -dimensional row vector $\pi = (\pi_i)_{i \in S}$ with $\pi_i \geq 0$ for all i and $\sum_{i \in S} \pi_i = 1$, is said to be a stationary distribution if $\pi = \pi P(t)$ for all $t \geq 0$.

Thus, a vector π which satisfies $\pi = \pi P(t)$ for all $t \geq 0$ is called a stationary distribution. This makes the process stationary. That is, if one sets the initial distribution of $X(0)$ to be such a π , then the distribution of $X(t)$ will also be π for all $t > 0$. That is $P(X(t) = j) = \pi_j$ for all $j \in S$ and all $t > 0$. To see this, set the initial distribution of $X(0)$ to be π and compute $P(X(t) = j)$ by conditioning on $X(0)$. This gives Equation (3.17)

$$\begin{aligned} P(X(t) = j) &= \sum_{i \in S} P(X(t) = j | X(0) = i) P(X(0) = i) \\ &= \sum_{i \in S} P_{ij}(t) \pi_i = [\pi P(t)]_j = \pi_j \end{aligned} \quad (3.17)$$

It must be noted that, the relation between the generator matrix G and the definition of a stationary distribution can be represented as equivalence Equation (3.18)

$$\Leftrightarrow \pi = \pi P(t) \text{ for all } t \geq 0 \quad (3.18)$$

$P(t)$ in the definition of π in Equation (3.18) can be replaced with e^{tG} . By so doing, one obtains an equivalence as Equation (3.19)

$$\Leftrightarrow \pi = \pi \sum_{n=0}^{\infty} \frac{(tG)^n}{n!} \text{ for all } t \geq 0 \quad (3.19)$$

Rewriting Equation (3.19) with the summation sign starting from $n=1$ gives Equation (3.20)

$$\Leftrightarrow \pi = \pi + \pi \sum_{n=1}^{\infty} \frac{(tG)^n}{n!} \text{ for all } t \geq 0 \quad (3.20)$$

Equation (3.20) then simplifies to Equation (3.21)

$$\Leftrightarrow 0 = \sum_{n=1}^{\infty} \frac{t^n}{n!} \pi G^n \text{ for all } t \geq 0 \quad (3.21)$$

For $n \geq 1$, Equation (3.21) converges to Equation (3.22)

$$\Leftrightarrow 0 = \pi G^n \text{ for all } n \geq 1 \quad (3.22)$$

And finally settles as Equation (3.23)

$$\Leftrightarrow 0 = \pi G \quad (3.23)$$

To be convinced that the implications are true in both directions in each of the lines above, it could be seen that the condition $\pi = \pi P(t)$ for all $t \geq 0$, which would be quite difficult to check, reduces to the much simpler condition $0 = \pi G$ in terms of the generator matrix G . The equation $0 = \pi G$ is a set of $|S|$ linear equations which, together with the normalization constraint $\sum_{i \in S} \pi_i = 1$ determines the stationary distribution π if one exists.

The j th equation in $0 = \pi G$ is given by Equation (3.24)

$$0 = -v_j \pi_j + \sum_{i \neq j} q_{ij} \pi_i \quad (3.24)$$

and Equation (3.24) is equal to Equation (3.25)

$$\pi_j v_j = \sum_{i \neq j} \pi_i q_{ij} \quad (3.25)$$

This Equation (3.25) has the following interpretation. On the left-hand side, π_j is the long run proportion of time that the process is in state j , while v_j is that rate of leaving state j when the process is in state j . Thus, the product $\pi_j v_j$ is interpreted as the long run rate of leaving state j . On the right hand side, q_{ij} is the rate of going to state j when the process is in state i , so the product $\pi_i q_{ij}$ is interpreted as the long run rate of going from state i to state j . Summing overall $i \neq j$ then gives the long run rate of going to state j given by Equation (3.26)

$$\pi_j v_j = \sum_{i \neq j} \pi_i q_{ij} \quad (3.26)$$

The Equation (3.26) is interpreted as “the long run rate out of state j” equals “the long run rate into state j”. For this reason, the equations $\pi G=0$ are called the Global Balance Equations, or just Balance Equations. Equation (3.26) expresses the fact that when the process is made stationary, there must be equality, or balance, in the long run rates into and out of any state.

3.3 Linearisation of Nonlinear Systems

Consider the linearisation of systems described by nonlinear partial differential equations. The procedure is based on the Taylor series expansion and on knowledge of nominal system trajectories and nominal system inputs. Suppose one has a simple scalar first-order nonlinear dynamic system given by Equation (3.27)

$$\frac{\partial x}{\partial t} = F(x(t), f(t)), \quad x(t_0) \text{ given} \quad (3.27)$$

Assume that this system operates along the trajectory $x_n(t)$ while it is driven by the system input $f_n(t)$. $x_n(t)$ and $f_n(t)$ are the nominal system trajectory and the nominal system input respectively. On the nominal trajectory the partial differential equation in Equation (3.28) is satisfied

$$\frac{\partial x_n(t)}{\partial t} = F(x_n(t), u_n(t)) \quad (3.28)$$

Assume that the motion of the nonlinear system is in the neighbourhood of the nominal system trajectory given by (3.29),

$$x(t) = x_n(t) + \Delta x(t) \quad (3.29)$$

where $\Delta x(t)$ represents a small quantity. It is natural for one to assume that the system motion in close proximity to the nominal trajectory will be sustained by a system input which is obtained by adding a small quantity to the nominal system input given by Equation (3.30)

$$f(t) = f_n(t) + \Delta f(t) \quad (3.30)$$

For the system motion in close proximity to the nominal trajectory, one obtains Equations (3.31)

$$\frac{\partial x_n(t)}{\partial t} + \Delta \dot{x}(t) = F(x_n(t) + \Delta x(t), f_n(t) + \Delta f(t)) \quad (3.31)$$

Since $\Delta x(t)$ and $\Delta f(t)$ are small quantities, the right-hand side can be expanded into a Taylor series about the nominal system trajectory and input, which produces Equation (3.32)

$$\frac{\partial x_n(t)}{\partial t} + \Delta \dot{x}(t) = F(x_n, f_n) + \frac{\partial F}{\partial x}(x_n, f_n)\Delta x(t) + \frac{\partial F}{\partial f}(x_n, f_n)\Delta f(t) + \text{higher-order terms} \quad (3.32)$$

Cancelling higher-order terms (which contain very small quantities $\Delta x^2, \Delta f^2, \Delta x\Delta f, \Delta x^3, \dots$), the linear partial differential equation is obtained as Equation (3.33)

$$\Delta \dot{x}(t) = \frac{\partial F}{\partial x}(x_n, f_n)\Delta x(t) + \frac{\partial F}{\partial f}(x_n, f_n)\Delta f(t) \quad (3.33)$$

The partial derivatives in the linearisation procedure are evaluated at the nominal points. Introducing the notation given by Equation (3.34)

$$a_0 = -\frac{\partial F}{\partial x}(x_n, f_n) \quad b_0 = \frac{\partial F}{\partial f}(x_n, f_n) \quad (3.34)$$

the linearised system can be represented as Equation (3.35)

$$\Delta \dot{x}(t) + a_0(t)\Delta x(t) = b_0(t)\Delta f(t) \quad (3.35)$$

In general, the obtained linear system is time varying. One will therefore consider situations for which the linearisation procedure produces time invariant systems. The initial condition for the linearised system can be obtained from Equation (3.36)

$$\Delta x(t_0) = x(t_0) - x_n(t_0) \quad (3.36)$$

Similarly, one can linearise the second-order nonlinear dynamic system given by Equation (3.37)

$$\frac{\partial^2 x}{\partial t^2} = F\left(x(t), \frac{\partial x}{\partial t}, f(t), \frac{\partial f}{\partial t}\right), \quad x(t_0) \quad \frac{\partial x(t_0)}{\partial t} \text{ given} \quad (3.37)$$

by assuming Equations (3.38) and (3.39)

$$x(t) = x_n(t) + \Delta x(t) \quad \frac{\partial x(t)}{\partial t} = \frac{\partial x_n(t)}{\partial t} + \Delta \dot{x}(t) \quad (3.38)$$

$$f(t) = f_n(t) + \Delta f_n(t) \quad \frac{\partial f(t)}{\partial t} = \frac{\partial f_n(t)}{\partial t} + \Delta \dot{f}(t) \quad (3.39)$$

By expanding Equation (3.40)

$$\frac{\partial^2 x_n(t)}{\partial t^2} + \Delta \ddot{x}(t) = F \left(x_n + \Delta x_n, \frac{\partial x_n(t)}{\partial t} + \Delta \dot{x}, f_n + \Delta f, \frac{\partial f_n}{\partial t} + \Delta \dot{f} \right) \quad (3.40)$$

into a Taylor series about nominal points $x_n, \partial x_n(t)/\partial t, f_n, \partial f_n/\partial t$ leads to Equation (3.41)

$$\Delta \ddot{x}(t) + a_1(t) \Delta \dot{x}(t) + a_0(t) \Delta x(t) = b_1(t) \Delta \dot{f}(t) + b_0(t) \Delta f(t) \quad (3.41)$$

where the corresponding coefficients are evaluated at the nominal points given by Equations (3.42) and (3.43)

$$a_1 = \frac{\partial F}{\partial \dot{x}} \left(x_n, \frac{\partial x_n(t)}{\partial t}, f_n, \frac{\partial f_n}{\partial t} \right) \quad a_0 = - \frac{\partial F}{\partial x} \left(x_n, \frac{\partial x_n(t)}{\partial t}, f_n, \frac{\partial f_n}{\partial t} \right) \quad (3.42)$$

$$b_1 = \frac{\partial F}{\partial \dot{f}} \left(x_n, \frac{\partial x_n(t)}{\partial t}, f_n, \frac{\partial f_n}{\partial t} \right) \quad b_0 = \frac{\partial F}{\partial f} \left(x_n, \frac{\partial x_n(t)}{\partial t}, f_n, \frac{\partial f_n}{\partial t} \right) \quad (3.43)$$

The initial conditions for the second-order linearised system are obtained from Equation (3.44)

$$\Delta x(t_0) = x(t_0) - x_n(t_0), \quad \Delta \dot{x}(t_0) = \frac{\partial x(t_0)}{\partial t} - \frac{\partial x_n(t_0)}{\partial t} \quad (3.44)$$

The linearisation procedure to an n-order nonlinear dynamic system with one input and one output can be extended in straightforward way. However, for multi-input multi-output systems this procedure becomes cumbersome. Using the state space model, the linearisation procedure for the multi-input multi-output case is simplified.

Consider the general nonlinear dynamic control system in matrix form given by Equation (3.45)

$$\frac{d}{dt} x(t) = F(x(t), f(t)) \quad x(t_0) \text{ given} \quad (3.45)$$

where $x(t)$, $f(t)$, and F are respectively, the n-dimensional system state space vector, the r-dimensional input vector, and the n-dimensional vector function. Assume that the nominal (operating) system trajectory $x_n(t)$ is known and that the nominal system input that keeps the system on the nominal trajectory is given by $f_n(t)$. Using the same logic as for the scalar case, one can assume that the actual system dynamics in the immediate proximity of the system nominal trajectories by approximating the first terms of the Taylor series. Thus, one starts with Equations (3.46) and (3.47) respectively

$$x(t) = x_n(t) + \Delta x(t), \quad f(t) = f_n(t) + \Delta f(t) \quad (3.46)$$

$$\frac{d}{dt} x(t) = F(x_n(t), f_n(t)) \quad (3.47)$$

Expanding the right-hand side into a Taylor series yields Equation (3.48) and its simplified form as Equation (3.49)

$$\frac{dx_n(t)}{dt} + \frac{d}{dt} \Delta x(t) = F(x_n(t) + \Delta x(t), f_n(t) + \Delta f(t)) \quad (3.48)$$

$$= F(x_n, f_n) + \left(\frac{\partial F}{\partial x} \right) \Big|_{x_n(t), f_n(t)} \Delta x(t) + \left(\frac{\partial F}{\partial f} \right) \Big|_{x_n(t), f_n(t)} \Delta f(t) + \text{higher-order terms} \quad (3.49)$$

Higher-order terms contain at least quadratic quantities of Δx and Δf . Since Δx and Δf are small, their squares are even much smaller, and hence the high-order terms can be neglected. Neglecting higher-order terms, Equation (3.50) is obtained

$$\frac{d}{dt} \Delta x(t) = \left(\frac{\partial F}{\partial x} \right) \Big|_{x_n(t), f_n(t)} \Delta x(t) + \left(\frac{\partial F}{\partial f} \right) \Big|_{x_n(t), f_n(t)} \Delta f(t) \quad (3.50)$$

The partial derivatives represent the Jacobian matrices given by Equations (3.51) and (3.52)

$$= \left(\frac{\partial F}{\partial x} \right) \Big|_{x_n(t), f_n(t)} = A(n \times n) = \begin{bmatrix} \frac{\partial F_1}{\partial x_1} & \frac{\partial F_1}{\partial x_2} & \dots & \dots & \frac{\partial F_1}{\partial x_n} \\ \frac{\partial F_2}{\partial x_1} & \frac{\partial F_2}{\partial x_2} & \dots & \dots & \frac{\partial F_2}{\partial x_n} \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \frac{\partial F_n}{\partial x_1} & \frac{\partial F_n}{\partial x_2} & \dots & \dots & \frac{\partial F_n}{\partial x_n} \end{bmatrix} \Big|_{x_n(t), f_n(t)} \quad (3.51)$$

$$= \left(\frac{\partial F}{\partial f} \right) \Big|_{x_n(t), f_n(t)} = B(n \times r) = \begin{bmatrix} \frac{\partial F_1}{\partial f_1} & \frac{\partial F_1}{\partial f_2} & \dots & \dots & \frac{\partial F_1}{\partial f_r} \\ \frac{\partial F_2}{\partial f_1} & \frac{\partial F_2}{\partial f_2} & \dots & \dots & \frac{\partial F_2}{\partial f_r} \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \frac{\partial F_n}{\partial f_1} & \frac{\partial F_n}{\partial f_2} & \dots & \dots & \frac{\partial F_n}{\partial f_r} \end{bmatrix} \Big|_{x_n(t), f_n(t)} \quad (3.52)$$

The Jacobian matrices are evaluated at the nominal points, that is, at $x_n(t)$ and $f_n(t)$. The linearised system to Equation (3.50) has the form given by Equation (3.53)

$$\frac{d}{dt} \Delta x(t) = A \Delta x(t) + B \Delta u(t) \quad \Delta x(t_0) = x(t_0) - x_n(t_0) \quad (3.53)$$

The output of a nonlinear system satisfies a nonlinear algebraic equation of the form given by Equation (3.54)

$$y(t) = G(x(t), f(t)) \quad (3.54)$$

This equation can also be linearised by expanding its right-hand side into a Taylor series about nominal points $x_n(t)$ and $f_n(t)$. This leads to Equation (3.55)

$$y_n + \Delta y = G(x_n, f_n) + \left(\frac{\partial G}{\partial x} \right) \Big|_{x_n(t), f_n(t)} \Delta x(t) + \left(\frac{\partial G}{\partial f} \right) \Big|_{x_n(t), f_n(t)} \Delta f(t) + \text{higher-order terms} \quad (3.55)$$

It must be noted from Equation (3.54) that, $y_n(t)$ cancels the term $G(x_n(t), f_n(t))$ in Equation (3.55). By neglecting higher-order terms, the linearised part of the output Equation (3.55) is given by Equation (3.56)

$$\Delta y(t) = C\Delta x(t) + D\Delta f(t) \quad (3.56)$$

where the Jacobian matrices C and D are indicated by Equations (3.57) and (3.58)

$$= \left(\frac{\partial G}{\partial x} \right) \Big|_{x_n(t), f_n(t)} = C(p \times n) = \begin{bmatrix} \frac{\partial G_1}{\partial x_1} & \frac{\partial G_1}{\partial x_2} & \dots & \dots & \frac{\partial G_1}{\partial x_n} \\ \frac{\partial G_2}{\partial x_1} & \frac{\partial G_2}{\partial x_2} & \dots & \dots & \frac{\partial G_2}{\partial x_n} \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \frac{\partial G_p}{\partial x_1} & \frac{\partial G_p}{\partial x_2} & \dots & \dots & \frac{\partial G_p}{\partial x_n} \end{bmatrix} \Big|_{x_n(t), f_n(t)} \quad (3.57)$$

$$= \left(\frac{\partial G}{\partial f} \right) \Big|_{x_n(t), f_n(t)} = D(p \times r) = \begin{bmatrix} \frac{\partial F_1}{\partial f_1} & \frac{\partial F_1}{\partial f_2} & \dots & \dots & \frac{\partial F_1}{\partial f_r} \\ \frac{\partial F_2}{\partial f_1} & \frac{\partial F_2}{\partial f_2} & \dots & \dots & \frac{\partial F_2}{\partial f_r} \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \frac{\partial F_p}{\partial f_1} & \frac{\partial F_p}{\partial f_2} & \dots & \dots & \frac{\partial F_p}{\partial f_r} \end{bmatrix} \Big|_{x_n(t), f_n(t)} \quad (3.58)$$

3.4 Michaelis-Menten Kinetics

An expression widely used to model the rate of nutrient uptake by a cell follows what is known as Michaelis-Menten kinetics. According to Michaelis and Menten (1913), the rate of change of the nutrients concentration $N(t)$ used by a cell for growth and development is modeled by the differential equation given by Equation (3.59)

$$\frac{dN}{dt} = -K(N) = -\frac{k_{\max} N}{k_N + N} \quad (3.59)$$

where k_{\max} is the maximum rate of uptake of nutrient by the tree and k_N is the half-saturation constant, that is, the amount of nutrient such that $K(N) = \frac{k_{\max}}{2}$. The rate of growth $K(N)$ from Michaelis-Menten kinetics is also referred to as Michaelis-Menten-Monod kinetics (Smith and Waltman, 1995).

3.4.1 Description of Nutrient-Cell Plant Growth

A brief description of how nutrients enter the cell of the root of a tree and contribute to the growth of the tree is made by Edelstein-Keshet, (1988). Nutrient molecules N (substrate) enter the tree cell membrane by attaching to membrane-bound receptors x . If a nutrient molecule is captured by a cell of the tree, it is denoted as p for the product. The notation x_0 denotes a receptor not occupied by a nutrient molecule. x_1 denotes a receptor occupied by a nutrient molecule (or a complex formed from the tree and the nutrient molecule), and the resulting product is denoted by p . The following relationships summarize the direction and the rates of the reactions. This is given by Equation (3.60)



where the constants $k_i, i = -1, 1, 2$ are the rate constants. The arrows indicate that, the first reaction is reversible. An occupied receptor can lose the nutrient molecule before the nutrient molecule is captured by the tree cell. The reaction relationships between the molecules can be expressed as differential equations. Consider the law of mass action which states that, the rate of reaction between two quantities is proportional to the product of their concentrations, and let the variables N, x_0, x_1 and p denote the concentrations (average number per unit volume) of nutrient, unbound receptors, bound receptors and product respectively. The differential equations for these four variables are given by Equations (3.61), (3.62), (3.63) and (3.64)

$$\frac{dN}{dt} = -k_1 N x_0 + k_{-1} x_1 \quad (3.61)$$

$$\frac{dx_0}{dt} = -k_1 N x_0 + k_{-1} x_1 + k_2 x_1 \quad (3.62)$$

$$\frac{dx_1}{dt} = k_1 N x_0 - k_{-1} x_1 - k_2 x_1 \quad (3.63)$$

$$\frac{dp}{dt} = k_2 x_1 \quad (3.64)$$

(Edelstein-Keshet, 1988). It can be seen from Equations (3.62) and (3.63) that the total concentration of receptor cells is constant and can be represented as Equation (3.65)

$$\frac{dx_0}{dt} + \frac{dx_1}{dt} = 0 \quad (3.65)$$

Let $r = x_0 + x_1$ where r is the sum of the unbounded and bounded receptors and if one replaces x_0 in the differential equations for N and x_1 by $x_0 = r - x_1$, it follows that only differential equations for N and x_1 need to be considered. The differential equation for the product concentration p can be solved after the solution for x_1 is found. Simplifying the differential equations for N and x_1 yields Equations (3.66) and (3.67)

$$\frac{dN}{dt} = -k_1 r N + (k_{-1} + k_1 N) x_1 \quad (3.66)$$

$$\frac{dx_1}{dt} = k_1 r N - (k_{-1} + k_2 + k_1 N) x_1 \quad (3.67)$$

The nutrient concentration is usually much higher than the receptor concentration. The receptors work at maximum capacity so that their occupancy rate is approximately constant. Therefore, it is reasonable to make the assumption that $\frac{dx_1}{dt} = 0$. This assumption is known as the quasi-equilibrium hypothesis. From this assumption the equation for Michaelis-Menten kinetics is generated. Thus, let $\frac{dx_1}{dt} = 0$, then Equation (3.67) yields Equation (3.68)

$$k_1 r N - (k_{-1} + k_1 N) x_1 = k_2 x_1 \quad (3.68)$$

and Equation (3.66) reduces to Equation (3.69)

$$\frac{dN}{dt} = -k_2 x_1 \quad (3.69)$$

$$= -\frac{k_2 k_1 r N}{k_{-1} + k_2 + k_1 N} \quad (3.70)$$

$$= -\frac{k_2 r N}{\frac{k_{-1} + k_2}{k_1} + N} \quad (3.71)$$

$$\frac{dN}{dt} = -\frac{k_{\max} N}{k_N + N} \quad (3.72)$$

where $k_{\max} = k_2 r$ and $k_N = \frac{k_{-1} + k_2}{k_1}$.

3.5 Finite Difference Method

The finite difference method offers a more direct approach to the numerical solution of partial differential equations compared to most of the methods based on other formulations (Sauer, 2011). It consists of replacing each derivative by a difference quotient in its formulation. The method consists of different schemes (Forward, Backward and Central Schemes).

3.5.1 The Finite Difference Formula

Given the function $u(x, y, t)$, the first partial derivative of $u(x, y, t)$ with respect to x can be defined in one of the following ways as shown in equation (3.73)

$$\left. \begin{aligned} \frac{\partial u(x, y, t)}{\partial x} &= \lim_{\Delta x \rightarrow 0} \frac{u(x + \Delta x, y, t) - u(x, y, t)}{\Delta x} \\ \frac{\partial u(x, y, t)}{\partial x} &= \lim_{\Delta x \rightarrow 0} \frac{u(x, y, t) - u(x - \Delta x, y, t)}{\Delta x} \\ \frac{\partial u(x, y, t)}{\partial x} &= \lim_{\Delta x \rightarrow 0} \frac{u(x + \Delta x, y, t) - u(x - \Delta x, y, t)}{2\Delta x} \end{aligned} \right\} \quad (3.73)$$

Applying the Taylor series expansion for $u(x + \Delta x, y, t)$ about $u(x, y, t)$, yields Equation (3.74),

$$u(x + \Delta x, y, t) = u(x, y, t) + \frac{\partial u(x, y, t)}{\partial x} \cdot (\Delta x) + \frac{\partial^2 u(x, y, t)}{\partial x^2} \cdot \frac{(\Delta x)^2}{2!} + o((\Delta x)^2) \quad (3.74)$$

which can be simplified to Equation (3.75)

$$\frac{\partial u(x, y, t)}{\partial x} = \frac{u(x + \Delta x, y, t) - u(x, y, t)}{\Delta x} - \frac{\partial^2 u(x, y, t)}{\partial x^2} \cdot \frac{(\Delta x)}{2} \quad (3.75)$$

For linear approximation of $u(x + \Delta x, y, t)$, the terms of order $(\Delta x)^2$ and higher orders are dropped to obtain Equation (3.76)

$$\frac{\partial u(x, y, t)}{\partial x} = \frac{u(x + \Delta x, y, t) - u(x, y, t)}{\Delta x} \quad (3.76)$$

The equation (3.76) is referred to as the *forward difference formula* and approximates the derivative $\frac{\partial u}{\partial x}$ with error of the first order in Δx . Similarly, from the second equation in

Equation (3.73), one obtains Equation (3.77)

$$\frac{\partial u(x, y, t)}{\partial x} = \frac{u(x, y, t) - u(x - \Delta x, y, t)}{\Delta x} \quad (3.77)$$

The equation (3.77) is called the *backward difference formula*.

Next, applying the Taylor series expansion with remainders involving a third partial derivative of the function u gives equations (3.78) and (3.79)

$$\begin{aligned} u(x + \Delta x, y, t) = & u(x, y, t) + \frac{\partial u(x, y, t)}{\partial x} \cdot (\Delta x) + \frac{\partial^2 u(x, y, t)}{\partial x^2} \cdot \frac{(\Delta x)^2}{2!} \\ & + \frac{\partial^3 u(x, y, t)}{\partial x^3} \cdot \frac{(\Delta x)^3}{3!} + o((\Delta x)^3) \end{aligned} \quad (3.78)$$

$$\begin{aligned} u(x - \Delta x, y, t) = & u(x, y, t) - \frac{\partial u(x, y, t)}{\partial x} \cdot (\Delta x) + \frac{\partial^2 u(x, y, t)}{\partial x^2} \cdot \frac{(\Delta x)^2}{2!} \\ & - \frac{\partial^3 u(x, y, t)}{\partial x^3} \cdot \frac{(\Delta x)^3}{3!} + o((\Delta x)^3) \end{aligned} \quad (3.79)$$

Subtracting Equation (3.79) from Equation (3.78) yields Equation (3.80)

$$\begin{aligned} \frac{\partial u(x, y, t)}{\partial x} = & \frac{u(x + \Delta x, y, t) - u(x - \Delta x, y, t)}{2\Delta x} \\ & + \left(\frac{\partial^3 u(x, y, t)}{\partial x^3} + \frac{\partial^3 u(x, y, t)}{\partial x^3} \right) \cdot \frac{(\Delta x)^3}{3!} \end{aligned} \quad (3.80)$$

But for first difference approximation, higher derivative goes to zero. Hence, the Equation (3.80) reduces to Equation (3.81)

$$\frac{\partial u(x, y, t)}{\partial x} = \frac{u(x + \Delta x, y, t) - u(x - \Delta x, y, t)}{2\Delta x} \quad (3.81)$$

The equation (3.81) is referred to as the *central difference formula*.

For the second difference approximation indicated by Equations (3.82) and (3.83)

$$\begin{aligned} u(x + \Delta x, y, t) = & u(x, y, t) + \frac{\partial u(x, y, t)}{\partial x} \cdot (\Delta x) + \frac{\partial^2 u(x, y, t)}{\partial x^2} \cdot \frac{(\Delta x)^2}{2!} + \\ & \frac{\partial^3 u(x, y, t)}{\partial x^3} \cdot \frac{(\Delta x)^3}{3!} + \frac{\partial^4 u(x, y, t)}{\partial x^4} \cdot \frac{(\Delta x)^4}{4!} + o((\Delta x)^4) \end{aligned} \quad (3.82)$$

$$\begin{aligned} u(x - \Delta x, y, t) = & u(x, y, t) - \frac{\partial u(x, y, t)}{\partial x} \cdot (\Delta x) + \frac{\partial^2 u(x, y, t)}{\partial x^2} \cdot \frac{(\Delta x)^2}{2!} + \\ & \frac{\partial^3 u(x, y, t)}{\partial x^3} \cdot \frac{(\Delta x)^3}{3!} + \frac{\partial^4 u(x, y, t)}{\partial x^4} \cdot \frac{(\Delta x)^4}{4!} + o((\Delta x)^4) \end{aligned} \quad (3.83)$$

subtracting equation (3.83) from equation (3.82), and letting higher derivative other than second order derivative goes to zero, one obtains equation as (3.84) below

$$\frac{\partial^2 u(x, y, t)}{\partial x^2} = \frac{u(x + \Delta x, y, t) - 2u(x, y, t) + u(x - \Delta x, y, t)}{(\Delta x)^2} \quad (3.84)$$

The equation (3.84) is referred to as the centred second difference formula. In subscript or grid notation, Equations (3.76), (3.77), (3.81) and (3.84) become

- (i) The Forward Difference: $(u_x)_{i,j} \approx \frac{1}{(\Delta x)} [u_{i+1,j} - u_{i,j}]$
- (ii) The Backward Difference: $(u_x)_{i,j} \approx \frac{1}{(\Delta x)} [u_{i,j} - u_{i-1,j}]$
- (iii) The Centred Difference: $(u_x)_{i,j} \approx \frac{1}{2(\Delta x)} [u_{i+1,j} - u_{i-1,j}]$
- (iv). The Centred Second Difference: $(u_{xx})_{i,j} \approx \frac{1}{(\Delta x)^2} [u_{i+1,j} - 2u_{i,j} + u_{i-1,j}]$,

respectively. Suppose a mesh on the spatial domain (x, y) and a uniform time step Δt are defined as in equation (3.85)

$$\left. \begin{aligned} x_0 = 0, \quad x_1 = \frac{L}{M+1}, \quad x_2 = \frac{2L}{M+1}, \quad x_3 = \frac{3L}{M+1}, \quad \dots, \quad x_{m+1} = L, \\ y_0 = 0, \quad y_1 = \frac{L}{N+1}, \quad y_2 = \frac{2L}{N+1}, \quad y_3 = \frac{3L}{N+1}, \quad \dots, \quad y_{n+1} = L, \text{ and} \\ t_0 = 0, \quad t_1 = \frac{T}{K+1}, \quad t_2 = \frac{2T}{K+1}, \quad t_3 = \frac{3T}{K+1}, \quad \dots, \quad t_{K+1} = T \end{aligned} \right\} \quad (3.85)$$

$$\Delta x = \frac{1}{m+1}, \quad \Delta y = \frac{1}{n+1}, \quad \text{and} \quad \Delta t = \frac{1}{k+1}.$$

then, for one step forward in time n solving for u_{ij} for $i = 1, 2, \dots, m$ and $j = 1, 2, 3, \dots, n$ two different schemes: Explicit and Implicit schemes can be established.

An *explicit scheme* is one that estimates the state of the system at a future time from the current time. Suppose f_n denote the state of f at time n in a given grid, then for a linear system, there must be some defined matrix operator A which gives the explicit change from time n to $n + 1$ as shown in Equation (3.86)

$$f^{n+1} = A(f^n) + b \quad (3.86)$$

for some initial state b . If the system is nonlinear, then there exist some operator G such that one has the form indicated as Equation (3.87)

$$f^{n+1} = G(f^n) \quad (3.87)$$

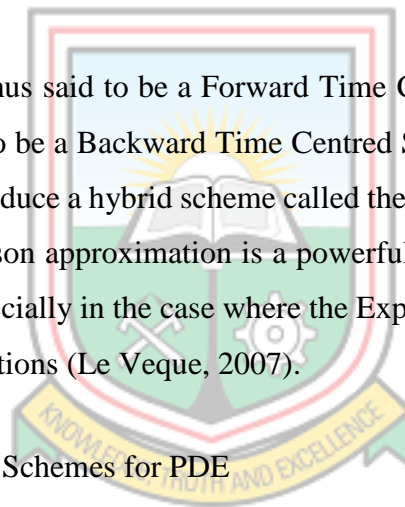
An *implicit scheme* on the other hand helps to determine a solution for the future time step by solving a system of equations involving future and current time steps. Thus, for a linear system, there must be some defined matrix operator B which gives an implicit change from time $n + 1$ to n as indicated as Equation (3.88)

$$f^n = B(f^{n+1}) + d, \quad (3.88)$$

for some initial state d . If the system is nonlinear, then an operator H can be defined as in Equation (3.89)

$$f^n = H(f^{n+1}). \quad (3.89)$$

The explicit scheme is thus said to be a Forward Time Centred Space (FTCS), whilst the implicit scheme is said to be a Backward Time Centred Space (BTCS). The combinations of these two schemes produce a hybrid scheme called the Crank-Nicolson method (Saucer, 2011). The Crank-Nicolson approximation is a powerful hybrid scheme used extensively for nonlinear PDE's especially in the case where the Explicit and the Implicit schemes fail to give approximate solutions (Le Veque, 2007).



3.5.2 Finite Difference Schemes for PDE

Consider the one-dimensional non-steady state diffusion equation with a diffusivity constant k . To demonstrate an explicit and implicit scheme, then the Initial Boundary Value Problem (IBVP) in Equation (3.90) can be used

$$\begin{cases} u_t = ku_{xx} & 0 \leq x \leq L, \quad k > 0 \\ u(x, 0) = f(x) & \text{initial condition} \\ u(0, t) = g(t), \quad u(L, t) = h(t), \quad 0 \leq t \leq t_f & \text{boundary conditions} \end{cases} \quad (3.90)$$

Applying first the explicit scheme to discretise the time dependent PDE using the subscript form of Equation (3.85) yields Equation (3.91)

$$\frac{u_i^{n+1} - u_i^n}{(\Delta t)} = k \left[\frac{u_{i+1}^n - 2u_i^n + u_{i-1}^n}{(\Delta x)^2} \right] \quad (3.91)$$

or further, Equation (3.92)

$$u_i^{n+1} = \alpha u_{i-1}^n + (1-2\alpha)u_i^n + \alpha u_{i+1}^n, \quad (3.92)$$

where $\alpha = \frac{k\Delta t}{(\Delta x)^2}$, and $1 \leq i \leq n$.

Equation (3.92) in matrix form is shown as in Equation (3.93)

$$\begin{bmatrix} (1-2\alpha) & \alpha & 0 & 0 & \cdots & 0 \\ \alpha & (1-2\alpha) & \alpha & 0 & \cdots & 0 \\ 0 & \alpha & (1-2\alpha) & \alpha & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \ddots & 0 & \alpha & (1-2\alpha) & \alpha \\ 0 & \dots & 0 & 0 & \alpha & (1-2\alpha) \end{bmatrix} \begin{bmatrix} u_1^n \\ u_2^n \\ u_3^n \\ \vdots \\ u_{m-1}^n \\ u_m^n \end{bmatrix} + \begin{bmatrix} \alpha u_0^n \\ 0 \\ 0 \\ \vdots \\ 0 \\ \alpha u_{m+1}^n \end{bmatrix} = \begin{bmatrix} u_1^{n+1} \\ u_2^{n+1} \\ u_3^{n+1} \\ \vdots \\ u_{m-1}^{n+1} \\ u_m^{n+1} \end{bmatrix} \quad (3.93)$$

with initial conditions given by Equation (3.94)

$$\begin{bmatrix} u_1^0 \\ u_2^0 \\ u_3^0 \\ \vdots \\ u_{m-1}^0 \\ u_m^0 \end{bmatrix} = \begin{bmatrix} f(x_1) \\ f(x_2) \\ f(x_3) \\ \vdots \\ f(x_{m-1}) \\ f(x_m) \end{bmatrix} \quad (3.94)$$

In similar vain, if an implicit scheme is used to discretise equation (3.90), one obtains Equation (3.95)

$$\begin{bmatrix} (1+2\alpha) & -\alpha & 0 & 0 & \cdots & 0 \\ -\alpha & (1+2\alpha) & -\alpha & 0 & \cdots & 0 \\ 0 & -\alpha & (1+2\alpha) & -\alpha & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \ddots & 0 & -\alpha & (1+2\alpha) & -\alpha \\ 0 & \dots & 0 & 0 & -\alpha & (1+2\alpha) \end{bmatrix} \begin{bmatrix} u_1^{n+1} \\ u_2^{n+1} \\ u_3^{n+1} \\ \vdots \\ u_{m-1}^{n+1} \\ u_m^{n+1} \end{bmatrix} + \begin{bmatrix} -\alpha u_0^{n+1} \\ 0 \\ 0 \\ \vdots \\ 0 \\ -\alpha u_{m+1}^{n+1} \end{bmatrix} = \begin{bmatrix} u_1^n \\ u_2^n \\ u_3^n \\ \vdots \\ u_{m-1}^n \\ u_m^n \end{bmatrix} \quad (3.95)$$

3.5.3 Stability of the Scheme

A finite difference scheme is stable if the effect of an error made in any stage of the computation is not propagated into large errors in later stages of the computations. A difference scheme can be examined for stability by substituting into it perturbed values, the

solution of the scheme (Chen, 2007). The stability of the scheme can be studied using the one-dimensional non-steady state *diffusion equation* with a constant parameter α as shown in Equation (3.96)

$$\frac{\partial u}{\partial t} = \alpha \frac{\partial^2 u}{\partial x^2} \quad (3.96)$$

Let u_i^n be a solution of the equation (3.92), and let its perturbation satisfy the same scheme, such that Equation (3.96) becomes Equation (3.97) using Equation (3.91)

$$\frac{(u_i^{n+1} + \varepsilon_i^{n+1}) - (u_i^n + \varepsilon_i^n)}{\Delta t} = \alpha \left[\frac{(u_{i+1}^n + \varepsilon_{i+1}^n) - 2(u_i^n + \varepsilon_i^n) + (u_{i-1}^n + \varepsilon_{i-1}^n)}{h^2} \right], \quad (3.97)$$

where $h = \Delta x$. From Equation (3.97), one can deduce Equation (3.98)

$$\left(\frac{\varepsilon_i^{n+1} - \varepsilon_i^n}{\Delta t} \right) = \alpha \left(\frac{\varepsilon_{i+1}^n - 2\varepsilon_i^n + \varepsilon_{i-1}^n}{h^2} \right). \quad (3.98)$$

If the error factor ε_i^n is expanded using Fourier series of the form as shown in Equation (3.99)

$$\varepsilon_i^n = \sum_k \bar{\gamma}_k^n \exp(ikx_i), \text{ where } i = \sqrt{-1} \quad (3.99)$$

then, the analysis can be simplified if one assumes that a solution to the error equation (3.98) has one term, by dropping the subscript k in Equation (3.99) to obtain Equation (3.100)

$$\varepsilon_i^n = \bar{\gamma}^n \exp(ikx_i) \quad (3.100)$$

Substituting equation (3.100) into Equation (3.98), and solving for the *amplification factor* becomes Equation (3.101)

$$\bar{\gamma} = \bar{\gamma}^{n+1} / \bar{\gamma}^n \quad (3.101)$$

Applying the *von Neumann* Criterion for stability, that stipulates that the modulus of the amplification factor must not be greater than one (Thomas, 1995), using Equations (3.100) and (3.98) yields Equation (3.102)

$$\frac{\bar{\gamma}^{n+1} - \bar{\gamma}^n}{\Delta t} = \alpha \left(\frac{\bar{\gamma}^n \exp(ikh) - 2\bar{\gamma}^n + \bar{\gamma}^n \exp(-ikh)}{h^2} \right) \quad (3.102)$$

Since $\exp(ikh) - 2 + \exp(-ikh) = 2\cos(kh) - 2 = -4\sin^2(kh/2)$, this leads from Equation (3.102) into Equation (3.103)

$$\bar{\gamma}^{n+1} = \left(1 - \frac{4\alpha\Delta t}{h^2} \sin^2(kh/2)\right) \bar{\gamma}^n \quad (3.103)$$

Dividing through equation (3.103) by $\bar{\gamma}^n$, one obtains equation (3.104)

$$\bar{\gamma}^n = 1 - \frac{4\alpha\Delta t}{h^2} \sin^2(kh/2) \quad (3.104)$$

Thus, the von Neumann criterion for stability is satisfied for Equation (3.105) as

$$\left|1 - \frac{4\alpha\Delta t}{h^2} \sin^2(kh/2)\right| \leq 1 \quad (3.105)$$

The inequality (3.105) is satisfied if the stability condition in equation (3.106) is satisfied

$$\frac{4\alpha\Delta t}{h^2} \leq \frac{1}{2} \quad (3.106)$$

Therefore, the forward difference scheme for equation (3.97) is stable under condition (3.106). For the backward difference scheme, a similar von Neumann stability analysis can be done. The error equation in (3.103) for the backward difference scheme takes the form in Equation (3.107)

$$\frac{(\varepsilon_i^{n+1} - \varepsilon_i^n)}{\Delta t} = \alpha \left(\frac{\varepsilon_{i+1}^{n+1} - 2\varepsilon_i^{n+1} + \varepsilon_{i-1}^{n+1}}{h^2} \right) \quad (3.107)$$

Substituting equation (3.100) into equation (3.107), and simplifying the algebraic expression yields the equation for the amplification factor as shown in Equation (3.108)

$$\bar{\gamma} = \frac{1}{\left|1 + (4\alpha\Delta t / h^2) \sin^2(kh/2)\right|} \quad (3.108)$$

From the von Neumann criterion, the equation (3.108) is always less than or equal to one for any choice of $\alpha, k, \Delta t$ and h . Hence the backward heat equation is unconditionally stable. A similar analysis can be done for the central difference scheme.

3.6 Sensitivity Analysis

Sensitivity Analysis is a method for quantifying uncertainty and its objective is to identify

critical inputs such as parameters and initial conditions of a model and quantifying how the input uncertainty impacts models outcome (Marino *et al.*, 2008). The behaviour of physical and chemical systems is affected by many parameters that characterise the system. The analysis of how a system responds to changes in the parameters is called parametric sensitivity (Varma *et al.*, 1999). In most cases, when some parameters are varied slightly, while keeping the remaining parameters fixed, the response of a system also changes slightly. However, other set of parameter combinations can cause the system to respond enormously, even if one or more parameters are varied only slightly. In this case, it is said that the system behaves in a parametrically sensitive manner (Varma *et al.*, 1999). In this section, the use of sensitivity analysis to evaluate an influence of parametric variations on the model predictions by local and global sensitivity methods is discussed.

3.6.1 Local Sensitivity Analysis

A local sensitivity analysis investigates the impact on the model output based on changes in the parameters only very close to the nominal values (Marino *et al.*, 2008). When the input factors such as parameters or initial conditions are known with a little uncertainty, one can examine the partial derivative of the output function with respect to the input factors. In the following, brief overviews about the local sensitivity analysis and for more details can be seen in the works of (Varma *et al.*, 1999; Salfelli *et al.*, 2000). In most of these studies, a system described by an ordinary differential equation in Equation (3.109) is considered

$$\frac{dy}{dt} = f(y, \phi, t) \quad (3.109)$$

with the initial condition $y(0) = y_0$ where y is the dependent variable, t is the time, and ϕ represents the vector containing the m -system input parameters. The function $f \in C^1$ is a continuously differentiable function. That is, all partial derivatives of f with respect to x_j , $\partial f_i / \partial x_j$ with $i, j = 1, 2, 3, \dots, n$ exist and are continuous. This guarantees that the above equation has a unique solution $y = y(t, \phi)$, which is continuous in t and ϕ . Let $\phi_j + \Delta\phi_j$ denote the change from ϕ_j in the j th parameter in the parameter vector ϕ . Then the corresponding solution becomes Equation (3.110)

$$y = y(t, \phi_j + \Delta\phi_j) \quad (3.110)$$

This solution is continuous in ϕ_j and can be expanded into a Taylor series as indicated in Equation (3.111)

$$y(t, \phi_j + \Delta\phi_j) = y(t, \phi_j) + \frac{\partial y(t, \phi_j)}{\partial \phi_j} \Delta\phi_j + \frac{\partial^2 y(t, \phi_j + \theta\Delta\phi_j)}{\partial \phi_j^2} \cdot \frac{\Delta\phi_j^2}{2} \quad (3.111)$$

where $0 < \theta < 1$ is sufficiently small, i.e. $\Delta\phi_j < \phi_j$. Truncating the second and higher order terms on the right-hand side leads to Equation (3.112)

$$\Delta y = y(t, \phi_j + \Delta\phi_j) - y(t, \phi_j) + \frac{\partial y(t, \phi_j)}{\partial \phi_j} \Delta\phi_j \quad (3.112)$$

where Δy represents the variation of y due to the change of the input parameter ϕ_j given by $\Delta\phi_j$. When both sides of equation (3.112) is divided by $\Delta\phi_j$ and an infinitesimal variation ($\Delta\phi_j \rightarrow 0$) is considered, one obtains Equation (3.113)

$$s(y; \phi_j) = \frac{\partial y(t, \phi_j)}{\partial \phi_j} = \lim_{\Delta\phi_j \rightarrow 0} \frac{y(t, \phi_j + \Delta\phi_j) - y(t, \phi_j)}{\Delta\phi_j} \quad (3.113)$$

The Equation (3.113) defines a local sensitivity of the variable, y , with respect to parameter, ϕ_j (Varma *et al.*, 1999). Higher order local sensitivity can be defined using similar procedure. In order to compare the computed sensitivities among the different input parameters, a normalised sensitivity is commonly used. The normalised sensitivity of y with respect to ϕ_j is defined as indicated in Equation (3.114)

$$s(y; \phi_j) = \frac{\phi_j}{y} \cdot \frac{\partial \ln y}{\partial \ln \phi_j} = \frac{\phi_j}{y} s(y; \phi_j) \quad (3.114)$$

The magnitudes of the input parameter ϕ_j and the variable y in Equation (3.114) are normalised. Thus, if the local sensitivity $s(y; \phi_j)$ is known, the computation of $s(y; \phi_j)$ is much easier. When the system is described by dependent variables of size n , this leads to Equation (3.115)

$$\frac{dy_i}{dt} = f(y_i, \phi, t), \quad y_i(0) = y^i \quad (3.115)$$

where $i = 1, 2, \dots, n$, the sensitivity measure can be generated by the column sensitivity vector given by Equation (3.116).

$$s(y_i, \phi) = \frac{\partial y_i}{\partial \phi_j} = \left[\frac{\partial y_1}{\partial \phi_j}, \frac{\partial y_2}{\partial \phi_j}, \dots, \frac{\partial y_n}{\partial \phi_j} \right]^T = \left[s(y_1; \phi_j), s(y_2; \phi_j), \dots, s(y_n; \phi_j) \right] \quad (3.116)$$

By combining all the row and column sensitivity vectors, an $n \times m$ sensitivity matrix which comprises sensitivity indices as elements is obtained as Equation (3.117)

$$S(y_i, \phi) = \frac{\partial y_i}{\partial \phi_j} = \begin{bmatrix} \frac{\partial y_1}{\partial \phi_1} & \frac{\partial y_1}{\partial \phi_2} & \dots & \frac{\partial y_1}{\partial \phi_m} \\ \frac{\partial y_2}{\partial \phi_1} & \frac{\partial y_2}{\partial \phi_2} & \dots & \frac{\partial y_2}{\partial \phi_m} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial y_n}{\partial \phi_1} & \frac{\partial y_n}{\partial \phi_2} & \dots & \frac{\partial y_n}{\partial \phi_m} \end{bmatrix} \quad (3.117)$$

3.6.2 Global Sensitivity Analysis

The local sensitivity methods estimate the effects of infinitesimal variations of each factor having on the model output, in the region of a fixed nominal point. The local methods are widely used on steady-state models and on studies dealing with the stability of a nominal point. The local methods can only account for small variations from the nominal values and fail to capture the large variations in a parameter set. Global sensitivity methods are advantageous when performing a full search of the parameter space, hence providing information independent of nominal points. Furthermore, the global methods can account for the total uncertainty in the model output, while all parameters are varied at the same time. In addition, the global sensitivity analysis methods evaluate the effect of a parameter while all other parameters are varied simultaneously, accounting for interactions between parameters without depending on the stipulation of the nominal point. The most widely used methods in global sensitivity analysis are Fourier Amplitude Sensitivity Testing (FAST) method (Cukier *et al.*, 1978; Morris, 1991; Sabal, 2001) and Derivative based Global sensitivity methods (Kucherenko *et al.*, 2009).

CHAPTER 4

MATHEMATICAL MODEL FORMULATION

4.1 Preamble

This chapter looks at the theoretical aspect of the mathematical models for the growth, spread and vegetation pattern formation under variable environmental conditions. In the theoretical aspect, a modified mathematical model was constructed for plant growth, spread and vegetation patterns formation using the model by Li *et al.*, (2003). Li *et al.* (2003), modelled crop growth process under the multi-environment external force action. This was used to modify Klausmeier (1999), model of regular and irregular patterns in semiarid vegetation. Their study include the prominent components for the growth, spread and pattern formation of the vegetation.

4.2 Model Development

In modelling plant growth, spread and vegetation pattern formation, the Klausmeier (1999) model of regular and irregular patterns in semiarid vegetation was adopted and modified to form the basis of this research. Klausmeier's (1999) model consists of biomass dynamics equation and water dynamics equation thought to be responsible for pattern formation. In his model, the water dynamics equation is controlled by a uniform supply of water at rate A , and loss of water due to evaporation at rate LW . Water uptake by plant was represented by an expression $RG(W)F(P)P = RWP^2$ where $G(W) = W$ represents the functional response of plants to water, $F(P) = P$ represents an increasing function that describes how plants increase water infiltration. The biomass dynamics equation, is governed by biomass accumulation $JRWP^2$ where J is the yield of plant biomass per unit water consumed, loss of plant biomass through density-independent mortality and maintenance at a constant rate MP and biomass movement due to spatial components. Klausmeier (1999) model therefore consists of two state variables: a water variable (W) and plant Biomass variable (P) defined on an infinite two-dimensional domain indexed by X and Y . The model is therefore a system of two partial differential equations given by the Equation (4.1)

$$\left. \begin{aligned}
\frac{\partial W}{\partial T} &= \underbrace{A}_{\text{Water source}} - \underbrace{LW}_{\text{Water loss due to evaporation}} - \underbrace{RWP^2}_{\text{Water uptake by plants}} + \underbrace{V \frac{\partial W}{\partial X}}_{\text{Water movement at uniform speed}} \\
\frac{\partial P}{\partial T} &= \underbrace{JRWP^2}_{\text{Biomass accumulation}} - \underbrace{MP}_{\text{Biomass loss}} - \underbrace{D_p \left(\frac{\partial^2}{\partial X^2} + \frac{\partial^2}{\partial Y^2} \right) P}_{\text{Biomass movement}}
\end{aligned} \right\} \quad (4.1)$$

where T is the time coordinate, and (X, Y) represents the spatial domain.

The limitation with regard to Klausmeier (1999) model is the absence of soil water dynamics which in this thesis was presumed to be different from surface water dynamics and cannot be merged together. This is due to the fact that, these two operate at different time scales and must be considered as two separate entities. The proposed model in this study therefore seeks to address this deficiency. The Klausmeier's (1999) model is further refined by use of Li *et al.* (2003) model for comprehensive analysis.

4.2.1 Refining the Model

This study considered modifying the water dynamics equation of Klausmeier (1999) model by separating this equation into two: the surface water dynamics (component) and soil water dynamics (component) and merge them with the third equation which is the population (biomass) density component.

Surface Water Dynamics

During and after an intense rainfall, a major proportion of the rainfall first collects above ground. This is as a result of relatively slow process of water infiltration into the soil. This water will either infiltrate into the soil or flow towards other areas and subsequently infiltrate in those regions (surface water motion). The amount of water on the soil surface at a particular position and time is denoted by $W(t, x, y)$. The rate of change of the amount of water on the surface given by $\partial W / \partial T$ is controlled by a uniform supply of water at rate A , loss of water due to evaporation at rate LW , surface water infiltration into the soil and the expression $V \partial W / \partial X$ that represents downhill water flow and measures slope gradient or $D_w (\partial^2 W / \partial X^2 + \partial^2 W / \partial Y^2)$ that represents the net displacement of surface water on a perfectly horizontal terrain during rainfall. This is due to the fact that water infiltration in vegetated ground is much faster than in unvegetated ground. Thus, the water on the bare

surface will then flow to places with vegetation where all water has already infiltrated. Induced by pressure differences measured by the slope of the thickness of the water layer, the surface water motion incorporates the flow due to pressure differences into a single parameter, D_w , so that the surface water movement can be described by this term. According to Walker *et al.* (1981), infiltration rate $N_f(t, x, y)$ depends on the amount of water on the surface, plant density, and soil characteristics. The surface water infiltration into the soil is therefore a saturation function represented as in Equation (4.2).

$$\text{Surface Water Infiltration Rate} = JW(x, y, t) \times \frac{P(x, y, t) + s_2 N_0}{P(x, y, t) + s_2} \quad (4.2)$$

where $P(x, y, t)$ represents the plant population (biomass) density, $JW(x, y, t)$ describes maximum infiltration rate of surface water, $JW(x, y, t)N_0$ is the minimum water infiltration in the absence of plants and s_2 is a half-saturation constant. Parameter s_2 corresponds to the rate at which water infiltration increases with plant density. When the expression on the right-hand side of Equation (4.2) is substituted for surface water infiltration into the soil, the surface water dynamics of the proposed model in this research is represented by Equation (4.3)

$$\underbrace{\frac{\partial W}{\partial T}}_{\text{Rate of change of surface water}} = \underbrace{A}_{\text{Rainfall}} - \underbrace{LW}_{\text{water loss due to evaporation}} - \underbrace{JW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{water infiltration into the soil}} + \left\{ \underbrace{V \frac{\partial W}{\partial X}}_{\text{water movement at uniform speed}} \right\} \text{ or } \left\{ \underbrace{D_w \left(\frac{\partial^2 W}{\partial X^2} + \frac{\partial^2 W}{\partial Y^2} \right)}_{\text{surface water movement}} \right\} \quad (4.3)$$

Soil Water Dynamics

Soil water at a particular position and time would involve infiltration into the soil from surface water, what may be taken up by plants growing at that particular position and time, the reduction that may be experienced due to evaporation and drainage, or flow to other parts. The soil water dynamics is therefore controlled by infiltration into the soil from surface water, loss due to evaporation and drainage, loss due to water uptake by plants, and movement due to spatial components. The infiltration rate at a particular position and time is given earlier by the expression on the right-hand side of Equation (4.2). According to

Rietkerk *et al.* (1997), soil water loss as a result of plant uptake is assumed to be a saturation function of soil water. Soil water loss by plant uptake is therefore given by Equation (4.4).

$$\text{Soil Water Loss by plant uptake} = J \times \frac{N(x, y, t)}{N(x, y, t) + s_1} \times P(x, y, t) \quad (4.4)$$

where J is as defined earlier and s_1 is a half-saturation constant. When the expression on the right hand side of Equation (4.4) is substituted for soil water loss by plant uptake, the soil water dynamics of the proposed model in this research is represented as in Equation (4.5)

$$\frac{\partial N}{\partial T} = \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{Infiltration into the soil from surface water}} - \underbrace{MN}_{\text{Evaporation and drainage}} - \underbrace{J \times \left(\frac{N}{N + s_1} \right) P}_{\text{Soil water loss by plants uptake}} + \underbrace{D_N \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right)}_{\text{Soil water movement}} \quad (4.5)$$

Rate of change of soil water

Plant Biomass Dynamics

The plant biomass dynamics of the proposed model of this study compares with Biomass equation in Klausmeier's model but with slight modification. The modification to the Klausmeier (1999) model in relation to plant biomass dynamics is the plant growth function β which was introduced as an improvement factor. The plant biomass dynamics of this study is therefore controlled by soil water uptake by plants leading to plant growth, plant loss as a result of density-independent mortality and maintenance, and plant dispersal. This is represented by Equation (4.6).

$$\frac{\partial P}{\partial T} = [\text{Plant Growth}] + [\text{Plant Loss}] + [\text{Plant Dispersal}] \quad (4.6)$$

It is assumed that plant growth increases linearly with soil water uptake. This is at its maximum when the availability of soil water permits maximum specific soil water uptake (De Wit, 1958). The Li *et al.* (2003), growth model was introduced into the growth component of the plant biomass dynamics as β . This is to determine the dynamics of the model at different levels of β . The plant growth at a particular position and time is therefore represented by Equation (4.7)

$$\text{Plant Growth at a Particular Point and Time} = (\beta + J) \times \left(\frac{N}{N + s_1} \right) P \quad (4.7)$$

where J is the specific plant growth with β modelled as in Li *et al.* (2003) growth model for comprehensive analysis. Plant population (biomass) density may be lost (decrease) through natural mortality (U) and be defined as in Equation (4.8)

$$\text{Plant Loss at a Particular Point and Time} = U \times P \quad (4.8)$$

Plant movement, either through seed dispersal or any other form is given by the diffusion term indicated by Equation (4.9)

$$\text{Plant Dispersal} = D_p \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right) \quad (4.9)$$

When the Equations (4.7), (4.8) and (4.9) are substituted into Equation (4.6) for plant growth, plant loss and plant dispersal respectively in the plant population dynamics relation given by Equation (4.6), one obtains Equation (4.10).

$$\underbrace{\frac{\partial P}{\partial T}}_{\text{Rate of change of plant density}} = \underbrace{\left(J + \beta \right) \times \left(\frac{N}{N + s_1} \right) P}_{\text{Soil water uptake by plants/growth}} - \underbrace{UP}_{\text{Plant loss as a result of mortality}} + \underbrace{D_p \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right)}_{\text{Plant dispersal}} \quad (4.10)$$

Further, the plant growth function, β which was introduced into the model as a constant improvement factor is modelled by using Li *et al.* (2003) model for crop growth process under the multi-environment external force action through continuous-time Markov process. This involves synthesising the combined effects of the multiple resources (light, water, temperature and nutrients) and defined as in Equation (4.11)

$$\beta = \frac{1 - F_1 N}{F_2 + F_3 N} \quad (4.11)$$

where F_1 , F_2 and F_3 are three aggregate parameters, and are defined respectively by the Equations (4.12), (4.13) and (4.14)

$$F_1 = \frac{\alpha_6 (\lambda_{21} + \lambda_{23})}{\lambda_{12} \lambda_{23}} \quad (4.12)$$

$$F_2 = \frac{(\lambda_{21} + \lambda_{23}) \lambda_{61}}{\lambda_{12} \lambda_{23} \lambda_{61}} + \frac{\lambda_{12} \lambda_{61}}{\lambda_{12} \lambda_{23} \lambda_{61}} + \frac{\lambda_{45} \lambda_{51} + \lambda_{34} \lambda_{51} + \lambda_{34} \lambda_{45}}{\lambda_{34} \lambda_{45} \lambda_{51}}$$

or in other simplified form as Equation (4.13).

$$F_2 = \frac{\lambda_{21}}{\lambda_{12}\lambda_{23}} + \frac{1}{\lambda_{12}} + \frac{1}{\lambda_{23}} + \frac{1}{\lambda_{34}} + \frac{1}{\lambda_{45}} + \frac{1}{\lambda_{51}} \quad (4.13)$$

$$F_3 = \frac{\alpha_6(\lambda_{21} + \lambda_{23})}{\lambda_{12}\lambda_{23}} \cdot \frac{1}{\lambda_{61}} = \frac{F_1}{\lambda_{61}} \quad (4.14)$$

where λ_{ij} are state transition rates and are considered as parameters of interest. However, these parameters are restricted by the input of resources such as light, temperature, water and soil nutrients. Each of these transition rates are considered to be proportional to each resource. Thus, the transition rates are related to the resources as indicated in Equation (4.15)

$$\lambda_{12} = \alpha_1 I, \lambda_{23} = \alpha_2 T, \lambda_{34} = \alpha_3 H \text{ and } \lambda_{45} = \alpha_4 N \quad (4.15)$$

where I , T , H and N represent the measure indices of light, temperature, water and soil nutrients, respectively. The α_1 , α_2 , α_3 and α_4 are the utilization coefficients of the corresponding resource. Substituting Equation (4.15) into (4.12), (4.13) and (4.14) for F_1 , F_2 and F_3 , respectively, as defined by Li *et al.* (2003), one obtains Equations (4.16), (4.17) and (4.18).

$$F_1 = \frac{\alpha_6(\lambda_{21} + \alpha_2 T)}{\alpha_1 \alpha_2 I T} \quad (4.16)$$

$$F_2 = \frac{(\lambda_{21} + \alpha_2 T)\lambda_{61}}{\alpha_1 I \alpha_2 T \lambda_{61}} + \frac{\alpha_1 I \lambda_{61}}{\alpha_1 I \alpha_2 T \lambda_{61}} + \frac{\alpha_4 N \lambda_{51} + \alpha_3 H \lambda_{51} + \alpha_3 H \alpha_4 N}{\alpha_3 H \alpha_4 N \lambda_{51}}$$

or further,

$$F_2 = \frac{\lambda_{21}}{\alpha_1 \alpha_2 I T} + \frac{1}{\alpha_1 I} + \frac{1}{\alpha_2 T} + \frac{1}{\alpha_3 H} + \frac{1}{\alpha_4 N} + \frac{1}{\lambda_{51}} \quad (4.17)$$

$$F_3 = \frac{\alpha_6(\lambda_{21} + \lambda_{23})}{\lambda_{12}\lambda_{23}} \cdot \frac{1}{\lambda_{61}} = \frac{F_1}{\lambda_{61}} \quad (4.18)$$

4.2.2 Assumptions of the Model

The proposed model factored into it four assumptions as follows:

- (i) The descriptive variable of vegetation increase during vegetation growth is

proportional to the surface water infiltration into the soil together with the contribution from multi environment external force action;

- (ii) During rain showers of at least some considerable length, a steady state develops between rainfall, surface water motion, and water infiltration. This steady state is calculated from $[\partial W(x, y, t)]/\partial T = 0$. Though, rain showers are discrete events, for the sake of model analysis, it is assumed that water infiltration rate is at steady state. This is to say that, water infiltration is a continuous water supply to the system at a position in space.
- (iii) The per capita rate of water uptake is proportional to increase in plant population (biomass) density, reflecting the positive correlation between infiltration rate and plant population (biomass) density on the basis that water is the limiting resource.
- (iv) Stationary assumption: Changes in surface water terms occur so rapidly in comparison to the plant population (biomass) density and soil water dynamics. This allows the surface water dynamics to be approximated as stationary during plant population (biomass) growth.

4.2.3 The Models

Two different but very similar models were formulated in this study. The first model relates to the situation where the surface water dynamics represents downhill water flow and measures slope gradient. This together with the assumptions in section 4.2.2 leads to a system of three partial differential equations as modelled in Equation (4.19).

$$\left. \begin{aligned}
 \underbrace{\frac{\partial W}{\partial T}}_{\text{Rate of change of surface water}} &= \underbrace{A}_{\text{Rainfall}} - \underbrace{LW}_{\text{water loss due to evaporation}} - \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{surface water infiltration into the soil}} + \underbrace{V \frac{\partial W}{\partial X}}_{\text{water movement at uniform speed}} \\
 \underbrace{\frac{\partial N}{\partial T}}_{\text{Rate of change of soil water}} &= \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{infiltration into the soil from surface water}} - \underbrace{MN}_{\text{evaporation and drainage}} - \underbrace{J \times \left(\frac{N}{N + s_1} \right) P}_{\text{Soil water loss by plants uptake}} + \underbrace{D_N \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right)}_{\text{Soil water movement}} \\
 \underbrace{\frac{\partial P}{\partial T}}_{\text{Rate of change of plant density}} &= \underbrace{(\beta + J) \times \left(\frac{N}{N + s_1} \right) P}_{\text{soil water uptake by plants / growth}} - \underbrace{UP}_{\text{Plant loss as a result of mortality}} + \underbrace{D_P \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right)}_{\text{plant dispersal}}
 \end{aligned} \right\} (4.19)$$

The second model formulated uses the same assumptions, together with the situation where the surface water dynamics represents the net displacement of surface water on an overly evenly horizontal terrain during rainfall. Thus, the water on the bare surface then flows by pressure differences measured by the slope of the thickness of the water layer. The surface water motion incorporates the flow due to pressure differences into a single parameter, D_w such that the surface water movement can be described by the term $D_w \left(\frac{\partial^2 W}{\partial X^2} + \frac{\partial^2 W}{\partial Y^2} \right)$. The second model for this study is also a coupled, three partial differential equations linking surface water dynamics, soil water dynamics and plant population (biomass) density. The system of equations is labeled as Equation (4.20)

$$\left. \begin{aligned}
 \frac{\partial W}{\partial T} &= \underbrace{A}_{\text{Rainfall}} - \underbrace{LW}_{\text{water loss due to evaporation}} - \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{surface water infiltration into the soil}} + \underbrace{D_w \left(\frac{\partial^2 W}{\partial X^2} + \frac{\partial^2 W}{\partial Y^2} \right)}_{\text{Surface water movements}} \\
 \frac{\partial N}{\partial T} &= \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{infiltration into the soil from surface water}} - \underbrace{\frac{MN}{\beta}}_{\text{evaporation and drainage}} - \underbrace{J \times \left(\frac{N}{N + s_1} \right) P}_{\text{Soil water loss by plants uptake}} + \underbrace{D_N \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right)}_{\text{Soil water movement}} \\
 \frac{\partial P}{\partial T} &= \underbrace{(\beta + J) \times \left(\frac{N}{N + s_1} \right) P}_{\text{soil water uptake by plants / growth}} - \underbrace{UP}_{\text{Plant loss as a result of mortality}} + \underbrace{D_p \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right)}_{\text{plant dispersal}}
 \end{aligned} \right\} (4.20)$$

where T is the time, (X, Y) represent the spatial domain. The parameters associated with the two models are merged together and defined in Table 4.1.

Table 4.1 Parameters of the Models and their meanings and units

Parameter	Meaning	Units
A	Mean water supply or mean rainfall	m year^{-1}
L	Rate of evaporation of surface water	year^{-1}
R	Rate of infiltration into the soil	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
M	Rate of evaporation and drainage of soil water	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
D_N	Diffusion coefficient of soil water	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
D_p	Dispersal coefficient of plant density	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
D_w	Diffusion coefficient of surface water	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
U	Plant mortality rate	$\text{Kg m}^{-2} \text{ year}^{-1}$
V	Speed of flow of water downhill	$\text{Kg H}_2\text{O m year}^{-1}$
J	Yield of plant density per unit of soil water consumed	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
β	Plant growth function representing a multi-environment external force action	$\text{Kg H}_2\text{O m}^{-2} \text{ year}^{-1}$
s_1	Half-saturation constant of specific plant growth and water uptake	M
s_2	Rate at which infiltration increases with specific plant density	Kg m^{-1}
N_0	Minimum water infiltration in the absence of plant	---

4.3 Non-Dimensionalisation of the Models

Generally, computations of null clines, steady states and the stability of systems of equations could be done by the normal procedure. However, at most times, when the number of variables involved are huge, it becomes cumbersome and very tedious to solve

such systems. It is therefore beneficial in the analysis of complex phenomena to transform the system of species balance equations into dimensionless form. The first benefit is related to the generalization of the results of theoretical and experimental investigations by presenting the numerical calculation measurements in the form of dependences between dimensionless parameters. The second reason is related to the problem of modelling the species balance equations to determine the actual conditions of the problem and finally to make computations easier. Thus, one proceeds with the non-dimensionalisation of the models as follow: the variables of the equations in Equations (4.19) and (4.20) were separated into a part without unit and a unit carrying part. The time, space and concentration scales to balance the surface water (W), soil water (N) and plant (biomass) density variables (P) were chosen as indicated in Equation (4.21).

$$W = \bar{W} \cdot w, \quad N = \bar{N} \cdot n, \quad P = \bar{P} \cdot p, \quad T = \bar{T} \cdot t, \quad X = \bar{X} \cdot x \quad \text{and} \quad Y = \bar{Y} \cdot y \quad (4.21)$$

with $\bar{T} = 1/(J + \beta)$, $\bar{X} = (D_N/(J + \beta))^{1/2}$, $\bar{Y} = (D_N/(J + \beta))^{1/2}$, $\bar{N} = s_1$, $\bar{W} = (J + \beta)s_1/R$ and $\bar{P} = s_2$ with β as defined earlier by Equation (4.11) and F_1 , F_2 and F_3 are three aggregate parameters defined respectively in Equations (4.12), (4.13) and (4.14). The α_i 's are the rate coefficients and λ_{ij} 's as the mean transition rates from one state i to another state j . The dimensionless form of the first proposed model is given by Equation (4.22)

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - lw - r \left(\frac{p + N_0}{p + 1} \right) w + v \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \left(\frac{p + N_0}{p + 1} \right) w - mn - g \left(\frac{n}{n + 1} \right) p + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left(\frac{n}{n + 1} \right) p - up + D_{PN} \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\} \quad (4.22)$$

The following representations labelled as Equation (4.23) are the dimensionless parameters and the variables that resulted into the system of dimensionless equations are indicated in Equation (4.21).

$$\left. \begin{aligned} a &= \frac{AR}{(\beta+J)^2 s_1}, \quad l = \frac{L}{(\beta+J)}, \quad r = \frac{R}{(\beta+J)}, \quad m = \frac{M}{(\beta+J)}, \quad g = \frac{Js_2}{(\beta+J)s_1}, \\ u &= \frac{U}{(\beta+J)}, \quad y = \left(\frac{(\beta+J)}{D_N} \right)^{1/2} Y, \quad x = \left(\frac{(\beta+J)}{D_N} \right)^{1/2} X, \quad v = \left(\frac{1}{(\beta+J)D_N} \right)^{1/2} V, \\ w &= \frac{WR}{(\beta+J)s_1}, \quad D_{PN} = \frac{D_P}{D_N}, \quad t = (\beta+J)T, \quad n = \frac{N}{s_1}, \quad p = \frac{P}{s_2} \end{aligned} \right\} \quad (4.23)$$

In similar manner, the dimensionless form of the second proposed model is given by Equation (4.24)

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - lw - r \left(\frac{p + N_0}{p + 1} \right) w + \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \left(\frac{p + N_0}{p + 1} \right) w - mn - g \left(\frac{n}{n + 1} \right) p + D_{NW} \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left(\frac{n}{n + 1} \right) p - up + D_{PW} \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\} \quad (4.24)$$

The second dimensionless model labelled as Equation (4.24) has similar but slightly different dimensionless parameters and variables from the first model parameters and variables and indicated by Equation (4.25).

$$\left. \begin{aligned} a &= \frac{AR}{(\beta+J)^2 s_1}, \quad l = \frac{L}{(\beta+J)}, \quad r = \frac{R}{(\beta+J)}, \quad m = \frac{M}{(\beta+J)}, \quad g = \frac{Js_2}{(\beta+J)s_1}, \\ u &= \frac{U}{(\beta+J)}, \quad y = \left(\frac{(\beta+J)}{D_W} \right)^{1/2} Y, \quad x = \left(\frac{(\beta+J)}{D_W} \right)^{1/2} X, \quad D_{PW} = \frac{D_P}{D_W}, \\ w &= \frac{WR}{(\beta+J)s_1}, \quad D_{NW} = \frac{D_N}{D_W}, \quad t = (\beta+J)T, \quad n = \frac{N}{s_1}, \quad p = \frac{P}{s_2} \end{aligned} \right\} \quad (4.25)$$

The full text of the dimensionless form of both models are indicated in appendices A1 and A2 of the thesis.

4.4 Components of the Analysis

The analysis of the models formulated dwells on two main aspects. The first aspect dwells on conditions or properties for pattern formation. This involves some basic conditions or features and theorems associated with both reaction systems and reaction-diffusion systems for pattern formation. In order to illustrate the validity of the theoretical results, some

numerical simulations were considered. The second aspect therefore involves comparison of the patterns formed from simulations run under different water fertility conditions. The patterns formed from different fertility levels within a particular water condition display the multi-dimension effect of the resource utilisation.



CHAPTER 5

ANALYSIS OF THE MODELS

5.1 The Proposed Models

The proposed models are systems for which each consists of three nonlinear partial differential equations for surface water balance (W), Soil water balance (N) and Plant biomass density variable (P). The models are Reaction-Diffusion types and they are expressed in dimensionless form. The first system is the dimensionless model for which its dimensional form relates to a situation where the surface water dynamics involves an expression that represents downhill water flow which measures the topography of the land. This is referenced from Equation (4.21) and now indicated as Equations (5.1)

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - lw - r \left(\frac{p + N_0}{p + 1} \right) w + v \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \left(\frac{p + N_0}{p + 1} \right) w - mn - g \left(\frac{n}{n + 1} \right) p + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left(\frac{n}{n + 1} \right) p - up + d \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\} \quad (5.1)$$

Similarly, the other system is a dimensionless model for which its dimensional form relates to a situation where the surface water dynamics incorporates the flow due to pressure differences into a single parameter D_w , so that the surface water dynamics can be described by the term $D_w \left(\frac{\partial^2 W}{\partial X^2} + \frac{\partial^2 W}{\partial Y^2} \right)$. This is also referenced from Equation (4.23) and indicated as Equation (5.2).

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - lw - r \left(\frac{p + N_0}{p + 1} \right) w + \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \left(\frac{p + N_0}{p + 1} \right) w - mn - g \left(\frac{n}{n + 1} \right) p + D_{nw} \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left(\frac{n}{n + 1} \right) p - up + D_{pw} \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\} \quad (5.2)$$

Table 5.1 gives the meaning of the dimensional and dimensionless model parameters and their values used in the analysis.

Table 5.1 Dimensional and Dimensionless Parameters used in the Model Simulations

Dimensional Parameters with meanings	Value	Dimensionless Parameter	Value
A : Mean water supply or mean rainfall	Varied	$a = \frac{AR}{(J + \beta)^2 s_1}$	Varied
L : Rate of evaporation of surface water	0.15	$l = \frac{L}{(J + \beta)}$	Varied
R : Rate of infiltration	0.05	$g = \frac{Js_2}{(J + \beta)s_1}$	Varied
M : Rate of evaporation and drainage of soil water	0.02	$m = \frac{M}{(J + \beta)}$	Varied
D_N : Diffusion coefficient of soil water	0.1	$r = \frac{R}{J + \beta}$	Varied
D_P : Dispersal coefficient of plant density	20	$u = \frac{U}{J + \beta}$	Varied
D_W : Diffusion coefficient of surface water	0.4	$v = \left(\frac{1}{\{J + \beta\} D_N} \right)^{\frac{1}{2}} V$	Varied
U : Plant mortality rate	0.10		
V : Speed of flow of water downhill	4		
J : Yield of plant density per unit of soil water consumed	0.35	$D_{NW} = \frac{D_N}{D_W}$	0.25
β : Plant growth function representing a multi-environment force action	Varied	$D_{PN} = \frac{D_P}{D_N}$	200
s_1 : Half-saturation constant of specific plant growth and water uptake	3	$D_{PW} = \frac{D_P}{D_W}$	50
s_2 : Rate at which infiltration increases with specific plant density	5		
N_0 : Minimum water infiltration in the absence of plant	0.03		

The plant growth function representing a multi-environment force action is categorised into water condition and soil fertility level. A range of values of β are therefore obtained based on the water condition and soil fertility level. As a result of this, all dimensionless relations with parameter β will constitute a range of values.

5.2 Conditions for Pattern Formation

The first step in the investigation of the pattern-forming potential of the systems of Equations (5.1) and (5.2) is to determine the spatially homogeneous steady states of the system Equation (5.3) as indicated in section 5.3. If the steady state is stable, then it implies that, the λ 's of the Jacobian matrix associated with the system must have negative real part and hence pattern formation of Equations (5.1) and (5.2) are possible. The next step is to linearise the system of the nonlinear models at the steady states as indicated in Section 5.4.

5.3 Equilibrium Solutions (Steady States)

The initial stage of analysing the proposed model of Equations (5.1) and (5.2) is to determine the equilibrium solutions (critical points) of the non-spatial form of the models. The relevant homogeneous steady states of Equations (5.1) and (5.2) are obtained by setting the space derivatives of the dimensionless models to zero. Thus, the equilibrium solutions of the model equations in Equation (5.1) and Equation (5.2) are obtained by reducing Equation (5.1) and Equation (5.2) to Equation (5.3).

$$\left. \begin{aligned} a - lw - r \left(\frac{p + N_0}{p + 1} \right) w &= 0 \\ \left(\frac{p + N_0}{p + 1} \right) w - mn - g \left(\frac{n}{n + 1} \right) p &= 0 \\ \left(\frac{n}{n + 1} \right) p - up &= 0 \end{aligned} \right\} \quad (5.3)$$

The equilibrium solutions to equation (5.3) are qualitatively analysed to investigate the stability of the associated equilibriums. To obtain the system of equations in Equation (5.3), it is assumed that all the parameters in Equations (5.1) and (5.2) are non-negative by setting $\partial w / \partial t = 0$, $\partial n / \partial t = 0$ and $\partial p / \partial t = 0$. The derivative functions $d(\partial^2 n / \partial x^2 + \partial^2 n / \partial y^2)$, $dv \partial w / \partial x$, and $(\partial^2 p / \partial x^2 + \partial^2 p / \partial y^2)$ representing the diffusive terms are also discarded.

Estimating the steady state conditions, the following two steady states $E_1^* = (w^*, n^*, 0)$ and $E_2^* = (w^*, n^*, p^*)$ were obtained. E_1^* which is the trivial equilibrium point, biologically represents a trivial situation and was obtained as shown in Equation (5.4)

$$E_1^* = \left[w^* = \frac{a}{rN_0 + l}, \quad n^* = \frac{aN_0}{m(rN_0 + l)}, \quad p^* = 0 \right] \quad (5.4)$$

In similar manner, E_2^* which is the non-trivial equilibrium situation and ecologically plausible admits the equilibrium point provided for as in Equation (5.5)

$$E_2^* = \left[w = \frac{a(p_s + 1)}{l(p_s + 1) + r(p_s + N_0)}, \quad n = \frac{u}{1 - u}, \quad p = \frac{a - lw - rmu}{gru} \right] \quad (5.5)$$

5.4 Linearisation of the Proposed Nonlinear Models

The nonlinear system was linearised in order to understand the behaviour of the system at the equilibrium points. This was represented as a linear system in a much-localised region specifically near where these equilibrium points lie. Thus, if (w^*, n^*, p^*) is an equilibrium point of equation (5.3) then the solution of the linearised system corresponding to (w^*, n^*, p^*) is obtained from the relation given by Equation (5.6)

$$\frac{\partial v_0}{\partial t} = J(f, g, h) \Big|_{(w^*, n^*, p^*)} v_0 \quad (5.6)$$

where $J(f, g, h) \Big|_{(w^*, n^*, p^*)} = \begin{pmatrix} \frac{\partial f}{\partial w} & \frac{\partial f}{\partial n} & \frac{\partial f}{\partial p} \\ \frac{\partial g}{\partial w} & \frac{\partial g}{\partial n} & \frac{\partial g}{\partial p} \\ \frac{\partial h}{\partial w} & \frac{\partial h}{\partial n} & \frac{\partial h}{\partial p} \end{pmatrix} \Big|_{(w^*, n^*, p^*)}$ and $v_0(w^*, n^*, p^*, t) \propto e^{\lambda t}$ is the

solution of the linearised system provided from Equation (5.2) with state functions $f(w, n, p)$, $g(w, n, p)$ and $h(w, n, p)$.

5.4.1 The Dynamics of the Model

Let $x \cong 0$ be the equilibrium point of the nonlinear system of partial differential equations $\dot{x} = f(t, x)$. The right hand side of $\dot{x} = f(t, x)$ satisfies the conditions of existence and uniqueness theorem and is of the form $f(t, x) = A(t)x + F(t, x)$ where $A(t)$ is a parameter dependent matrix and that $\lim_{|x| \rightarrow 0} (|F(t, x)|/|x|) = 0$. The linear homogeneous system of equations $\dot{x} = A(t)x$ is called the first approximation or linearisation of $\dot{x} = f(t, x)$.

In this section, the linearisation of the proposed model described by nonlinear partial differential equations in Equation (5.1) was considered. The procedure is based on the Taylor series expansion and on knowledge of nominal system trajectories and nominal system inputs. Suppose, one assumes slight perturbation given by Equation (5.7)

$$\left. \begin{aligned} w &= w_s + \bar{w} \\ n &= n_s + \bar{n} \\ p &= p_s + \bar{p} \end{aligned} \right\} \quad (5.7)$$

then, the Taylor series expansion is applied to the dimensionless model Equation (5.1) as follows:

$$\frac{\partial \bar{w}}{\partial t} = f(w, n, p) \Big|_{(w_s, n_s, p_s)} + \frac{\partial f}{\partial w} \Big|_{(w_s, n_s, p_s)} \bar{w} + \frac{\partial f}{\partial n} \Big|_{(w_s, n_s, p_s)} \bar{n} + \frac{\partial f}{\partial p} \Big|_{(w_s, n_s, p_s)} \bar{p} + \dots + v \frac{\partial \bar{w}}{\partial x} \quad (5.8)$$

$$\frac{\partial \bar{n}}{\partial t} = g(w, n, p) \Big|_{(w_s, n_s, p_s)} + \frac{\partial g}{\partial w} \Big|_{(w_s, n_s, p_s)} \bar{w} + \frac{\partial g}{\partial n} \Big|_{(w_s, n_s, p_s)} \bar{n} + \frac{\partial g}{\partial p} \Big|_{(w_s, n_s, p_s)} \bar{p} + \dots + d \left(\frac{\partial^2 \bar{n}}{\partial x^2} + \frac{\partial^2 \bar{n}}{\partial y^2} \right) \quad (5.9)$$

$$\frac{\partial \bar{p}}{\partial t} = h(w, n, p) \Big|_{(w_s, n_s, p_s)} + \frac{\partial h}{\partial w} \Big|_{(w_s, n_s, p_s)} \bar{w} + \frac{\partial h}{\partial n} \Big|_{(w_s, n_s, p_s)} \bar{n} + \frac{\partial h}{\partial p} \Big|_{(w_s, n_s, p_s)} \bar{p} + \dots + \left(\frac{\partial^2 \bar{p}}{\partial x^2} + \frac{\partial^2 \bar{p}}{\partial y^2} \right) \quad (5.10)$$

When the partial derivatives of $f(w, n, p) = a - lw - r\left(\frac{p + N_0}{p + 1}\right)w$ is evaluated with respect to surface water, w , one obtains Equation (5.11)

$$\frac{\partial f}{\partial w} = -l - r\left(\frac{p + N_0}{p + 1}\right) \quad (5.11)$$

When Equation (5.11) is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.12)

$$\left.\frac{\partial f}{\partial w}\right|_{E_1^*=(w_s, n_s, 0)} = -l - r \cdot N_0 = -(l + rN_0) \quad (5.12)$$

The partial derivative of $f(w, n, p) = a - lw - r\left(\frac{p + N_0}{p + 1}\right)w$ is again determined with respect to soil water, n to obtain Equation (5.13)

$$\frac{\partial f}{\partial n} = 0 \quad (5.13)$$

When Equation (5.13) is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.14)

$$\left.\frac{\partial f}{\partial n}\right|_{E_1^*=(w_s, n_s, 0)} = 0 \quad (5.14)$$

The partial derivative of $f(w, n, p) = a - lw - r\left(\frac{p + N_0}{p + 1}\right)w$ is finally determined with respect to plant population (biomass) density, p , to obtain Equation (5.15)

$$\frac{\partial f}{\partial p} = -rw \cdot \frac{\partial}{\partial p} \left[\frac{p + N_0}{p + 1} \right] = -rw \cdot \left[\frac{(p + 1) - (p + N_0)}{(p + 1)^2} \right] = -\frac{rw(1 - N_0)}{(p + 1)^2} \quad (5.15)$$

and when evaluated at $E_1^* = (w_s, n_s, 0)$, gives Equation (5.16)

$$\left.\frac{\partial f}{\partial p}\right|_{E_1^*=(w_s, n_s, 0)} = -r \cdot \left[\frac{a}{rN_0 + l} \right] \cdot \left[\frac{1 - N_0}{(0 + 1)^2} \right] = -\frac{ar(1 - N_0)}{rN_0 + l} \quad (5.16)$$

The point $E_1^* = (w_s, n_s, 0)$ is the equilibrium solution of the linearised system of equations in Equation (5.2). This implies that, it must satisfy the system in Equation (5.2). Therefore if $f(w, n, p)$ is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.17)

$$f(w, n, p) \Big|_{E_1^* = (w_s, n_s, 0)} = 0 \quad (5.17)$$

The linearised form of the surface water dynamics of the dimensionless system in Equation (5.1) is therefore obtained as in Equation (5.18)

$$\frac{\partial \bar{w}}{\partial t} = 0 = A_{11} \bar{w} + A_{12} \bar{n} + A_{13} \bar{p} + \left(\frac{\partial^2 \bar{w}}{\partial x^2} + \frac{\partial^2 \bar{w}}{\partial y^2} \right) \quad (5.18)$$

where

$$A_{11} = -(l + rN_0), \quad A_{12} = 0 \quad \text{and} \quad A_{13} = -\frac{ar(1-N_0)}{rN_0+l}$$

Similarly, the partial derivatives of $g(w, n, p) = \left(\frac{p+N_0}{p+1} \right) w - mn - g \left(\frac{n}{n+1} \right) p$ was evaluated with respect to surface water, w to obtain Equation (5.19)

$$\frac{\partial g}{\partial w} = \frac{p+N_0}{p+1} \quad (5.19)$$

When Equation (5.19) was evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.20)

$$\frac{\partial g}{\partial w} \Big|_{(w_s, n_s, 0)} = N_0 \quad (5.20)$$

The partial derivative of $g(w, n, p) = \left(\frac{p+N_0}{p+1} \right) w - mn - g \left(\frac{n}{n+1} \right) p$ was again determined with respect to soil water, n to obtain Equation (5.21)

$$\begin{aligned} \frac{\partial g}{\partial n} &= -m - gp \frac{\partial}{\partial n} \left[\left(\frac{n}{n+1} \right) \right] \\ \frac{\partial g}{\partial n} &= -m - gp \left[\frac{(n+1) - n}{(n+1)^2} \right] = -m - gp \left[\frac{1}{(n+1)^2} \right] = - \left[m + \frac{gp}{(n+1)^2} \right] \end{aligned} \quad (5.21)$$

When Equation (5.21) is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.22)

$$\left. \frac{\partial g}{\partial n} \right|_{(w_s, n_s, 0)} = - \left[m + \frac{g \cdot (0)}{(n+1)^2} \right] = -m \quad (5.22)$$

The partial derivative of $g(w, n, p) = \left(\frac{p + N_0}{p + 1} \right) w - mn - g \left(\frac{n}{n+1} \right) p$ is finally determined with respect to plant population density, p to obtain Equation (5.23)

$$\begin{aligned} \frac{\partial g}{\partial p} &= w \frac{\partial}{\partial p} \left[\frac{p + N_0}{p + 1} \right] - g \left[\frac{n}{n+1} \right] = w \left[\frac{(p+1) - (p+N_0)}{(p+1)^2} \right] - g \left[\frac{n}{n+1} \right] \\ &= w \left[\frac{1 - N_0}{(p+1)^2} \right] - g \left[\frac{n}{n+1} \right] \end{aligned} \quad (5.23)$$

When Equation (5.23) was evaluated at $E_1^* = (w_s, n_s, 0)$ gives Equation (5.24)

$$\begin{aligned} \Rightarrow \left. \frac{\partial g}{\partial p} \right|_{(w_s, n_s, 0)} &= \left[\frac{a}{rN_0 + l} \right] \left[\frac{1 - N_0}{(0+1)^2} \right] - g \left[\frac{\left\{ \frac{aN_0}{m(rN_0 + l)} \right\}}{\left\{ \frac{aN_0}{m(rN_0 + l)} \right\} + 1} \right] \\ &= \left[\left(\frac{a}{rN_0 + l} \right) (1 - N_0) \right] - \left[\frac{agN_0}{aN_0 + m(rN_0 + l)} \right] \\ \Rightarrow \left. \frac{\partial g}{\partial p} \right|_{(w_s, n_s, 0)} &= \frac{a(1 - N_0)}{rN_0 + l} - \frac{agN_0}{aN_0 + m(rN_0 + l)} \end{aligned} \quad (5.24)$$

Since the point $E_1^* = (w_s, n_s, 0)$ is the equilibrium solution of the linearised system of equations in Equation (5.2), it implies that it must satisfy the system. Therefore if $g(w, n, p)$ is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.25)

$$g(w, n, p) \Big|_{E_1^* = (w_s, n_s, 0)} = 0 \quad (5.25)$$

The linearised form of the soil water dynamics of the dimensionless system Equation (5.2) is therefore obtained as Equation (5.26)

$$\frac{\partial \bar{n}}{\partial t} = A_{21} \bar{w} + A_{22} \bar{n} + A_{23} \bar{p} + D_{NW} \left(\frac{\partial^2 \bar{n}}{\partial x^2} + \frac{\partial^2 \bar{n}}{\partial y^2} \right) \quad (5.26)$$

where

$$A_{21} = N_0, A_{22} = -m, \text{ and } A_{23} = \frac{a(1-N_0)}{rN_0+l} - \frac{agN_0}{aN_0+m(rN_0+l)}$$

Finally, the partial derivatives of $h(w, n, p) = \left(\frac{n}{n+1} \right) p - up$ is evaluated with respect to surface water, w to obtain Equation (5.27)

$$\frac{\partial h}{\partial w} = 0 \quad (5.27)$$

When Equation (5.27) is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.28)

$$\frac{\partial h}{\partial w} \Big|_{(w_s, n_s, 0)} = 0 \quad (5.28)$$

The partial derivative of $h(w, n, p) = \left(\frac{n}{n+1} \right) p - up$ is again determined with respect to soil water, n to obtain Equation (5.29)

$$\frac{\partial h}{\partial n} = p \frac{\partial}{\partial n} \left[\left(\frac{n}{n+1} \right) \right] = p \left[\frac{1}{(n+1)^2} \right] = \frac{p}{(n+1)^2} \quad (5.29)$$

When this is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.30)

$$\frac{\partial h}{\partial n} \Big|_{E_1^*=(w_s, n_s, 0)} = \frac{p}{(n+1)^2} = \frac{(0)}{(n+1)^2} = 0 \quad (5.30)$$

The partial derivative of $h(w, n, p) = \left(\frac{n}{n+1} \right) p - up$ is finally determined with respect to plant population (biomass) density, p to obtain Equation (5.31)

$$\frac{\partial h}{\partial p} = \left(\frac{n}{n+1} \right) - u \quad (5.31)$$

When Equation (5.31) is evaluated at $E_1^* = (w_s, n_s, 0)$, gives Equation (5.32)

$$\begin{aligned} \Rightarrow \frac{\partial h}{\partial p} \Big|_{E_1^*=(w_s, n_s, 0)} &= \frac{\left[\frac{\left\{ \frac{aN_0}{m(rN_0+l)} \right\}}{\left\{ \frac{aN_0}{m(rN_0+l)} + 1 \right\}} \right] - u}{\left[\frac{\left\{ \frac{aN_0}{m(rN_0+l)} \right\}}{\left\{ \frac{aN_0}{m(rN_0+l)} + 1 \right\}} \right] - u} = \frac{\left[\frac{aN_0/m(rN_0+l)}{aN_0+m(rN_0+l)} \right] - u}{\left[\frac{aN_0/m(rN_0+l)}{aN_0+m(rN_0+l)} \right] - u} \\ &= \frac{aN_0}{aN_0+m(rN_0+l)} - u = \frac{aN_0 - u(aN_0+m(rN_0+l))}{aN_0+m(rN_0+l)} \end{aligned} \quad (5.32)$$

Since the point $E_1^* = (w_s, n_s, 0)$ is the equilibrium solution of the linearised system of equations in Equation (5.2), it implies that it must satisfy the system equation. Therefore if $h(w, n, p)$ is evaluated at $E_1^* = (w_s, n_s, 0)$, one obtains Equation (5.33)

$$h(w, n, p) \Big|_{(w_s, n_s, 0)} = 0 \quad (5.33)$$

The linearised form of the plant population dynamics of the dimensionless system in Equation (5.2) is therefore obtained as Equation (5.34)

$$\frac{\partial \bar{p}}{\partial t} = A_{31} \bar{w} + A_{32} \bar{n} + A_{33} \bar{p} + D_{PW} \left(\frac{\partial^2 \bar{p}}{\partial x^2} + \frac{\partial^2 \bar{p}}{\partial y^2} \right) \quad (5.34)$$

where

$$A_{31} = 0, A_{32} = 0 \text{ and } A_{33} = \frac{aN_0 - u[aN_0 + m(rN_0 + l)]}{aN_0 + m(rN_0 + l)}$$

Hence, the overall linearised form of the system Equation (5.2) is given by Equations (5.35)

$$\left. \begin{aligned} \frac{\partial \bar{w}}{\partial t} &= 0 = A_{11} \bar{w} + A_{12} \bar{n} + A_{13} \bar{p} + \left(\frac{\partial^2 \bar{w}}{\partial x^2} + \frac{\partial^2 \bar{w}}{\partial y^2} \right) \\ \frac{\partial \bar{n}}{\partial t} &= A_{21} \bar{w} + A_{22} \bar{n} + A_{23} \bar{p} + D_{NW} \left(\frac{\partial^2 \bar{n}}{\partial x^2} + \frac{\partial^2 \bar{n}}{\partial y^2} \right) \\ \frac{\partial \bar{p}}{\partial t} &= A_{31} \bar{w} + A_{32} \bar{n} + A_{33} \bar{p} + D_{PW} \left(\frac{\partial^2 \bar{p}}{\partial x^2} + \frac{\partial^2 \bar{p}}{\partial y^2} \right) \end{aligned} \right\} \quad (5.35)$$

where A_{ij} is given by

$$A_{11} = -(rN_0 + l), A_{12} = 0, A_{13} = -\frac{ar(1-N_0)}{rN_0 + l}, A_{21} = N_0, A_{22} = -m, A_{23} = 0, A_{31} = 0, A_{32} = 0$$

$$A_{23} = \frac{a(1-N_0)}{rN_0+l} - \frac{agN_0}{aN_0+m(rN_0+l)}, \text{ and } A_{33} = \frac{aN_0-u[aN_0+m(rN_0+l)]}{aN_0+m(rN_0+l)}$$

5.5 Linear Stability Analysis of $E_1^* = [w^*, n^*, 0]$ in the Absence of Spatial Variation

For any diffusion-driven instability in a reaction diffusion system, the first condition that must be satisfied is that, the homogeneous steady state must be linearly stable to small perturbations in the absence of diffusion (Bentil and Murray, 1992). Thus, with no spatial variation, the linearised system of equations as obtained earlier in Equations (5.35) is represented as a system of Equation (5.36)

$$\left. \begin{aligned} \frac{\partial \bar{w}}{\partial t} &= 0 = A_{11}\bar{w} + A_{12}\bar{n} + A_{13}\bar{p} \\ \frac{\partial \bar{n}}{\partial t} &= A_{21}\bar{w} + A_{22}\bar{n} + A_{23}\bar{p} \\ \frac{\partial \bar{p}}{\partial t} &= A_{31}\bar{w} + A_{32}\bar{n} + A_{33}\bar{p} \end{aligned} \right\} \quad (5.36)$$

where A_{ij} 's are given by

$$A_{11} = -(rN_0+l), A_{12} = 0, A_{13} = -\frac{ar(1-N_0)}{rN_0+l}, A_{21} = N_0, A_{31} = 0, A_{32} = 0, A_{22} = -m$$

$$A_{23} = \frac{a(1-N_0)}{rN_0+l} - \frac{agN_0}{aN_0+m(rN_0+l)}, \text{ and } A_{33} = \frac{aN_0-u[aN_0+m(rN_0+l)]}{aN_0+m(rN_0+l)}$$

From the first equation of the system in Equation (5.36), one obtains Equation (5.37) since

$$A_{12} = 0$$

$$\bar{w} = \frac{-(A_{12}\bar{n} + A_{13}\bar{p})}{A_{11}} = -\frac{A_{13}\bar{p}}{A_{11}} \quad (5.37)$$

Therefore, with no spatial variation, the homogeneous form given by Equation (5.36) reduces to the system of equations as shown in Equation (5.38)

$$\left. \begin{aligned} \frac{\partial \bar{n}}{\partial t} &= A_{22}\bar{n} + \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \bar{p} \\ \frac{\partial \bar{p}}{\partial t} &= A_{32}\bar{n} + \left(A_{33} - \frac{A_{13}A_{31}}{A_{11}} \right) \bar{p} \end{aligned} \right\} \quad (5.38)$$

Since $A_{31} = 0$ and $A_{32} = 0$, Equation (5.38) further reduces to Equation (5.39)

$$\left. \begin{aligned} \frac{\partial \bar{n}}{\partial t} &= A_{22}\bar{n} + \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \bar{p} \\ \frac{\partial \bar{p}}{\partial t} &= (A_{33}) \bar{p} \end{aligned} \right\} \quad (5.39)$$

The relation in Equation (5.39) was then represented as Equation (5.40) below

$$\begin{bmatrix} \frac{\partial \bar{n}}{\partial t} \\ \frac{\partial \bar{p}}{\partial t} \end{bmatrix} = \begin{bmatrix} A_{22} & \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \\ 0 & A_{33} \end{bmatrix} \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.40)$$

The representation indicated by Equation (5.40) can also be represented generally by Equation (5.41)

$$\frac{\partial k}{\partial t} = Hk, \quad \text{where } H = \begin{bmatrix} A_{22} & \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \\ 0 & A_{33} \end{bmatrix} \text{ and } k = \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.41)$$

and H is the stability matrix. A solution is sought for k in the form given as Equation (5.42)

$$k \propto e^{\lambda t} \quad (5.42)$$

where λ is the eigenvalue. The steady state $k = 0$ is linearly stable if $\text{Re } \lambda < 0$ since in this case the perturbation $k \rightarrow 0$ as $t \rightarrow \infty$. Substituting Equation (5.42) into H in Equation (5.41) determines the eigenvalues λ as the solution of Equation (5.43) below

$$|H - \lambda I| = \begin{vmatrix} A_{22} - \lambda & A_{23} - \frac{A_{13}A_{21}}{A_{11}} \\ 0 & A_{33} - \lambda \end{vmatrix} = 0 \quad (5.43)$$

Evaluating the determinant represented by Equation (5.43) leads to the quadratic Equation (5.44)

$$\lambda^2 - (\text{tr } H)\lambda + \det H = \lambda^2 - (A_{22} + A_{33})\lambda + A_{22}A_{33} = 0 \quad (5.44)$$

Thus, linear stability, that is $\text{Re } \lambda < 0$ is guaranteed if Equations (5.45) and (5.46) are satisfied:

$$\text{tr } H = A_{22} + A_{33} = -m + \left[-u + \frac{aN_0}{aN_0 + m(rN_0 + l)} \right] < 0 \quad (5.45)$$

and

$$\text{Det } H = A_{22}A_{33} = -m \times \left[-u + \frac{aN_0}{aN_0 + m(rN_0 + l)} \right] > 0 \quad (5.46)$$

Now as $a \rightarrow 0$, $\frac{aN_0}{aN_0 + m(rN_0 + l)} \rightarrow 0$ and Equations (5.45) and (5.46) are reduced to Equations (5.47) and (5.48).

$$\text{tr } H = -m - u = -(m + u) < 0 \quad (5.47)$$

and

$$\text{Det } H = -m[-u] = mu > 0 \quad (5.48)$$

5.6 Local Stability and Hopf Bifurcation

In this section, the local stability of the equilibria and the existence of the Hopf bifurcation of constant periodic solutions surrounding the positive equilibria of system Equation (5.2) was studied. There are two equilibrium solutions for the system Equation (5.2). These are indicated in (i) and (ii) respectively:

$$(i). \quad E_1^* = \left[w^* = \frac{a}{rN_0 + l}, \quad n^* = \frac{aN_0}{m(rN_0 + l)}, \quad p^* = 0 \right]$$

$$(ii). \quad E_2^* = \left[w = \frac{a(p_s + 1)}{l(p_s + 1) + r(p_s + N_0)}, \quad n = \frac{u}{1 - u}, \quad p = \frac{a - lw - rmu}{gru} \right]$$

In (i), the biomass dynamics goes into extinction. The (ii) is the non-trivial steady state representing the coexistence of the surface water dynamics, soil water dynamics and the biomass density. Now, by analysing the characteristic equation, in Equation (5.44), the

discussion of the geometrical properties of the equilibria of the system Equation (5.2) can be discussed by theorem 5. 1.

Theorem 5.1: If $m+u > \frac{aN_0}{aN_0+m(rN_0+l)}$ and $u > \frac{aN_0}{aN_0+m(rN_0+l)}$ for the system in

Equation (5.2), then the trivial equilibrium point E_1^* of the system of partial differential equations in Equation (5.2) is locally asymptotically stable, if all the eigenvalues of the Jacobian matrix evaluated at E_1^* have negative real parts. However, if either

$u < \frac{aN_0}{aN_0+m(rN_0+l)}$ or $m+u < \frac{aN_0}{aN_0+m(rN_0+l)}$ hold for the system Equation (5.2),

then the trivial equilibrium point E_1^* of the system of partial differential Equation (5.2) is said to be unstable if at least one of the eigenvalues of the jacobian matrix is positive, or has positive real part.

Proof: For equilibrium point $E_1^* = [w^* = a/(rN_0+l), n^* = aN_0/m(rN_0+l), p^* = 0]$, the characteristic equation of system Equation (5.2) was obtained as Equation (5.57a).

$$\lambda^2 - \left(-m-u + \frac{aN_0}{aN_0+m(rN_0+l)} \right) \lambda + mu - \frac{aN_0m}{aN_0+m(rN_0+l)} = 0 \quad (5.57a)$$

The roots of the characteristic Equation (5.57a) are

$$\lambda_{1,2} = -\frac{1}{2} \left(m+u - \frac{aN_0}{aN_0+m(rN_0+l)} \right) \pm \frac{1}{2} \sqrt{\left(m+u - \frac{aN_0}{aN_0+m(rN_0+l)} \right)^2 - 4 \left(u - \frac{aN_0}{aN_0+m(rN_0+l)} \right)}$$

Assume that $m+u > \frac{aN_0}{aN_0+m(rN_0+l)}$ then $\left(m+u - \frac{aN_0}{aN_0+m(rN_0+l)} \right) = h > 0$. Similarly, if

$u > \frac{aN_0}{aN_0+m(rN_0+l)}$, then $u - \frac{aN_0}{aN_0+m(rN_0+l)} = h_0 > 0$. Substituting h and h_0 into the

expression for the roots of the characteristic equation reduces the expression to Equaton (5.58a)

$$\lambda_{1,2} = -\frac{1}{2} h \pm \frac{1}{2} \sqrt{h^2 - 4h_0} \quad (5.58a)$$

For locally asymptotic stability, all the eigenvalues of the Jacobian matrix evaluated at E_1^* must have negative real part. From Equation (5.58a), one obtains Equations (5.59a) and (5.60a) respectively.

$$h^2 - 4h_0 > 0 \Rightarrow h_0 < \frac{1}{4}h^2 \quad (5.59a)$$

$$h^2 \geq h^2 - 4h_0 \Rightarrow 4h_0 \geq h^2 - h^2 = 0 \Rightarrow h_0 \geq 0 \quad (5.60a)$$

When Equations (5.59a) and (5.60a) are put together, one obtains Equation (5.61a)

$$0 \leq h_0 < \frac{1}{4}h^2 \quad (5.61a)$$

From Equation (5.60a), $h_0 \geq 0$. Since $h_0 = u - aN_0/[aN_0 + m(rN_0 + l)]$ implies that $u - aN_0/[aN_0 + m(rN_0 + l)] \geq 0$. If $h_0 = 0$, then one of the eigenvalues becomes zero and therefore nullifies the condition for stability. Hence h_0 should be strictly positive and hence the condition that $u > aN_0/[aN_0 + m(rN_0 + l)]$ is satisfied. Again, $h = m + h_0 = m + u - \frac{aN_0}{aN_0 + m(rN_0 + l)}$ and therefore if $u > aN_0/[aN_0 + m(rN_0 + l)]$ then it follows that, $m + u > \frac{aN_0}{aN_0 + m(rN_0 + l)}$. Hence, the trivial equilibrium point E_1^* of the system of partial differential Equation (5.2) is locally asymptotically stable

5.7 Linear Instability Analysis of $E_1^* = [w^*, n^*, 0]$ in the Presence of Spatial Variation

Diffusion-driven instability is concerned with instability in the presence of spatial variation. The interest is on linear instability of the steady states that is solely spatially dependent. Thus, the full reaction diffusion system given by Equation (5.35) is considered. One thus considers the substitution of perturbations of the following forms given by Equations (5.49), (5.50) and (5.51):

$$\bar{w}(x, y; t) = \bar{w}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.49)$$

$$\bar{n}(x, y, t) = \bar{n}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.50)$$

$$\bar{p}(x, y, t) = \bar{p}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.51)$$

Now differentiating Equation (5.49) partially into the second order forms with respect to spatial components (x, y) , one obtains Equations (5.52) and (5.53) respectively.

$$\frac{\partial^2 \bar{w}(x, y, t)}{\partial x^2} = -q_1^2 \bar{w}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.52)$$

$$\frac{\partial^2 \bar{w}(x, y, t)}{\partial y^2} = -q_2^2 \bar{w}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.53)$$

Adding Equations (5.52) and (5.53) leads to Equation (5.54)

$$\begin{aligned} \frac{\partial^2 \bar{w}(x, y, t)}{\partial x^2} + \frac{\partial^2 \bar{w}(x, y, t)}{\partial y^2} &= -q_1^2 \bar{w}(t) \cos(q_1 x) \cos(q_2 y) - q_2^2 \bar{w}(t) \cos(q_1 x) \cos(q_2 y) \\ &= -(q_1^2 + q_2^2) \bar{w}(t) \cos(q_1 x) \cos(q_2 y) \end{aligned} \quad (5.54)$$

Similarly, Equation (5.50) is differentiated partially into the second order forms with respect to spatial components (x, y) , to obtain Equations (5.55) and (5.56) respectively

$$\frac{\partial^2 \bar{n}(x, y, t)}{\partial x^2} = -q_1^2 \bar{n}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.55)$$

$$\frac{\partial^2 \bar{n}(x, y, t)}{\partial y^2} = -q_2^2 \bar{n}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.56)$$

Adding Equations (5.55) and (5.56) also leads to Equation (5.57)

$$\begin{aligned} \frac{\partial^2 \bar{n}(x, y, t)}{\partial x^2} + \frac{\partial^2 \bar{n}(x, y, t)}{\partial y^2} &= -q_1^2 \bar{n}(t) \cos(q_1 x) \cos(q_2 y) - q_2^2 \bar{n}(t) \cos(q_1 x) \cos(q_2 y) \\ &= -(q_1^2 + q_2^2) \bar{n}(t) \cos(q_1 x) \cos(q_2 y) \end{aligned} \quad (5.57)$$

Finally, Equation (5.51) is differentiated partially into the second order forms with respect to spatial components (x, y) , to obtain Equations (5.58) and (5.59) respectively

$$\frac{\partial^2 \bar{p}(x, y, t)}{\partial x^2} = -q_1^2 \bar{p}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.58)$$

$$\frac{\partial^2 \bar{p}(x, y, t)}{\partial y^2} = -q_2^2 \bar{p}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.59)$$

Adding Equations (5.58) and (5.59) leads to Equation (5.60)

$$\begin{aligned} \frac{\partial^2 \bar{p}(x, y, t)}{\partial x^2} + \frac{\partial^2 \bar{p}(x, y, t)}{\partial y^2} &= -q_1^2 \bar{p}(t) \cos(q_1 x) \cos(q_2 y) - q_2^2 \bar{p}(t) \cos(q_1 x) \cos(q_2 y) \\ &= -(q_1^2 + q_2^2) \bar{p}(t) \cos(q_1 x) \cos(q_2 y) \end{aligned} \quad (5.60)$$

The Equations (5.54), (5.57) and (5.60) were substituted into the linearised system of equations in Equation (5.35) to obtain the system of Equation (5.61)

$$\left. \begin{aligned} 0 &= A_{11} \bar{w}(t) + A_{12} \bar{n}(t) + A_{13} \bar{p}(t) - (q_1^2 + q_2^2) \bar{w}(t) \\ \frac{\partial \bar{n}(t)}{\partial t} &= A_{21} \bar{w}(t) + A_{22} \bar{n}(t) + A_{23} \bar{p}(t) - D_{NW} (q_1^2 + q_2^2) \bar{n}(t) \\ \frac{\partial \bar{p}(t)}{\partial t} &= A_{31} \bar{w}(t) + A_{32} \bar{n}(t) + A_{33} \bar{p}(t) - D_{PW} (q_1^2 + q_2^2) \bar{p}(t) \end{aligned} \right\} \quad (5.61)$$

Let $Q^2 = q_1^2 + q_2^2$, then the system of Equation (5.61) becomes Equation (5.62)

$$\left. \begin{aligned} 0 &= A_{11} \bar{w}(t) + A_{12} \bar{n}(t) + A_{13} \bar{p}(t) - \bar{w}(t) Q^2 \\ \frac{\partial \bar{n}(t)}{\partial t} &= A_{21} \bar{w}(t) + A_{22} \bar{n}(t) + A_{23} \bar{p}(t) - D_{NW} \bar{n}(t) Q^2 \\ \frac{\partial \bar{p}(t)}{\partial t} &= A_{31} \bar{w}(t) + A_{32} \bar{n}(t) + A_{33} \bar{p}(t) - D_{PW} \bar{p}(t) Q^2 \end{aligned} \right\} \quad (5.62)$$

A quasi-steady state approach was adopted. It was therefore assumed that the rate of change of surface water is zero, and hence the rate of change of surface water around its equilibrium is also equal to zero. Thus, from surface water balance equation of Equation (5.62) one obtains Equation (5.63)

$$\bar{w}(t) = \frac{A_{12} \bar{n}(t) + A_{13} \bar{p}(t)}{Q^2 - A_{11}} \quad (5.63)$$

But since $A_{12} = 0$, Equation (5.63) reduces to Equation (5.64)

$$\bar{w}(t) = \frac{A_{13}\bar{p}(t)}{Q^2 - A_{11}} \quad (5.64)$$

Equation (5.64) was substituted back into the system of equations in Equation (5.62) together with $A_{12} = 0, A_{31} = 0$ and $A_{32} = 0$ to obtain the system of equations in Equation (5.65)

$$\left. \begin{aligned} \frac{\partial \bar{n}(t)}{\partial t} &= A_{21} \times \left[\frac{A_{13}\bar{p}(t)}{Q^2 - A_{11}} \right] + A_{22} \times \bar{n}(t) + A_{23}\bar{p}(t) - D_{NW}\bar{n}(t)Q^2 \\ \frac{\partial \bar{p}(t)}{\partial t} &= [0] \times \left[\frac{A_{13}\bar{p}(t)}{Q^2 - A_{11}} \right] + [0] \times \bar{n}(t) + A_{33}\bar{p}(t) - D_{PW}\bar{p}(t)Q^2 \end{aligned} \right\} \quad (5.65)$$

Equation (5.65) finally reduces to a system of two partial differential equations as Equation (5.66)

$$\left. \begin{aligned} \frac{\partial \bar{n}(t)}{\partial t} &= (A_{22} - D_{NW}Q^2)\bar{n}(t) + A_{23} \left[A_{21} \times \frac{A_{13}}{Q^2 - A_{11}} + A_{23} \right] \bar{p}(t) \\ \frac{\partial \bar{p}(t)}{\partial t} &= (A_{33} - D_{PW}Q^2)\bar{p}(t) \end{aligned} \right\} \quad (5.66)$$

The relation represented as Equation (5.66) was then re-written as Equation (5.67)

$$\begin{bmatrix} \frac{\partial \bar{n}}{\partial t} \\ \frac{\partial \bar{p}}{\partial t} \end{bmatrix} = \begin{bmatrix} (A_{22} - D_{NW}Q^2) & \left(A_{21} \times \frac{A_{13}}{Q^2 - A_{11}} + A_{23} \right) \\ 0 & (A_{33} - D_{PW}Q^2) \end{bmatrix} \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.67)$$

The representation indicated by Equation (5.67) can also be represented generally by Equation (5.68)

$$\frac{\partial \gamma}{\partial t} = J\gamma, \quad \text{where } J = \begin{bmatrix} A_{22} - D_{NW}Q^2 & \left(A_{21} \times \frac{A_{13}}{Q^2 - A_{11}} + A_{23} \right) \\ 0 & A_{33} - D_{PW}Q^2 \end{bmatrix} \text{ and } \gamma = \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.68)$$

where J is the stability matrix. The stability or Jacobian matrix from the system of Equations (5.68) is indicated as Equation (5.69)

$$J = \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix} \quad (5.69)$$

where the elements of the Jacobian matrix are as follows:

$$B_{11} = (A_{22} - D_{NW}Q^2), \quad B_{12} = A_{21} \times \frac{A_{13}}{Q^2 - A_{11}} + A_{23}, \quad B_{21} = 0 \quad \text{and} \quad B_{22} = (A_{33} - D_{PW}Q^2).$$

The eigenvalues λ_i for $i = 1, 2$ for the Jacobian matrix was obtained from an equation given by Equation (5.70)

$$|J - \lambda I| = 0 \quad \Rightarrow \quad \lambda^2 - (trJ)\lambda + \det J = 0 \quad (5.70)$$

For the stability condition, $\text{Re} \lambda < 0$ and a necessary and sufficient conditions for linear stability is that $trJ < 0$ as indicated in Equation (5.71)

$$trJ = B_{11} + B_{22} < 0 \quad (5.71)$$

Also, the $\det J = f(Q^2) > 0$ as indicated in Equation (5.72)

$$\det J = f(Q^2) = B_{11}B_{22} - B_{21}B_{12} > 0 \quad (5.72)$$

However, if $B_{21} = 0$, the condition given by Equation (5.72) reduces to Equation (5.73)

$$f(Q^2) = B_{11}B_{22} > 0 \quad (5.73)$$

However, for pattern formation to occur, instability is required. This is only possible if one of Equations (5.71) and (5.73) is not satisfied or both of Equations are not satisfied. Thus, for pattern formation, the following situations labelled Equations (5.71) and (5.73) must be violated. If Equation (5.71) is violated, the system will be unstable. Thus, substituting B_{11} and B_{22} in Equation (5.71) for the trace of the Jacobian (first stability condition), one obtains the following:

- (i) the parameter set equations in Equation (5.71) which is unstable was obtained as Equation (5.74)

$$B_{11} + B_{22} = [A_{22} - D_{NW}Q^2] + [A_{33} - D_{PW}Q^2] > 0$$

$$\begin{aligned} &\Rightarrow \left[-m - D_{NW}Q^2 \right] + \left[-D_{PW}Q^2 - u + \frac{aN_0}{aN_0 + m(rN_0 + l)} \right] > 0 \\ &\Rightarrow m + u + D_{NW}Q^2 + D_{PW}Q^2 < \frac{aN_0}{aN_0 + m(rN_0 + l)} \end{aligned} \quad (5.74)$$

(ii) Similarly, for instability, it is required that $f(Q^2) = B_{11}B_{22} < 0$ leading to Equation (5.75)

$$\begin{aligned} B_{11}B_{22} &= \left[A_{22} - D_{NW}Q^2 \right] \times \left[A_{33} - D_{PW}Q^2 \right] < 0 \\ &\Rightarrow \left[-m - D_{NW}Q^2 \right] \times \left[-D_{PW}Q^2 - u + \frac{aN_0}{aN_0 + m(rN_0 + l)} \right] < 0 \\ &\Rightarrow (m + D_{NW}Q^2)(u + D_{PW}Q^2) - (m + D_{NW}Q^2) \left[\frac{aN_0}{aN_0 + m(rN_0 + l)} \right] < 0 \end{aligned} \quad (5.75)$$

Thus, pattern formation is possible provided that Equations (5.76) or (5.77), or both hold as indicated.

$$(m + D_{NW}Q^2 + u + D_{PW}Q^2) < \left[\frac{aN_0}{aN_0 + m(rN_0 + l)} \right] \quad (5.76)$$

$$(u + D_{PW}Q^2) < \left[\frac{aN_0}{aN_0 + m(rN_0 + l)} \right] \quad (5.77)$$

5.8 Linear Stability Analysis of $E_2^* = [w_s, n_s, p_s]$ in the Absence of Spatial Variation

The non-trivial steady state solutions indicated in Equation (5.5) is restated as Equation (5.78).

$$E_2^* = \left[w_s = \frac{a(p_s + 1)}{l(p_s + 1) + r(p_s + N_0)}, \quad n_s = \frac{u}{1 - u}, \quad p_s = \frac{a - lw - rmu}{gru} \right] \quad (5.78)$$

From Equation (5.11), $\partial f / \partial w$ was given as Equation (5.79)

$$\frac{\partial f}{\partial w} = -l - r \left(\frac{p + N_0}{p + 1} \right) \quad (5.79)$$

When Equation (5.79) is evaluated at $E_2^* = (w_s, n_s, p_s)$, one obtains Equation (5.80)

$$\left. \frac{\partial f}{\partial w} \right|_{(w_s, n_s, p_s)} = -l - \frac{r(a - lw - rmu + gruN_0)}{a - lw - rmu + gru} \quad (5.80)$$

From Equation (5.13), the partial derivative of $f(w, n, p) = a - lw - r\left(\frac{p + N_0}{p + 1}\right)w$ determined with respect to soil water, n , is as indicated in Equation (5.81)

$$\frac{\partial f}{\partial n} = 0 \quad (5.81)$$

Similarly, when Equation (5.81) is evaluated at (w_s, n_s, p_s) , one obtains Equation (5.82)

$$\left. \frac{\partial f}{\partial n} \right|_{(w_s, n_s, p_s)} = 0 \quad (5.82)$$

Finally, from Equation (5.15), the partial derivative of $f(w, n, p) = a - lw - r\left(\frac{p + N_0}{p + 1}\right)w$ determined with respect to plant population (biomass) density (p), is as shown in Equation (5.83)

$$\frac{\partial f}{\partial p} = -rw \cdot \left[\frac{(p+1) - (p+N_0)}{(p+1)^2} \right] = -\frac{rw(1-N_0)}{(p+1)^2} \quad (5.83)$$

When Equation (5.83) is evaluated at (w_s, n_s, p_s) , leads to Equation (5.84)

$$\begin{aligned} \left. \frac{\partial f}{\partial p} \right|_{(w_s, n_s, p_s)} &= -r \cdot \left[\frac{a(p_s+1)(1-N_0)}{l(p_s+1)+r(p_s+N_0)} \right] \cdot \left[\frac{1}{(p_s+1)^2} \right] \\ &= -\frac{ar(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)} \end{aligned} \quad (5.84)$$

The point (w_s, n_s, p_s) is the non-trivial equilibrium solution of the linearised system of equations in Equation (5.2). This implies that it must satisfy the system equation. Therefore if $f(w, n, p)$ is evaluated at (w_s, n_s, p_s) , one obtains Equation (5.85)

$$f(w, n, p) \Big|_{(w_s, n_s, p_s)} = 0 \quad (5.85)$$

The linearised form of the surface water dynamics of the dimensionless system in Equation (5.2) is therefore obtained as Equation (5.86)

$$\frac{\partial \bar{w}}{\partial t} = 0 = A_{11}\bar{w} + A_{12}\bar{n} + A_{13}\bar{p} + \left(\frac{\partial^2 \bar{w}}{\partial x^2} + \frac{\partial^2 \bar{w}}{\partial y^2} \right) \quad (5.86)$$

where

$$A_{11} = -l - \frac{r(a-lw-rmu+gruN_0)}{a-lw-rmu+gru}, A_{12} = 0, \text{ and } A_{13} = -\frac{ar(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)}$$

Similarly, the partial derivative of $g(w, n, p) = \left(\frac{p+N_0}{p+1} \right) w - mn - g \left(\frac{n}{n+1} \right) p$ evaluated with respect to surface water, w as obtained from Equation (5.19) is restated as Equation (5.87)

$$\frac{\partial g}{\partial w} = \frac{p+N_0}{p+1} \quad (5.87)$$

When Equation (5.87) is evaluated at (w_s, n_s, p_s) , one obtains Equation (5.88)

$$\frac{\partial g}{\partial w} \Big|_{(w_s, n_s, p_s)} = \frac{a-lw-rmu+gruN_0}{a-lw-rmu+gru} \quad (5.88)$$

When the partial derivative of $g(w, n, p) = \left(\frac{p+N_0}{p+1} \right) w - mn - g \left(\frac{n}{n+1} \right) p$ was determined with respect to soil water, n as shown earlier in Equation (5.21), one obtains Equation (5.89)

$$\frac{\partial g}{\partial n} = - \left[m + \frac{gp}{(n+1)^2} \right] \quad (5.89)$$

When Equation (5.89) is evaluated at (w_s, n_s, p_s) , one obtains Equation (5.90)

$$\frac{\partial g}{\partial n} \Big|_{(w_s, n_s, p_s)} = -m - (1-u)^2 \left[\frac{a-lw-rmu}{ur} \right] \quad (5.90)$$

The partial derivative of $g(w, n, p) = \left(\frac{p+N_0}{p+1}\right)^{w-mn} - g\left(\frac{n}{n+1}\right)p$ was finally determined with respect to plant population (biomass) density, (p) at earlier stages by Equation (5.23) to obtain Equation (5.91)

$$\frac{\partial g}{\partial p} = w \left[\frac{1-N_0}{(p+1)^2} \right] - g \left[\frac{n}{n+1} \right] \quad (5.91)$$

Also, when Equation (5.91) is evaluated at (w_s, n_s, p_s) , one gets Equation (5.92)

$$\begin{aligned} \Rightarrow \frac{\partial g}{\partial p} \Big|_{(w_s, n_s, p_s)} &= \left[\frac{a(p_s+1)}{l(p_s+1)+r(p_s+N_0)} \right] \left[\frac{1-N_0}{(p_s+1)^2} \right] - g \left[\frac{\left\{ \frac{u}{1-u} \right\}}{\left\{ \frac{u}{1-u} \right\} + 1} \right] \\ &= \frac{a(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)} - gu \end{aligned} \quad (5.92)$$

Since the point (w_s, n_s, p_s) is the equilibrium solution of the system in Equation (5.2), it implies that it satisfies the system in Equation (5.2). Thus, $g(w, n, p)$ evaluated at (w_s, n_s, p_s) gives Equation (5.93)

$$g(w, n, p) \Big|_{(w_s, n_s, p_s)} = 0 \quad (5.93)$$

The linearised form of the soil water dynamics of the dimensionless system in Equation (5.2) is given by Equation (5.94)

$$\frac{\partial \bar{n}}{\partial t} = A_{21} \bar{w} + A_{22} \bar{n} + A_{23} \bar{p} + D_{NW} \left(\frac{\partial^2 \bar{n}}{\partial x^2} + \frac{\partial^2 \bar{n}}{\partial y^2} \right) \quad (5.94)$$

where

$$A_{21} = \frac{a-lw-rmu+gruN_0}{a-lw-rmu+gru}, \quad A_{22} = -m - (1-u)^2 \left[\frac{a-lw-rmu}{ur} \right] \text{ and}$$

$$A_{23} = \frac{a(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)} - gu$$

Finally, the partial derivatives of $h(w, n, p) = \left(\frac{n}{n+1}\right)p - up$ was evaluated with respect to surface water, w in Equation (5.27) to obtain Equation (5.95).

$$\frac{\partial h}{\partial w} = 0 \quad (5.95)$$

When Equation (5.95) is evaluated at (w_s, n_s, p_s) , one obtains Equation (5.96)

$$\left. \frac{\partial h}{\partial w} \right|_{(w_s, n_s, p_s)} = 0 \quad (5.96)$$

The partial derivative of $h(w, n, p) = \left(\frac{n}{n+1}\right)p - up$ was again determined with respect to soil water, n in Equation (5.29) to obtain Equation (5.97).

$$\frac{\partial h}{\partial n} = p \frac{\partial}{\partial n} \left[\left(\frac{n}{n+1}\right) \right] = \frac{p}{(n+1)^2} \quad (5.97)$$

When Equation (5.97) is evaluated at (w_s, n_s, p_s) , one obtains Equation (5.98)

$$\Rightarrow \left. \frac{\partial h}{\partial n} \right|_{(w_s, n_s, p_s)} = \frac{p_s}{(n_s+1)^2} = \frac{1}{\left(\frac{u}{1-u} + 1\right)^2} \left[\frac{a-lw-rmu}{gru} \right] = (1-u)^2 \left[\frac{a-lw-rmu}{gru} \right] \quad (5.98)$$

The partial derivative of $h(w, n, p) = \left(\frac{n}{n+1}\right)p - up$ was finally determined with respect to plant population density, p , given in Equation (5.31) to obtain Equation (5.99)

$$\frac{\partial h}{\partial p} = \left(\frac{n}{n+1}\right) - u \quad (5.99)$$

and when Equation (5.99) is evaluated at (w_s, n_s, p_s) , gives Equation (5.100)

$$\Rightarrow \left. \frac{\partial h}{\partial p} \right|_{(w_s, n_s, p_s)} = \left[\frac{\left\{ \frac{u}{1-u} \right\}}{\left\{ \frac{u}{1-u} + 1 \right\}} \right] - u = \left[\frac{\frac{u}{1-u}}{\frac{u+1-u}{1-u}} \right] - u = 0 \quad (5.100)$$

Since the point (w_s, n_s, p_s) is the equilibrium solution of the system equation in Equation (5.2), it implies that it satisfies the system in Equation (5.2). Thus, $h(w, n, p)$ evaluated at (w_s, n_s, p_s) gives Equation (5.101)

$$h(w, n, p)\Big|_{(w_s, n_s, p_s)} = 0 \quad (5.101)$$

The linearised form of the plant population dynamics of the dimensionless system in Equation (5.2) is therefore obtained as Equation (5.102)

$$\frac{\partial \bar{p}}{\partial t} = A_{31} \bar{w} + A_{32} \bar{n} + A_{33} \bar{p} + D_{pW} \left(\frac{\partial^2 \bar{p}}{\partial x^2} + \frac{\partial^2 \bar{p}}{\partial y^2} \right) \quad (5.102)$$

where

$$A_{31} = 0, A_{32} = (1-u)^2 \left[\frac{a-lw-rmu}{gru} \right] \text{ and } A_{33} = 0$$

Hence, the overall linearised form about the point $E_2^* = (w_s, n_s, p_s)$ of the system in Equations (5.2) is given by Equation (5.103).

$$\left. \begin{aligned} \frac{\partial \bar{w}}{\partial t} &= 0 = A_{11} \bar{w} + A_{12} \bar{n} + A_{13} \bar{p} + \left(\frac{\partial^2 \bar{w}}{\partial x^2} + \frac{\partial^2 \bar{w}}{\partial y^2} \right) \\ \frac{\partial \bar{n}}{\partial t} &= A_{21} \bar{w} + A_{22} \bar{n} + A_{23} \bar{p} + D_{nW} \left(\frac{\partial^2 \bar{n}}{\partial x^2} + \frac{\partial^2 \bar{n}}{\partial y^2} \right) \\ \frac{\partial \bar{p}}{\partial t} &= A_{31} \bar{w} + A_{32} \bar{n} + A_{33} \bar{p} + D_{pW} \left(\frac{\partial^2 \bar{p}}{\partial x^2} + \frac{\partial^2 \bar{p}}{\partial y^2} \right) \end{aligned} \right\} \quad (5.103)$$

where A_{ij} 's are given by

$$A_{11} = -l - \frac{r(a-lw-rmu+gruN_0)}{a-lw-rmu+gru}, A_{12} = 0, A_{22} = -m - (1-u)^2 \left[\frac{a-lw-rmu}{ur} \right]$$

$$A_{13} = -\frac{ar(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)}, A_{21} = \frac{a-lw-rmu+gruN_0}{a-lw-rmu+gru}, A_{33} = 0$$

$$A_{23} = \frac{a(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)} - gu, A_{32} = (1-u)^2 \left[\frac{a-lw-rmu}{gru} \right] \text{ and}$$

$$A_{31} = 0$$

Thus, with no spatial variation, the system of Equations (5.2) is linearised about the non-trivial steady state and represented as a system of Equation (5.104)

$$\left. \begin{aligned} \frac{\partial \bar{w}}{\partial t} &= 0 = A_{11}\bar{w} + A_{12}\bar{n} + A_{13}\bar{p} \\ \frac{\partial \bar{n}}{\partial t} &= A_{21}\bar{w} + A_{22}\bar{n} + A_{23}\bar{p} \\ \frac{\partial \bar{p}}{\partial t} &= A_{31}\bar{w} + A_{32}\bar{n} + A_{33}\bar{p} \end{aligned} \right\} \quad (5.104)$$

where A_{ij} 's are given by

$$\begin{aligned} A_{11} &= -l - \frac{r(a-lw-rmu+gruN_0)}{a-lw-rmu+gru}, \quad A_{12} = 0, \quad A_{32} = (1-u)^2 \left[\frac{a-lw-rmu}{gru} \right] \\ A_{13} &= -\frac{ar(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)}, \quad A_{21} = \frac{a-lw-rmu+gruN_0}{a-lw-rmu+gru}, \quad A_{31} = 0 \\ A_{23} &= \frac{a(1-N_0)}{[l(p_s+1)+r(p_s+N_0)](p_s+1)} - gu, \quad A_{22} = -m - (1-u)^2 \left[\frac{a-lw-rmu}{ur} \right] \\ &, \text{ and } A_{33} = 0 \end{aligned}$$

From the first equation of the system in Equation (5.104), one obtains Equation (5.105)

given that $A_{12} = 0$

$$\bar{w} = \frac{-(A_{12}\bar{n} + A_{13}\bar{p})}{A_{11}} = -\frac{A_{13}\bar{p}}{A_{11}} \quad (5.105)$$

Therefore, with no spatial variation, the homogeneous form given by Equation (5.105) reduces to the system of equation indicated in Equation (5.106)

$$\left. \begin{aligned} \frac{\partial \bar{n}}{\partial t} &= A_{22}\bar{n} + \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \bar{p} \\ \frac{\partial \bar{p}}{\partial t} &= A_{32}\bar{n} + \left(A_{33} - \frac{A_{13}A_{31}}{A_{11}} \right) \bar{p} \end{aligned} \right\} \quad (5.106)$$

Since $A_{31} = 0$ and $A_{33} = 0$, Equation (5.106) reduces further to Equation (5.107)

$$\left. \begin{aligned} \frac{\partial \bar{n}}{\partial t} &= A_{22}\bar{n} + \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \bar{p} \\ \frac{\partial \bar{p}}{\partial t} &= A_{32}\bar{n} \end{aligned} \right\} \quad (5.107)$$

The relation in Equation (5.107) is then represented by Equation (5.108)

$$\begin{bmatrix} \frac{\partial \bar{n}}{\partial t} \\ \frac{\partial \bar{p}}{\partial t} \end{bmatrix} = \begin{bmatrix} A_{22} & \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \\ A_{32} & 0 \end{bmatrix} \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.108)$$

The representation indicated by Equation (5.108) can further be represented by Equation (5.109)

$$\frac{\partial k}{\partial t} = Hk, \quad \text{where } H = \begin{bmatrix} A_{22} & \left(A_{23} - \frac{A_{13}A_{21}}{A_{11}} \right) \\ A_{32} & 0 \end{bmatrix} \text{ and } k = \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.109)$$

where H is the stability matrix. A solution is sought for in the form given by Equation (5.110)

$$k \propto e^{\lambda t} \quad (5.110)$$

where λ is the eigenvalue. The steady state $k = 0$ is linearly stable if $\text{Re } \lambda < 0$. Thus, if $\text{Re } \lambda < 0$ the perturbation $k \rightarrow 0$ as $t \rightarrow \infty$. When Equation (5.110) is substituted into H in Equation (5.109) yields the eigenvalues λ as the solution of Equation (5.111)

$$|H - \lambda I| = \begin{vmatrix} A_{22} - \lambda & A_{23} - \frac{A_{13}A_{21}}{A_{11}} \\ A_{32} & -\lambda \end{vmatrix} = 0 \quad (5.111)$$

When the determinant represented by Equation (5.111) is evaluated leads to the quadratic Equation (5.112)

$$\lambda^2 - \lambda(\text{tr } H) + \det H = \lambda^2 - A_{22}\lambda + \left(A_{32} \times \frac{A_{13}A_{21}}{A_{11}} - A_{23}A_{32} \right) = 0 \quad (5.112)$$

Thus, for linear stability, the condition $\text{Re } \lambda < 0$ is guaranteed if the following in Equations (5.113) and (5.114) are satisfied:

$$tr H = A_{22} = -m - (1-u)^2 \left[\frac{a - lw_s - rmu}{ur} \right] < 0 \quad (5.113)$$

and

$$Det H = A_{32} \times \frac{A_{13}A_{21}}{A_{11}} - A_{23}A_{32} > 0$$

$$Det H = \frac{p_s}{(n_s + 1)^2} \left[\frac{ar(1-N_0)(p_s + N_0)}{[l(p_s + 1) + r(p_s + N_0)](p_s + 1)} - \frac{w_s - gu(p_s + 1)^2}{(p_s + 1)^2} \right] > 0 \quad (5.114)$$

Now, Equation (5.113) is satisfied if $a - lw_s - rmu > 0$ implying that $a > lw_s + rmu$.

Similarly, Equation (5.114) is satisfied if $\frac{ar(1-N_0)(p_s + N_0)}{[l(p_s + 1) + r(p_s + N_0)](p_s + 1)} - \frac{w_s - gu(p_s + 1)^2}{(p_s + 1)^2} > 0$.

This implies that $\frac{ar(1-N_0)(p_s + N_0)}{[l(p_s + 1) + r(p_s + N_0)](p_s + 1)} > \frac{w_s - gu(p_s + 1)^2}{(p_s + 1)^2}$.

5.9 Linear Instability Analysis of $E_2^* = [w_s, n_s, p_s]$ in the Presence of Spatial Variation

The purpose of this section is to further determine the linear instability of the steady state E_2^* that is solely spatially dependent. The substitution of perturbations of the following forms given by Equations (5.49), (5.50) and (5.51) and redefined as Equations (5.115), (1.116) and (5.117) were adopted:

$$\bar{w}(x, y; t) = \bar{w}(t) \cos(q_1 x) \times \cos(q_2 y) \quad (5.115)$$

$$\bar{n}(x, y; t) = \bar{n}(t) \cos(q_1 x) \times \cos(q_2 y) \quad (5.116)$$

$$\bar{p}(x, y; t) = \bar{p}(t) \cos(q_1 x) \times \cos(q_2 y) \quad (5.117)$$

The Equations (5.115) to (5.117) were differentiated partially into the second order forms with respect to spatial components (x, y) . The corresponding variables were added to obtain Equations (5.118), (5.119) and (5.120) respectively, which represents the first, second and third perturbations.

$$\frac{\partial^2 \bar{w}(x, y, t)}{\partial x^2} + \frac{\partial^2 \bar{w}(x, y, t)}{\partial y^2} = -(q_1^2 + q_2^2) \bar{w}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.118)$$

$$\frac{\partial^2 \bar{n}(x, y, t)}{\partial x^2} + \frac{\partial^2 \bar{n}(x, y, t)}{\partial y^2} = -(q_1^2 + q_2^2) \bar{n}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.119)$$

$$\frac{\partial^2 \bar{p}(x, y, t)}{\partial x^2} + \frac{\partial^2 \bar{p}(x, y, t)}{\partial y^2} = -(q_1^2 + q_2^2) \bar{p}(t) \cos(q_1 x) \cos(q_2 y) \quad (5.120)$$

Now, substituting Equations (5.118), (5.119) and (5.120) into the linearised system of equations in Equations (5.103), one obtains the system of equations in Equation (5.121)

$$\left. \begin{aligned} 0 &= A_{11} \bar{w}(t) + A_{12} \bar{n}(t) + A_{13} \bar{p}(t) - (q_1^2 + q_2^2) \bar{w}(t) \\ \frac{\partial \bar{n}(t)}{\partial t} &= A_{21} \bar{w}(t) + A_{22} \bar{n}(t) + A_{23} \bar{p}(t) - D_{NW} (q_1^2 + q_2^2) \bar{n}(t) \\ \frac{\partial \bar{p}(t)}{\partial t} &= A_{31} \bar{w}(t) + A_{32} \bar{n}(t) + A_{33} \bar{p}(t) - D_{PW} (q_1^2 + q_2^2) \bar{p}(t) \end{aligned} \right\} \quad (5.121)$$

Similarly, if we let $Q^2 = q_1^2 + q_2^2$, then the system of equations in Equation (5.121) becomes Equation (5.122)

$$\left. \begin{aligned} 0 &= A_{11} \bar{w}(t) + A_{12} \bar{n}(t) + A_{13} \bar{p}(t) - \bar{w}(t) Q^2 \\ \frac{\partial \bar{n}(t)}{\partial t} &= A_{21} \bar{w}(t) + A_{22} \bar{n}(t) + A_{23} \bar{p}(t) - D_{NW} \bar{n}(t) Q^2 \\ \frac{\partial \bar{p}(t)}{\partial t} &= A_{31} \bar{w}(t) + A_{32} \bar{n}(t) + A_{33} \bar{p}(t) - D_{PW} \bar{p}(t) Q^2 \end{aligned} \right\} \quad (5.122)$$

Suppose, one assumed a quasi-steady state approach with the rate of change of the surface water as zero, then the rate of change of surface water around its equilibrium position will also be equal to zero. Thus, from surface water balance equation of system Equation (5.122) one obtains Equation (5.123)

$$\bar{w}(t) = \frac{A_{12} \bar{n}(t) + A_{13} \bar{p}(t)}{Q^2 - A_{11}} \quad (5.123)$$

But $A_{12} = 0$ and hence equation (5.123) reduces to equation (5.124)

$$\bar{w}(t) = \frac{A_{13}\bar{p}(t)}{Q^2 - A_{11}} \quad (5.124)$$

When Equation (5.124) is substituted back into the system of Equation (5.122) together with $A_{12} = 0$, $A_{31} = 0$ and $A_{33} = 0$, one obtains a system of equations in Equation (5.125)

$$\left. \begin{aligned} \frac{\partial \bar{n}(t)}{\partial t} &= A_{21} \times \left[\frac{A_{13}\bar{p}(t)}{Q^2 - A_{11}} \right] + A_{22}\bar{n}(t) + A_{23}\bar{p}(t) - D_{NW}\bar{n}(t)Q^2 \\ \frac{\partial \bar{p}(t)}{\partial t} &= [0] \times \left[\frac{A_{13}\bar{p}(t)}{Q^2 - A_{11}} \right] + A_{32}\bar{n}(t) + [0]\bar{p}(t) - D_{PW}\bar{p}(t)Q^2 \end{aligned} \right\} \quad (5.125)$$

Equation (5.125) finally reduces to a system of two partial differential equations given by Equation (5.126):

$$\left. \begin{aligned} \frac{\partial \bar{n}(t)}{\partial t} &= \left(A_{22} - D_{NW}Q^2 \right) \bar{n}(t) + \left[A_{23} - \frac{A_{21}A_{13}}{Q^2 - A_{11}} + \right] \bar{p}(t) \\ \frac{\partial \bar{p}(t)}{\partial t} &= A_{32}\bar{n}(t) - D_{PW}Q^2\bar{p}(t) \end{aligned} \right\} \quad (5.126)$$

The relation in Equation (5.126) is then represented as Equation (5.127)

$$\begin{bmatrix} \frac{\partial \bar{n}}{\partial t} \\ \frac{\partial \bar{p}}{\partial t} \end{bmatrix} = \begin{bmatrix} A_{22} - D_{NW}Q^2 & \left(A_{23} - \frac{A_{21}A_{13}}{Q^2 - A_{11}} + \right) \\ A_{32} & -D_{PW}Q^2 \end{bmatrix} \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.127)$$

The representation indicated by Equation (5.127) can be represented by Equation (5.128)

$$\frac{\partial \gamma}{\partial t} = J\gamma, \quad \text{where } J = \begin{bmatrix} A_{22} - D_{NW}Q^2 & \left(A_{23} - \frac{A_{21}A_{13}}{Q^2 - A_{11}} \right) \\ A_{32} & -D_{PW}Q^2 \end{bmatrix} \text{ and } \gamma = \begin{bmatrix} \bar{n} \\ \bar{p} \end{bmatrix} \quad (5.128)$$

where J is the stability matrix. The stability matrix or Jacobian matrix from the system of Equations (5.128) is indicated by equation (5.129)

$$J = \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix} \quad (5.129)$$

where the elements of the Jacobian matrix are defined as follows:

$$B_{11} = A_{22} - D_{NW}Q^2, B_{12} = A_{23} - \frac{A_{21}A_{13}}{Q^2 - A_{11}}, B_{21} = A_{32}, \text{ and } B_{22} = -D_{PW}Q^2$$

The Jacobian matrix has eigenvalues λ given by Equation (5.130)

$$|J - \lambda I| = 0 \quad \Rightarrow \quad \lambda^2 - (trJ)\lambda + \det J = 0 \quad (5.130)$$

For stability one requires that, $\text{Re } \lambda < 0$. A necessary and sufficient conditions for linear stability are that $trJ < 0$ and $\text{Det } J > 0$ as indicated in Equations (5.131) and (5.132)

$$trJ = B_{11} + B_{22} < 0 \quad (5.131)$$

$$\det J = f(Q^2) = B_{11}B_{22} - B_{21}B_{12} > 0 \quad (5.132)$$

As stated earlier, for pattern formation to occur, instability is required. Thus, for pattern formation, one ascribes the following to the situations labelled as Equations (5.131) and (5.132). If Equations (5.131) and/or (5.132) are violated, the system will be unstable. Thus, substituting B_{11}, B_{12}, B_{21} and B_{22} in Equations (5.131) and (5.132) for the trace and the determinant of the Jacobian, one obtains the parameter set inequalities for unstable and instability in Equations (5.133) and (5.134) under (i) and (ii) respectively.

- (i) the parameter set such that Equation (5.131) is unstable and hence instability situation was obtained as Equation (5.133)

$$B_{11} + B_{22} = [A_{22} - D_{NW}Q^2] + [-D_{PW}Q^2] > 0$$

$$\Rightarrow -m - \frac{gp_s}{(n_s + 1)^2} - D_{NW}Q^2 - D_{PW}Q^2 > 0$$

But

$$-\left[m + \frac{gp_s}{(n_s + 1)^2} + D_{NW}Q^2 + D_{PW}Q^2 \right] < 0 \quad (5.133)$$

Hence, the trace condition cannot be violated. Thus, the instability of the system when diffusion is added is purely dependent on the determinant.

- (ii) Similarly for instability, it is required that $f(Q^2) = B_{11}B_{22} - B_{21}B_{12} < 0$ leading to Equation (5.134)

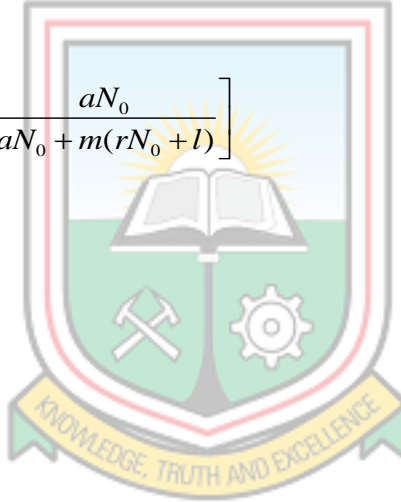
$$\begin{aligned}
B_{11}B_{22} - B_{21}B_{12} &= [A_{22} - D_{NW}Q^2] \times [-D_{PW}Q^2] - [A_{32}] \times \left[A_{23} - \frac{A_{21}A_{13}}{Q^2 - A_{11}} \right] < 0 \\
\Rightarrow \left[-m - \frac{gp_s}{(n_s + 1)^2} - D_{NW}Q^2 \right] \times [-D_{PW}Q^2] - \frac{p_s}{(n_s + 1)^2} \left[w_s \left(\frac{1 - N_0}{(p_s + 1)^2} \right) - g \left(\frac{n_s}{n_s + 1} \right) \right] \\
&\quad - \frac{p_s}{(n_s + 1)^2} \left[\frac{rw_s(p_s + N_0)(1 - N_0)}{[Q^2(p_s + 1) + l(p_s + 1) + r(p_s + N_0)](p_s + 1)^2} \right] < 0 \tag{5.134}
\end{aligned}$$

From Equations (5.133) and (5.134), it can be concluded that pattern formation is possible provided that Equations (5.135) or (5.136) or both hold as:

$$(m + D_{NW}Q^2 + u + D_{PW}Q^2) < \left[\frac{aN_0}{aN_0 + m(rN_0 + l)} \right] \tag{5.135}$$

or

$$(u + D_{PW}Q^2) < \left[\frac{aN_0}{aN_0 + m(rN_0 + l)} \right] \tag{5.136}$$



CHAPTER 6

SIMULATIONS AND DISCUSSION OF RESULTS

6.1 Preamble

In this chapter, the various simulations run on the proposed models represented by systems of Equations (5.1) and (5.2) for pattern formation and discussion of the results are presented. The parameter values used were obtained from literature and other parameters that were not available in literature were estimated. The chapter presents and discusses the following: the process analysis of the vegetation pattern formation; nature of pattern distribution of the vegetation at different values of the growth parameter β introduced in the model; and the validation of the numerical algorithm used for the simulations.

6.2 Process Analysis of the Vegetation Pattern Formation

The growth parameter β defined in Equation (4.11) was redefined by Equation (6.1)

$$\beta = \frac{1 - F_1 N}{F_2 + F_3 N} \quad (6.1)$$

where F_1 , F_2 and F_3 are three aggregate parameters, and are redefined by Equations (6.2), (6.3) and (6.4) respectively.

$$F_1 = \frac{\alpha_6 (\lambda_{21} + \lambda_{23})}{\lambda_{12} \lambda_{23}} = \frac{\alpha_6 (\lambda_{21} + \alpha_2 T)}{\alpha_1 I \alpha_2 T} \quad (6.2)$$

$$F_2 = \frac{(\lambda_{21} + \lambda_{23}) \lambda_{61}}{\lambda_{12} \lambda_{23} \lambda_{61}} + \frac{\lambda_{12} \lambda_{61}}{\lambda_{12} \lambda_{23} \lambda_{61}} + \frac{\lambda_{45} \lambda_{51} + \lambda_{34} \lambda_{51} + \lambda_{34} \lambda_{45}}{\lambda_{34} \lambda_{45} \lambda_{51}}$$

$$F_2 = \frac{(\lambda_{21} + \alpha_2 T) \lambda_{61}}{\alpha_1 I \alpha_2 T \lambda_{61}} + \frac{\alpha_1 I \lambda_{61}}{\alpha_1 I \alpha_2 T \lambda_{61}} + \frac{\alpha_4 N \lambda_{51} + \alpha_3 H \lambda_{51} + \alpha_3 H \alpha_4 N}{\alpha_3 H \alpha_4 N \lambda_{51}}$$

$$F_2 = \frac{\lambda_{21}}{\alpha_1 \alpha_2 I T} + \frac{1}{\alpha_1 I} + \frac{1}{\alpha_2 T} + \frac{1}{\alpha_3 H} + \frac{1}{\alpha_4 N} + \frac{1}{\lambda_{51}} \quad (6.3)$$

$$F_3 = \frac{\alpha_6 (\lambda_{21} + \lambda_{23})}{\lambda_{12} \lambda_{23}} \cdot \frac{1}{\lambda_{61}} = \frac{F_1}{\lambda_{61}} \quad (6.4)$$

The values of state transition parameters λ_{ij} , the utilisation coefficients α_i of each resource and the measure indices of light, temperature, water and soil nutrients were culled from Li *et al.* (2003) and are presented on Table 6.1 where CK, L, M and H represent control fertility, lower fertility, middle fertility and higher fertility respectively . Different values of β representing different levels of fertility under different water types were determined through multi environment external force action on the vegetation.

Table 6.1 Values of State Transition Parameters, Utilisation Coefficients and Measure Indices for Different Levels of Fertility under Different Water Conditions

Parameters	Rich water				Average water				Aridity			
	CK	L	M	H	CK	L	M	H	CK	L	M	H
I	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
T	0.766	0.766	0.766	0.766	0.766	0.766	0.766	0.766	0.766	0.766	0.766	0.766
H	0.875	0.875	0.875	0.875	0.75	0.75	0.75	0.75	0.588	0.588	0.588	0.588
N	0.690	0.793	0.896	1.000	0.690	0.793	0.896	1.000	0.690	0.793	0.896	1.000
α_1	0.589	0.733	0.786	0.900	0.426	0.692	0.917	0.876	0.292	0.367	0.444	0.419
α_2	0.662	0.662	0.662	0.662	0.662	0.662	0.662	0.662	0.662	0.662	0.662	0.662
α_3	0.91	0.91	0.91	0.91	0.91	0.91	0.91	0.91	0.90	0.90	0.90	0.90
α_4	0.87	0.82	0.91	0.95	0.86	0.89	0.86	1.00	0.77	0.65	0.62	0.45
α_6	0.076	0.084	0.071	0.071	0.127	0.118	0.092	0.092	0.122	0.131	0.100	0.096
λ_{21}	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
λ_{51}	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5
λ_{61}	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12

Source: Li *et al.* (2003)

From the aggregate parameter formulas given by Equations (6.2), (6.3) and (6.4), and the data in Table 6.1, the aggregate parameter values under each water-condition and fertility level are represented as shown in Table 6.2.

Table 6.2 Aggregate Parameters under each Water-Fertility Condition

Water Fertility		Aggregate Parameter		
		F_1	F_2	F_3
Rich	Control Fertility	0.1451	7.0147	1.2088
	Lower Fertility	0.1277	6.2045	1.0642
	Middle Fertility	0.1006	5.7342	0.8383
	Higher Fertility	0.0799	5.1725	0.6655
Average	Control Fertility	0.3321	7.9698	2.7674
	Lower Fertility	0.1907	6.3604	1.5891
	Middle Fertility	0.1121	5.7614	0.9340
	Higher Fertility	0.1176	5.4301	0.9798
Aridity	Control Fertility	0.4653	9.4369	3.8777
	Lower Fertility	0.3980	8.4110	3.3164
	Middle Fertility	0.2519	7.6452	2.0990
	Higher Fertility	0.2573	8.3001	2.1441

6.3 The Forward System Simulations Formula

The numerical simulation of the system Equations (5.1) and (5.2) are such that, they contain partial derivatives in both time and space. The partial derivatives of $w(x, y, t)$, $n(x, y, t)$ and $p(x, y, t)$ in Equations (5.1) and (5.2) were therefore approximated by Equations (6.5), (6.6) and (6.7) respectively as:

$$\frac{\partial^2 w}{\partial x^2} = \frac{w(x + \Delta x, y, t) - 2w(x, y, t) + w(x - \Delta x, y, t)}{\Delta x^2} \quad (6.5)$$

$$\frac{\partial^2 w}{\partial y^2} = \frac{w(x, y + \Delta y, t) - 2w(x, y, t) + w(x, y - \Delta y, t)}{\Delta y^2} \quad (6.6)$$

$$\frac{\partial w}{\partial t} = \frac{w(x, y, t + \Delta t) - w(x, y, t)}{\Delta t} \quad (6.7)$$

At each iteration, one approximates the values of $w(x, y, t)$, $n(x, y, t)$ and $p(x, y, t)$ by considering the change in space centered on a point in space (x, y) using values at $x + \Delta x$ and $y + \Delta y$ and the change in time as in the forward Euler method.

Let n be the index for the time steps, and m and q be the indices for position. Similarly, if $k = \Delta t$, $h = \Delta x$ and $l = \Delta y$ and write $w(x, y, t)$ as in Equation (6.8)

$$w(x, y, t) = w(m, q, n) = w_{m,q}^n \quad (6.8)$$

then, from Equation (6.8), the Equations (6.5), (6.6) and (6.7) can be expressed numerically by Equations (6.9), (6.10), and (6.11) respectively as

$$\begin{aligned} \frac{\partial^2 w}{\partial x^2} &= \frac{w(x + \Delta x, y, t) - 2w(x, y, t) + w(x - \Delta x, y, t)}{\Delta x^2} \\ &= \frac{w(m+1, q, n) - 2w(m, q, n) + w(m-1, q, n)}{h^2} \\ &= \frac{w_{m+1,q}^n - 2w_{m,q}^n + w_{m-1,q}^n}{h^2} \end{aligned} \quad (6.9)$$

$$\begin{aligned} \frac{\partial^2 w}{\partial y^2} &= \frac{w(x, y + \Delta y, t) - 2w(x, y, t) + w(x, y - \Delta y, t)}{\Delta y^2} \\ &= \frac{w(m, q+1, n) - 2w(m, q, n) + w(m, q-1, n)}{l^2} \\ &= \frac{w_{m,q+1}^n - 2w_{m,q}^n + w_{m,q-1}^n}{l^2} \end{aligned} \quad (6.10)$$

$$\begin{aligned} \frac{\partial w}{\partial t} &= \frac{w(x, y, t + \Delta t) - w(x, y, t)}{\Delta t} \\ &= \frac{w(m, q, n+1) - w(m, q, n)}{k} \\ &= \frac{w_{m,q}^{n+1} - w_{m,q}^n}{k} \end{aligned} \quad (6.11)$$

Similar expressions for $n(x, y, t)$ and $p(x, y, t)$ with respect to x, y and t are indicated by Equations (6.12) to (6.17)

$$\frac{\partial^2 n}{\partial x^2} = \frac{n(x + \Delta x, y, t) - 2n(x, y, t) + n(x - \Delta x, y, t)}{\Delta x^2} = \frac{n_{m+1,q}^n - 2n_{m,q}^n + n_{m-1,q}^n}{h^2} \quad (6.12)$$

$$\frac{\partial^2 n}{\partial y^2} = \frac{n(x, y + \Delta y, t) - 2n(x, y, t) + n(x, y - \Delta y, t)}{\Delta y^2} = \frac{n_{m,q+1}^n - 2n_{m,q}^n + n_{m,q-1}^n}{h^2} \quad (6.13)$$

$$\frac{\partial n}{\partial t} = \frac{n(x, y, t + \Delta t) - n(x, y, t)}{\Delta t} = \frac{w_{m,q}^{n+1} - w_{m,q}^n}{k} \quad (6.14)$$

$$\frac{\partial^2 p}{\partial x^2} = \frac{p(x + \Delta x, y, t) - 2p(x, y, t) + p(x - \Delta x, y, t)}{\Delta x^2} = \frac{p_{m+1,q}^n - 2p_{m,q}^n + p_{m-1,q}^n}{h^2} \quad (6.15)$$

$$\frac{\partial^2 p}{\partial y^2} = \frac{p(x, y + \Delta y, t) - 2p(x, y, t) + p(x, y - \Delta y, t)}{\Delta y^2} = \frac{p_{m,q+1}^n - 2p_{m,q}^n + p_{m,q-1}^n}{h^2} \quad (6.16)$$

$$\frac{\partial p}{\partial t} = \frac{p(x, y, t + \Delta t) - p(x, y, t)}{\Delta t} = \frac{p_{m,q}^{n+1} - p_{m,q}^n}{k} \quad (6.17)$$

The system of equations needed to simulate the model problem in Equation (5.2) is given by Equation (6.18)

$$\left. \begin{aligned} w_{m,q}^{n+1} &= w_{m,q}^n + ka - lk w_{m,q}^n - rk w_{m,q}^n \left[\frac{(p_{m,q}^n + N_0)}{(p_{m,q}^n + 1)} \right] \\ &\quad + \left(\frac{k}{h^2} + \frac{k}{l^2} \right) [w_{m+1,q}^n - 2w_{m,q}^n + w_{m-1,q}^n] \\ n_{m,q}^{n+1} &= n_{m,q}^n + k w_{m,q}^n \left[\frac{(p_{m,q}^n + N_0)}{(p_{m,q}^n + 1)} \right] - kmn_{m,q}^n \\ &\quad - kgp_{m,q}^n \left(\frac{n_{m,q}^n}{(n_{m,q}^n + 1)} \right) + \left(\frac{kD_{NW}}{h^2} + \frac{kD_{NW}}{l^2} \right) [w_{m+1,q}^n - 2w_{m,q}^n + w_{m-1,q}^n] \\ p_{m,q}^{n+1} &= p_{m,q}^n + k p_{m,q}^n \left(\frac{n_{m,q}^n}{(n_{m,q}^n + 1)} \right) - kup_{m,q}^n \\ &\quad + \left(\frac{kD_{PW}}{h^2} + \frac{kD_{PW}}{l^2} \right) [p_{m+1,q}^n - 2p_{m,q}^n + p_{m-1,q}^n] \end{aligned} \right\} \quad (6.18)$$

6.4 Distribution of the Vegetation Patterns at Different β - values

The spatial patterns associated with the different fertility levels for the different water conditions for the proposed models with the parameter set of values in Table 5.1 were numerically simulated. In order to corroborate the theoretical analysis in chapter 5, a direct numerical simulation of system Equation (5.2) was carried out with different fertility levels under different water conditions. The computations were performed on a two-dimensional grid. From the simulation equation given by Equation (6.18) and the data set of values in Tables 6.1 and 6.2, the vegetation patterns under each water condition and fertility level were obtained as follows.

6.4.1 Distribution of Vegetation Patterns for Different β - values under Rich Water Condition

The state transition parameters, utilisation coefficients and measure indices for Control fertility, Lower fertility, Middle fertility and Higher fertility under Rich water condition are given in Table 6.3

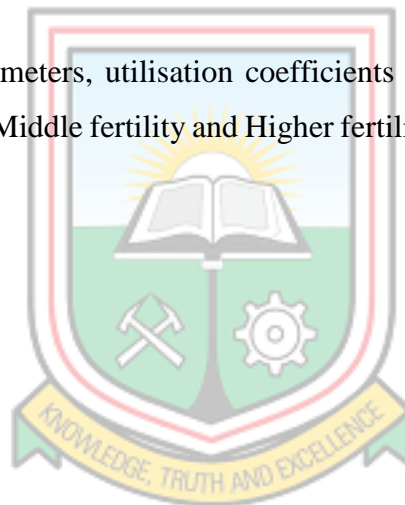


Table 6.3 State Transition Parameters, Utilisation Coefficients and Measure Indices for Control Fertility, Lower Fertility, Middle Fertility and Higher fertility under Rich Water Condition

Parameter	Control	Lower Fertility	Middle Fertility	Higher Fertility
I	1.000	1.000	1.000	1.000
T	0.766	0.766	0.766	0.766
H	0.875	0.875	0.875	0.875
N	0.793	0.793	0.896	1.000
α_1	0.733	0.733	0.786	0.990
α_2	0.662	0.662	0.662	0.662
α_3	0.910	0.910	0.910	0.910
α_4	0.820	0.82	0.91	0.950
α_6	0.0837	0.0837	0.0707	0.0707
λ_{21}	0.06	0.06	0.06	0.06
λ_{51}	4.5	4.5	4.5	4.5
λ_{61}	0.12	0.12	0.12	0.12

From Table 6.3, the aggregate parameters for the evaluation of different β -values representing fertility levels under rich-water condition is summarised in Table 6.4.

Table 6.4 The Aggregate Parameters for Evaluation of Different β -Values Representing Fertility Levels under Rich-Water Condition

Water fertility		Aggregate Parameter		
		F_1	F_2	F_3
Rich water	Control fertility	0.1451	7.0147	1.2088
	Lower fertility	0.1277	6.2045	1.0642
	Middle fertility	0.1006	5.7342	0.8383
	Higher fertility	0.0799	5.1725	0.6655

Vegetation Pattern of Control Fertility under Rich Water Condition

The stages of degradation into the final stage of simulated patterns of the vegetation with a β - value of $\beta = 0.1146524577$ for Control fertility under rich water condition is shown in Figure 6.1 and Figure 6.2.

s

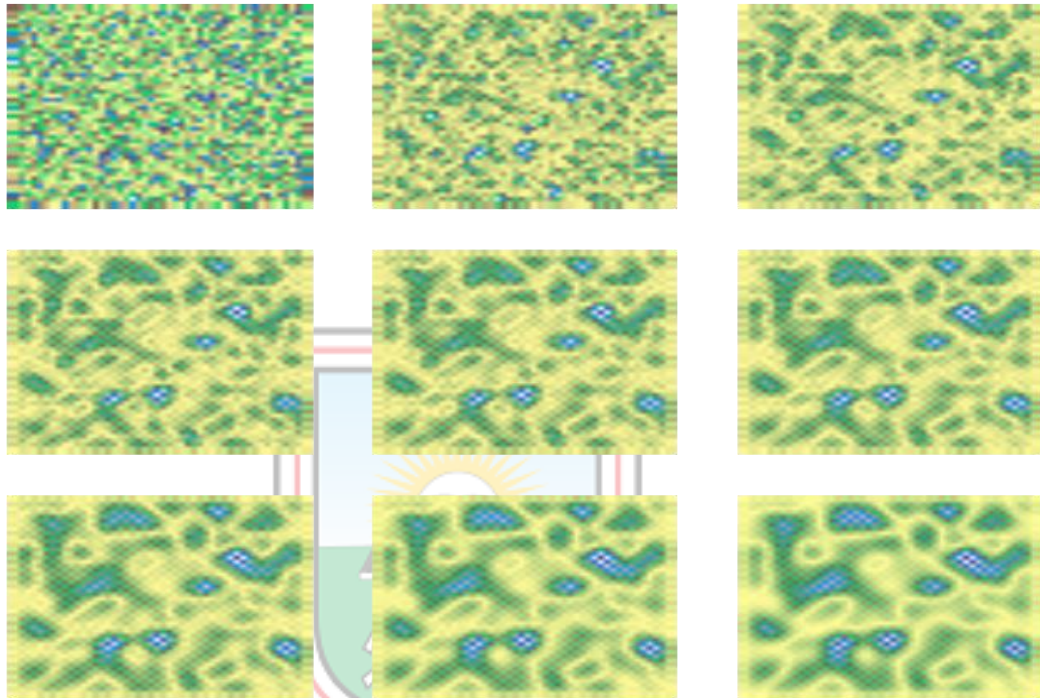


Figure 6.1 The Stages of Degradation into the Final Stage of Simulated Vegetation Pattern of Control Fertility under Rich Water Condition

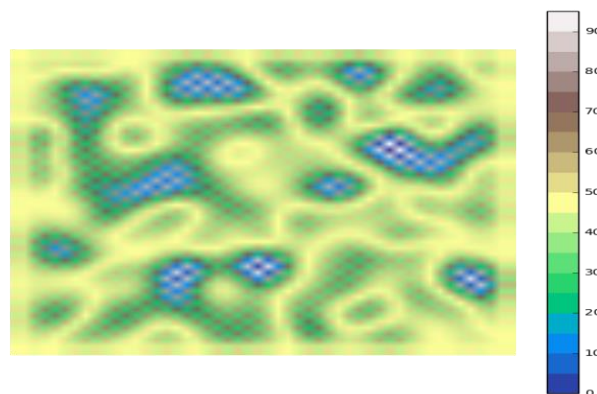


Figure 6.2 Final Vegetation Pattern of Control Fertility under Rich Water Condition with a β - value of $\beta = 0.1146524577$

Vegetation Pattern of Lower Fertility under Rich Water Condition

The stages of degradation into the final stage of simulated patterns of the vegetation with a β -value of $\beta = 0.1275087323$ for lower fertility under rich water condition is shown in Figures 6.3 and 6.4.

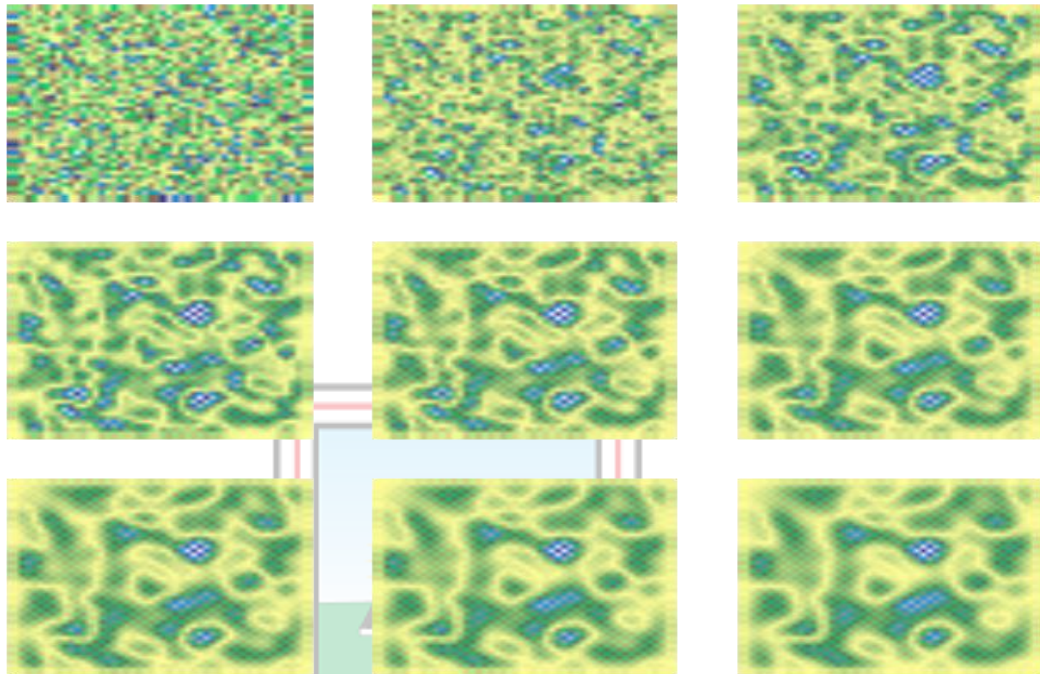


Figure 6.3 The Stages of Degradation into the Final Stage of Simulated Vegetation Patterns of Lower Fertility under Rich Water Condition

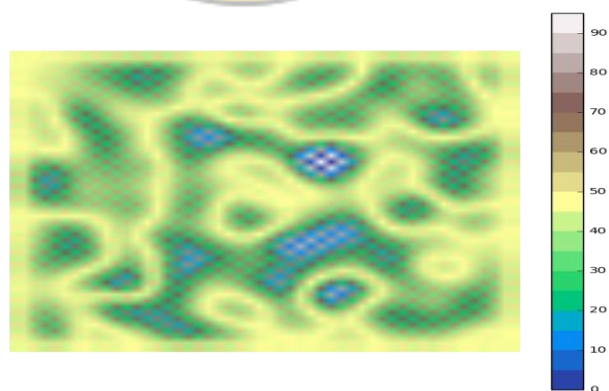


Figure 6.4 Final Vegetation Pattern of Lower Fertility under Rich Water Condition with a β -value of $\beta = 0.1275087323$

Vegetation Pattern of Middle Fertility under Rich Water Condition

The stages of degradation into the final stage of simulated patterns of the vegetation with a β - value of $\beta = 0.1402957524$ for middle fertility under rich water condition is also shown in the Figures 6.5 and 6.6.

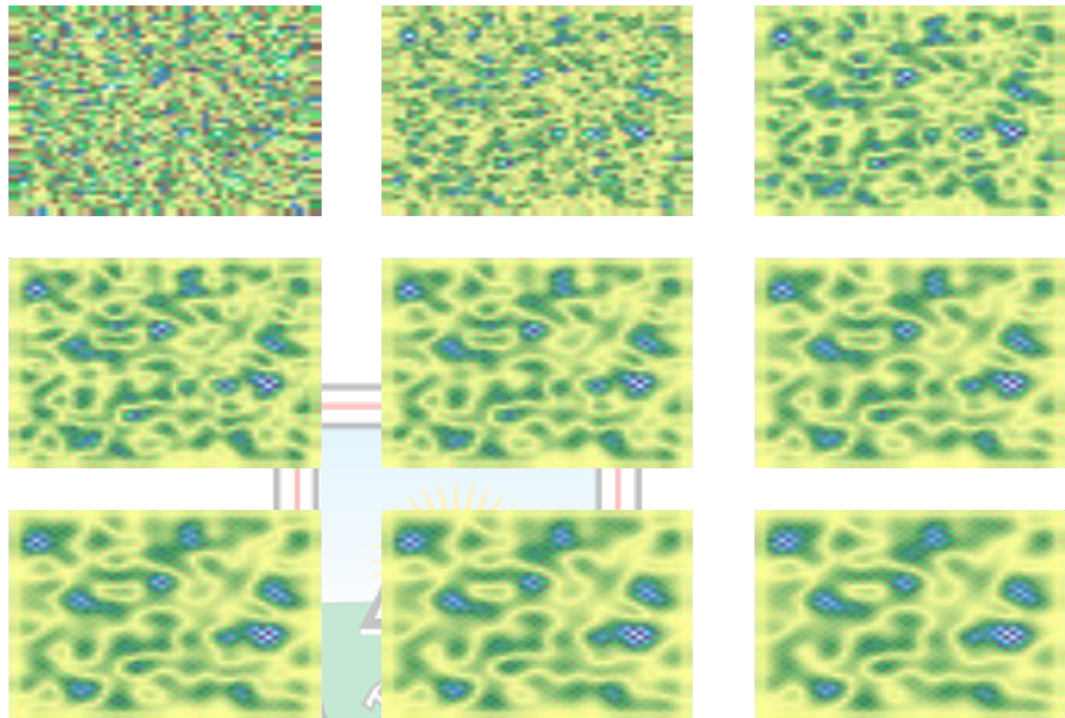


Figure 6.5 The Stages of Degradation into the Final Stage of Simulated Vegetation Patterns of Middle Fertility under Rich Water Condition

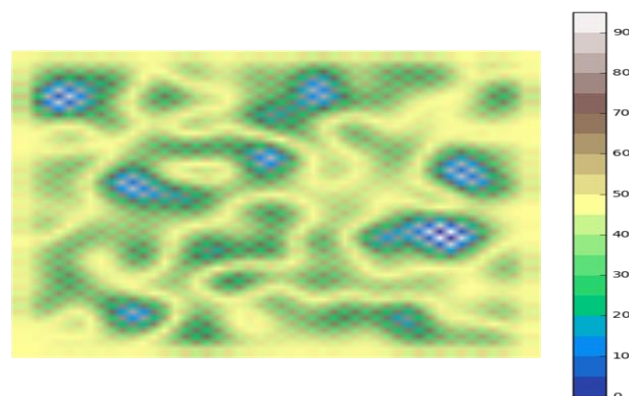


Figure 6.6 Final Vegetation Pattern of Middle Fertility under Rich Water Condition with a β - value of $\beta = 0.1402957524$

Vegetation Pattern of Higher Fertility under Rich Water Condition

The stages of degradation into the final stage of simulated patterns of the vegetation with a β -value of $\beta = 0.1576053443$ for higher fertility under rich water condition is indicated in Figures 6.7 and 6.8.

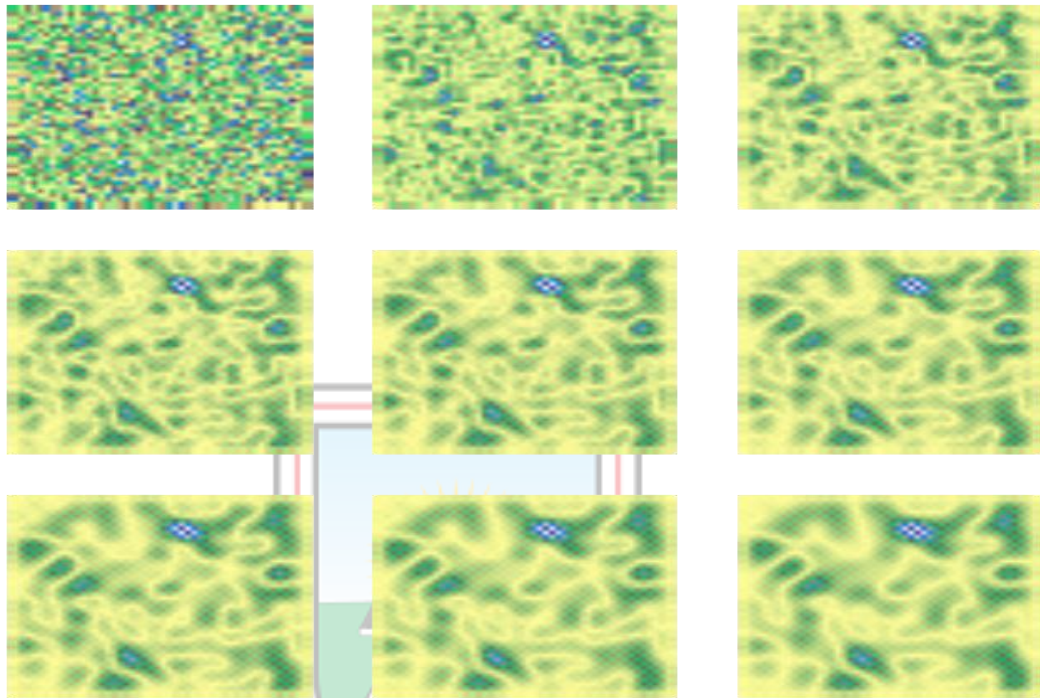


Figure 6.7 The Stages of Degradation into the Final Stage of Simulated Vegetation Patterns of Higher Fertility under Rich Water Condition

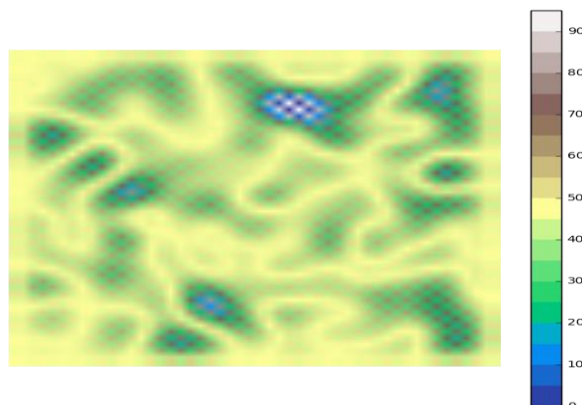


Figure 6.8 Final Vegetation Pattern of Higher Fertility under Rich Water Condition with a β -value of $\beta = 0.1576053443$

The final stages for various β - values representing control fertility, lower fertility, middle fertility and higher fertility under rich water condition were compared as shown in Figure 6.9.

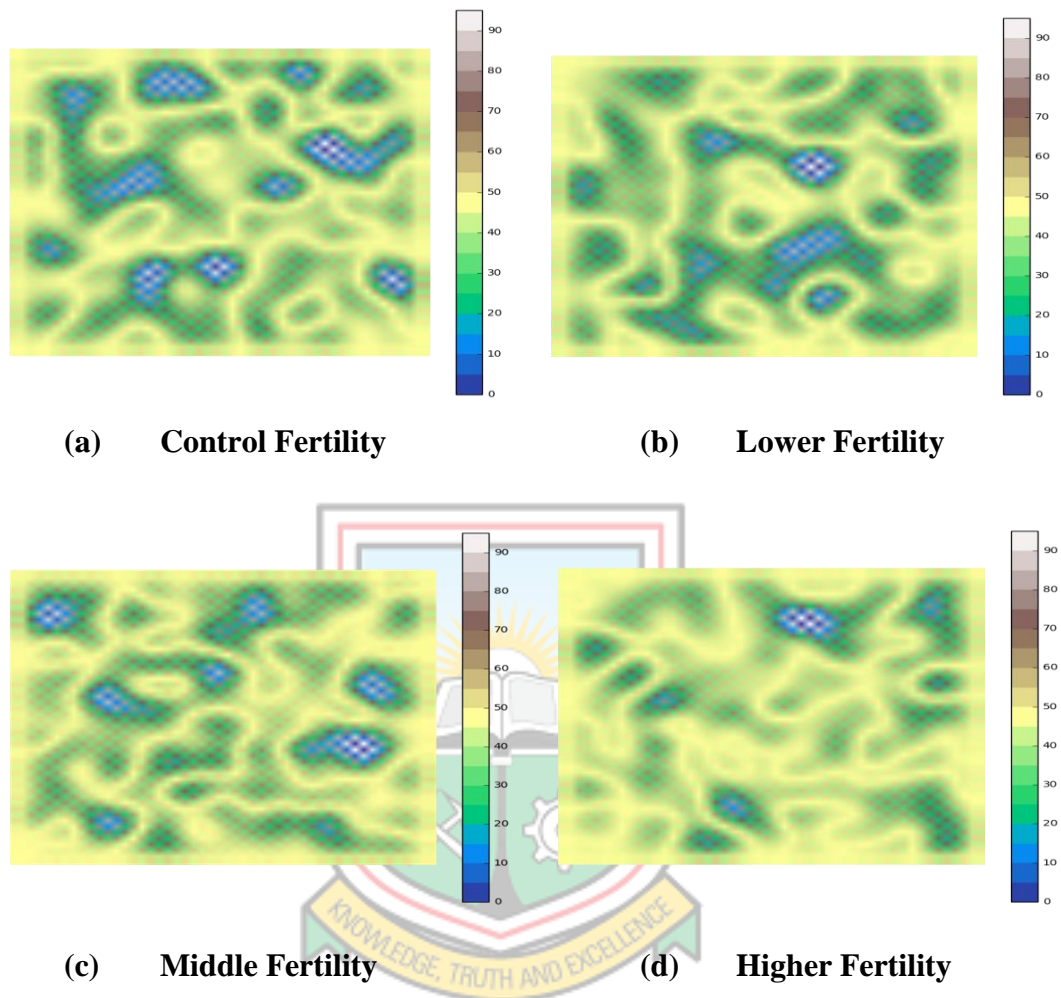


Figure 6.9 Spatial Patterns for Control Fertility, Lower Fertility, Middle Fertility and Higher Fertility Levels of the Soil under Rich Water Condition

The spatial patterns on overly evenly flat ground that are generated by the proposed model are revealed in a two-dimensional domain of a numerical simulations. Different levels of soil fertility namely control fertility, lower fertility, middle fertility and higher fertility based on their state transition parameters, utilisation coefficients and measure indices determined under Rich water condition were then compared.

The effects of changes in the fertility levels on the patterns formed by the vegetation under Rich water condition were examined. The β -value representing these fertility levels were

computed analytically based on the state transition parameters, utilisation coefficients and measure indices. Thus, the effects of β on the vegetation as predicted by the model Equation (5.2) were shown.

For a β -value of $\beta = 0.1146524577$ representing the Control fertility under rich water condition, the vegetation shows a pattern with quite a number of patches of bare or almost bare land as shown in Figure 6.9a. The number of patches of bare or almost bare land formed by the vegetation reduced and the area covered by these patches somehow dwindled for a β -value of $\beta = 0.1275087323$ representing lower fertility. This is as shown in figure 6.9b. Though the number of patches of bare or almost bare land seems numerous in the case of $\beta = 0.1402957524$ for middle fertility, the intensity of the vegetation is high as compared to that of lower fertility and the corresponding patches of bare land are narrower. This can best be looked at based on the colour bar associated with the vegetation pattern. This is equally represented by figure 6.9c. When the β -value is at $\beta = 0.1576053443$ representing higher fertility, patches of bare or almost bare land were barely absent compared to other fertility levels represented by figures 6.9a, 6.9b and 6.9c. However, the patches of bare or almost bare land is not wholly absent. Again, the colour bar shows that the intensity of the vegetation is very high compared to all the others. This is shown by Figure 6.9d.

6.4.2 Distribution of Vegetation Patterns for Different β -Values under Average Water Condition

Similar to Section 6.4.1, the state transition parameters, utilisation coefficients and measure indices for Control fertility, lower fertility, middle fertility and higher fertility under Average water condition are indicated in Table 6.5.

Table 6.5 State Transition Parameters, Utilisation Coefficients and Measure Indices for Control Fertility, Lower Fertility, Middle Fertility and Higher Fertility under Average Water Condition

Parameter	Control	Lower Fertility	Middle Fertility	Higher Fertility
I	1.000	1.000	1.000	1.000
T	0.766	0.766	0.766	0.766
H	0.750	0.750	0.750	0.750
N	0.690	0.793	0.896	1.000
α_1	0.426	0.692	0.917	0.876
α_2	0.662	0.662	0.662	0.662
α_3	0.910	0.910	0.910	0.910
α_4	0.860	0.890	0.86	1.000
α_6	0.1265	0.1180	0.0919	0.0921
λ_{21}	0.06	0.06	0.06	0.06
λ_{51}	4.5	4.5	4.5	4.5
λ_{61}	0.12	0.12	0.12	0.12

Extract from Table 6.1

From Table 6.5, the aggregate parameters for the evaluation of different β - values under Average-water condition for Control fertility, Lower fertility, Middle fertility and Higher fertility are summarised in Table 6.6.

Table 6.6 Aggregate Parameters for the Evaluation of Different Values under Average Water Condition

Water fertility		Aggregate Parameter		
		F_1	F_2	F_3
Average water	Control fertility	0.3321	7.9698	2.7674
	Lower fertility	0.1907	6.3604	1.5891
	Middle fertility	0.1121	5.7614	0.9340
	Higher fertility	0.1176	5.4301	0.9798

Vegetation Pattern of Control Fertility under Average Water Condition

The process of degradation into the final stage of simulated patterns of the vegetation with a β -value of $\beta = 0.0780268371$ for Control fertility under average water condition is shown in Figures 6.10 and 6.11.

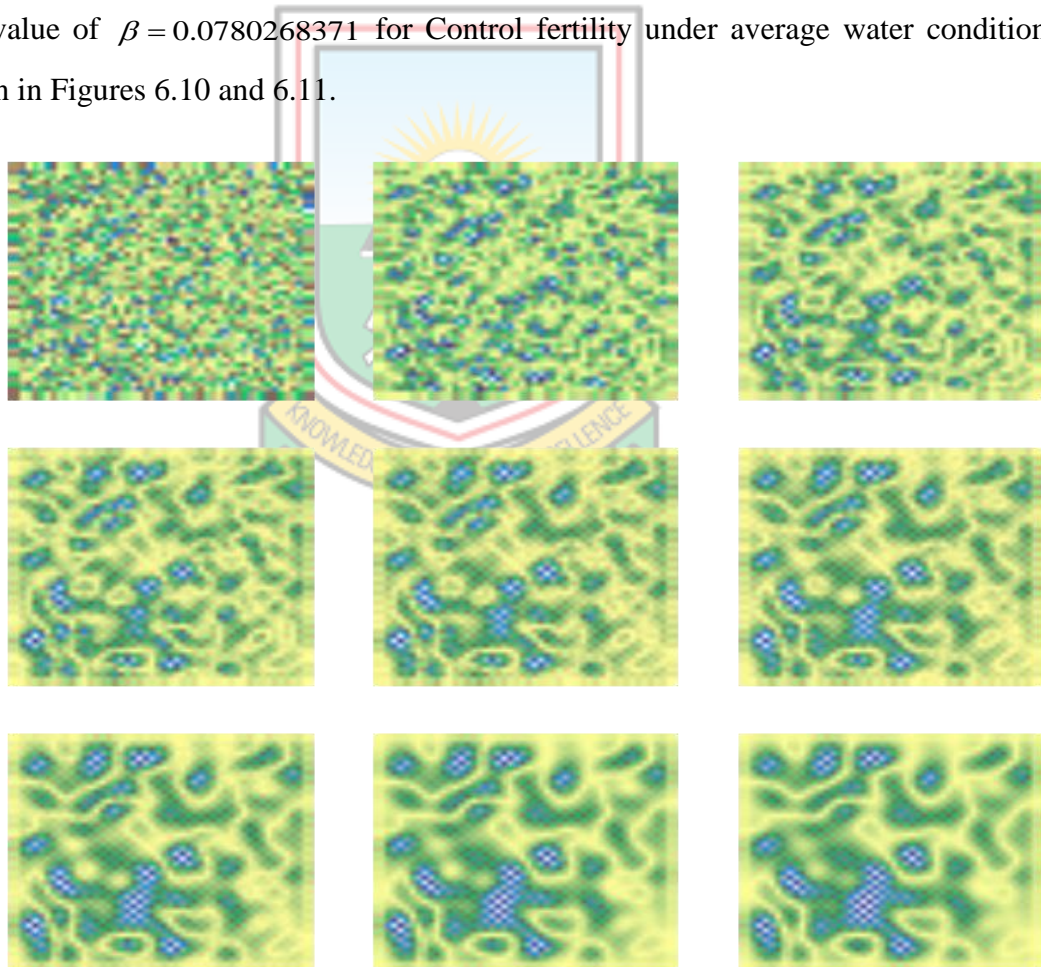


Figure 6.10 Stages of Degradation into the Final Stage of Simulated Vegetation Patterns of Control Fertility under Average Water Condition

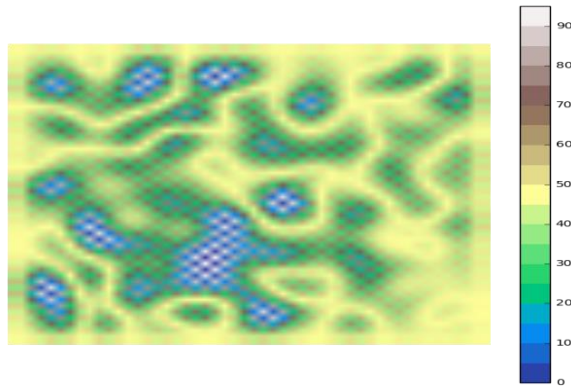


Figure 6.11 Final Vegetation Pattern of Control Fertility under Average Water with a β - Value of $\beta = 0.0780268371$

Vegetation Pattern for Lower Fertility under Average Water Condition

The process of degradation into the final stage of simulated patterns of the vegetation with a β -value of $\beta = 0.1113796509$ for lower fertility under average water condition is indicated in Figures 6.12 and 6.13.

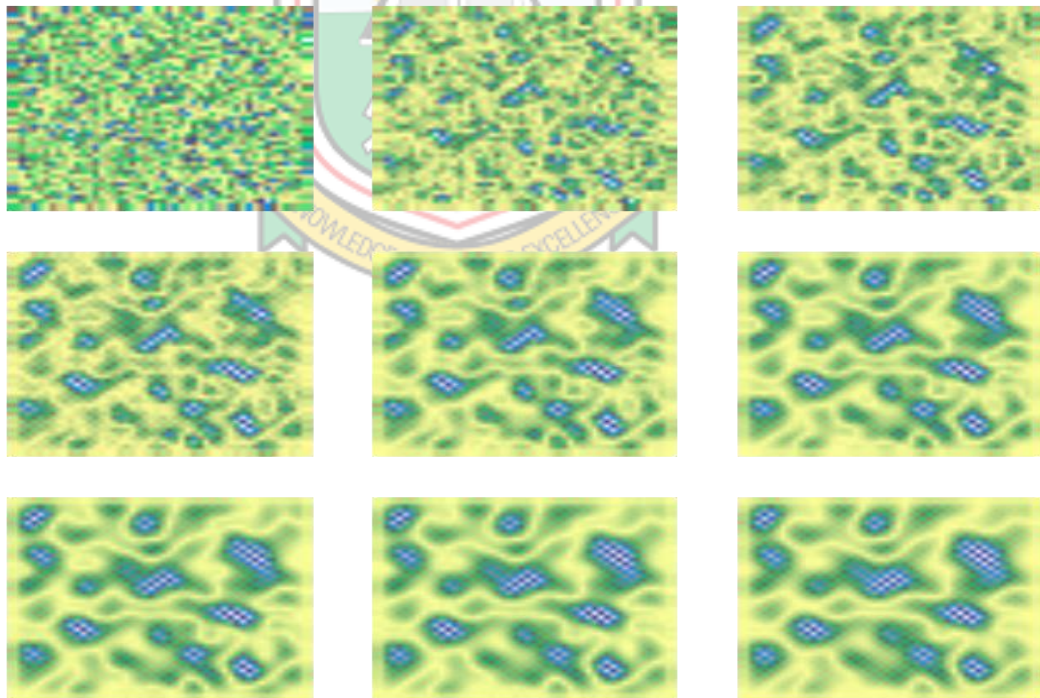


Figure 6.12 Stages of Degradation into the Final Stage of Simulated Patterns of Lower Fertility under Average Water Condition

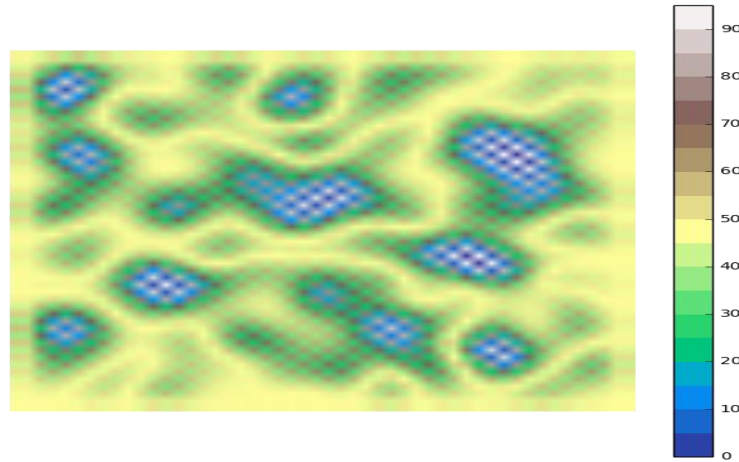


Figure 6.13 Final Vegetation Pattern of Lower Fertility under Average Water with a β - Value of $\beta = 0.1113796509$

Vegetation Pattern of Middle Fertility under Average Water

The process of degradation into the final stage of simulated growth patterns of the vegetation with a β -value of $\beta = 0.1363325869$ for middle fertility under average water condition is also shown in the Figures 6.14 and 6.15.

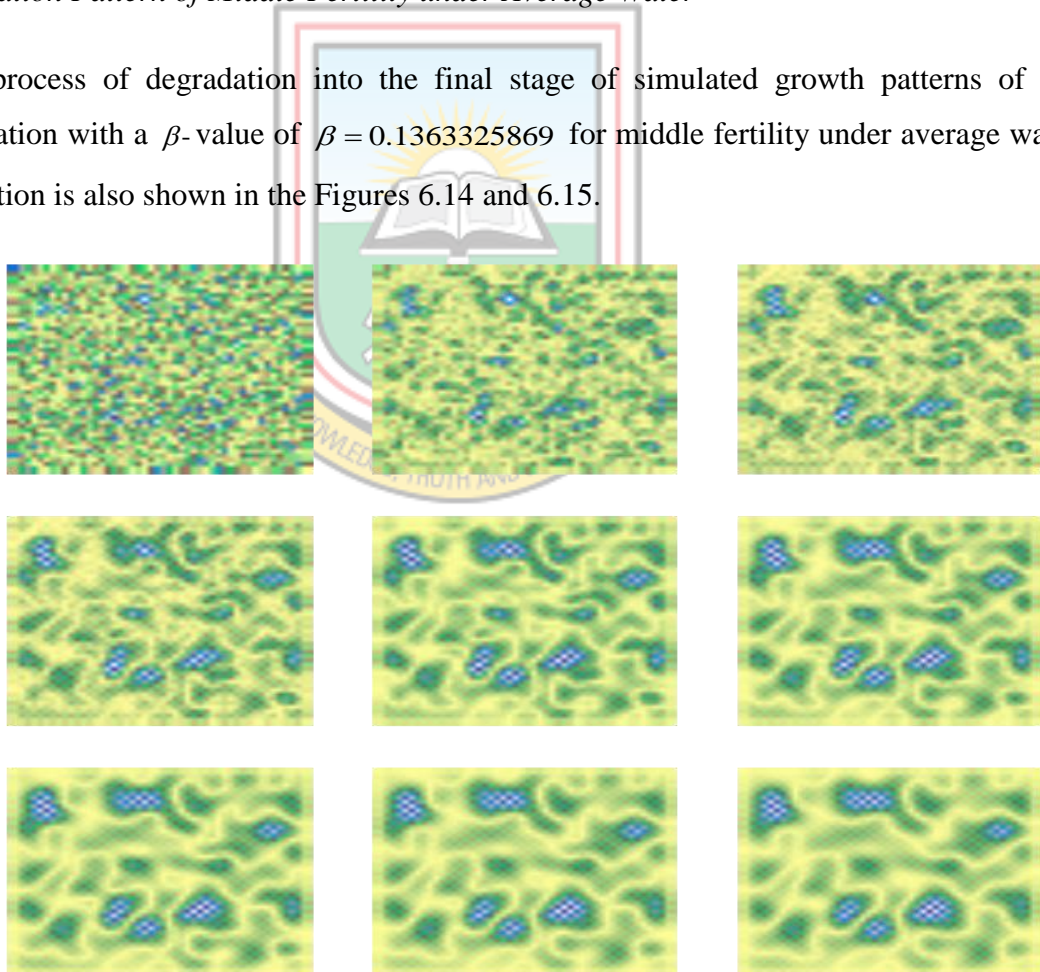


Figure 6.14 The Stages of Degradation into the Final Stage of Simulated Patterns of Middle Fertility under Average Water Condition

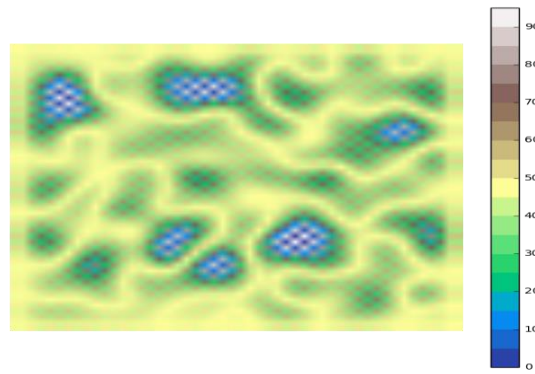


Figure 6.15 Final Vegetation Pattern of Middle Fertility under Average Water with a β - Value of $\beta = 0.1363325869$

Vegetation Pattern of Higher Fertility under Average Water Condition

The process of degradation into the final stage of simulated growth patterns of the vegetation with a β - value of $\beta = 0.137662054$ for higher fertility under average water is indicated in Figures 6.16 and 6.17.

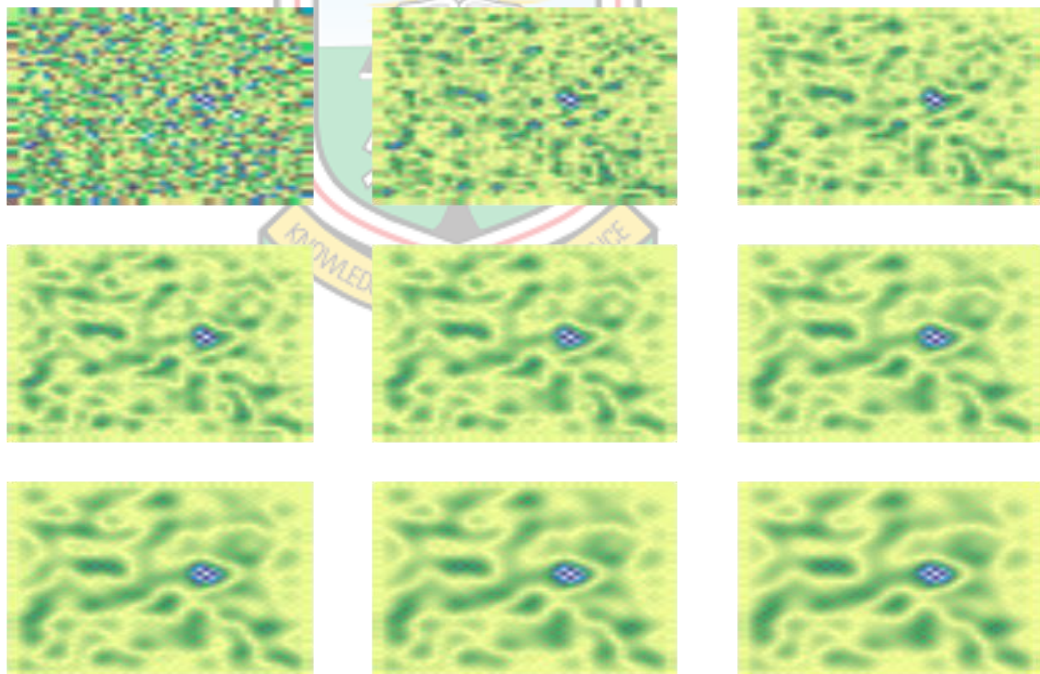


Figure 6.16 The Stages of Degradation into the Final Stage of Simulated Patterns of Higher Fertility under Average Water Condition

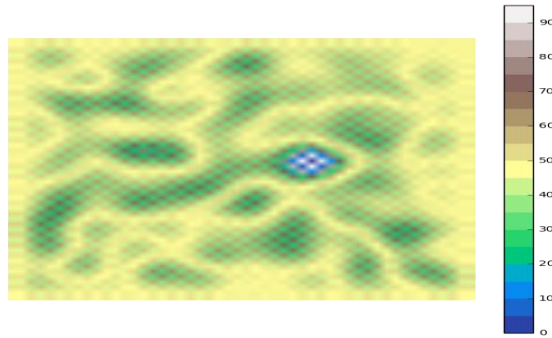


Figure 6.17 Final Vegetation Pattern of Higher Fertility under Average Water with a β - Value of $\beta = 0.137662054$

The final stages for various β - values representing Control fertility, lower fertility, middle fertility and higher fertility under Average Water Condition were compared as shown in Figure 6.18

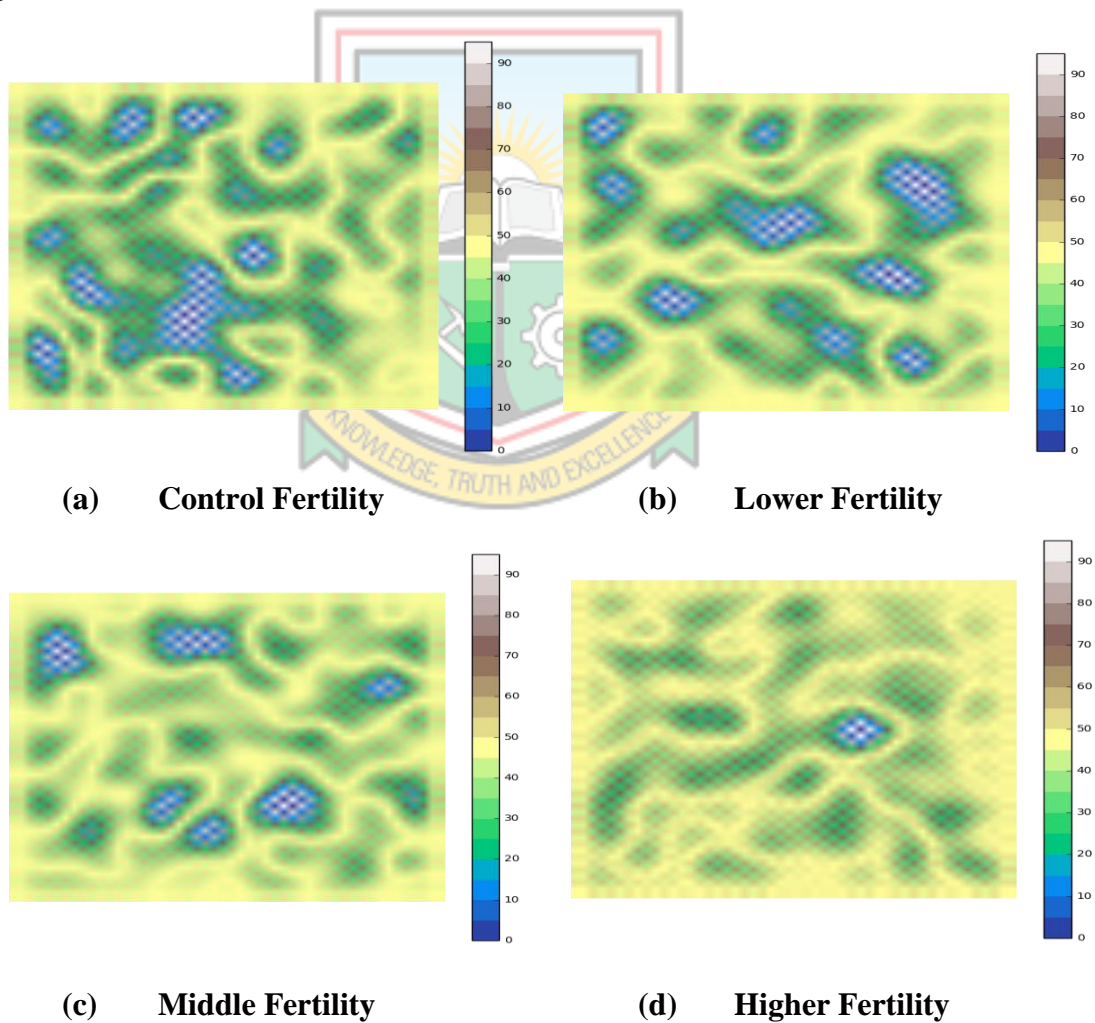


Figure 6.18 Spatial Patterns for Control Fertility, Lower Fertility, Middle Fertility and Higher Fertility of the Soil under Average Water Condition

The spatial patterns on evenly flat ground that are generated by the proposed model are again revealed in a two-dimensional domain of a numerical simulations. The different levels of soil fertility namely control fertility, lower fertility, middle fertility and higher fertility based on the state transition parameters, utilisation coefficients and measure indices were determined for Average water condition and then compared

The effects of different fertility levels on the patterns formed by the vegetation under Average water condition were examined. Thus, just as the various fertility levels were determined analytically under rich water condition, the same was done for the average water condition and the effects of β on the vegetation as predicted by the model Equation (5.2) was examined.

For β -value of 0.0780268371 representing the Control fertility under Average water condition, the vegetation shows a pattern with quite a number of patches of bare or almost bare land of which some are labyrinth in nature. These patches of bare land comparatively cover wider areas. This is shown in Figure 6.18a. Though the number of patches of bare or almost bare land formed by the vegetation under lower fertility appear to be more compared with the case of control fertility, the areas covered by these patches are somehow dwindled for $\beta = 0.1113796509$ representing the lower fertility. This is shown in Figure 6.18b. There was a further drastic decrease in the number of patches of bare or almost bare land and a corresponding dwindling of these patches of bare land at $\beta = 0.1363325869$ for middle fertility. This is equally represented by figure 6.18c. When the β -value is at $\beta = 0.137662054$ representing higher fertility, patches of bare or almost bare land reduced considerably. The intensity of the patches of vegetation is quite high as compared to all the others. This is shown by Figure 6.18d.

6.4.3 Distribution of Vegetation Patterns for Different β - Values under Arid Condition

In similar manner, the state transition parameters, utilisation coefficients and measure indices for Control fertility, lower fertility, middle fertility and higher fertility under Arid condition are given in Table 6.7.

Table 6.7 State Transition Parameters, Utilisation Coefficients and Measure Indices for Control Fertility, Lower Fertility, Middle Fertility and Higher fertility under Arid Environment

Parameter	Control	Lower Fertility	Middle Fertility	Higher Fertility
I	1.000	1.000	1.000	1.000
T	0.766	0.766	0.766	0.766
H	0.588	0.588	0.588	0.588
N	0.690	0.793	0.896	1.000
α_1	0.292	0.367	0.444	0.419
α_2	0.662	0.662	0.662	0.662
α_3	0.900	0.900	0.900	0.900
α_4	0.770	0.650	0.620	0.450
α_6	0.1215	0.1306	0.100	0.0964
λ_{21}	0.06	0.06	0.06	0.06
λ_{51}	4.5	4.5	4.5	4.5
λ_{61}	0.12	0.12	0.12	0.12

Extract from Table 6.1

From Table 6.7, the aggregate parameters for the evaluation of different β -values for Control fertility, lower fertility, middle fertility and higher fertility under Arid condition are indicated in Table 6.8.

Table 6.8 The Aggregate Parameters for the Evaluation of Different Values under Arid Condition

Water fertility		Aggregate Parameter		
		F_1	F_2	F_3
Aridity	Control fertility	0.4653	9.4369	3.8777
	Lower fertility	0.3980	8.4110	3.3164
	Middle fertility	0.2519	7.6452	2.990
	Higher fertility	0.2573	8.3001	2.1441

Vegetation Pattern of Control Fertility under Arid Condition

The process of degradation into the final stage of simulated growth patterns of the vegetation with a β -value of $\beta = 0.0560530255$ for Control fertility under arid condition is indicated in Figures 6.19 and 6.20.

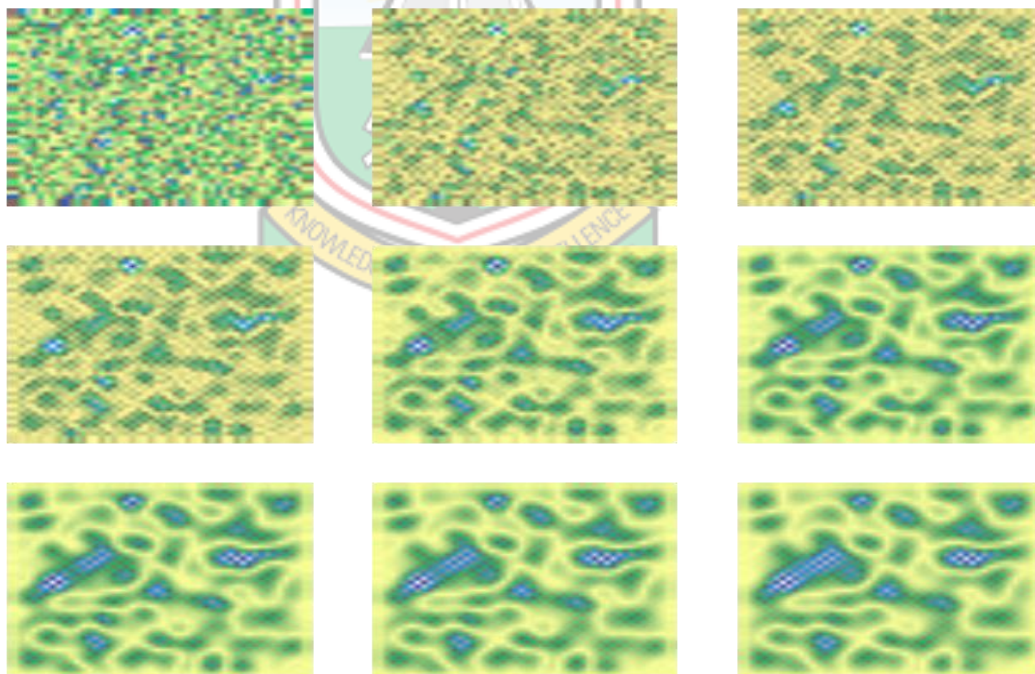


Figure 6.19 Stages of Degradation into the Final Stage of Simulated Patterns of Control Fertility under Arid Water Condition

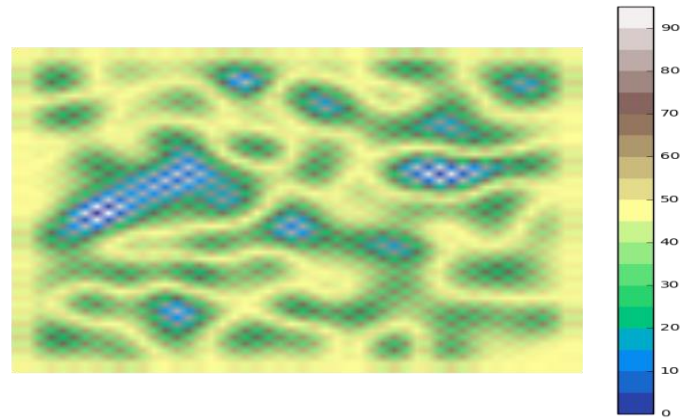


Figure 6.20 Final Vegetation Pattern of Control Fertility under Arid Water with a β - Value of $\beta = 0.0560530255$

Vegetation Pattern of Lower Fertility under Arid Condition

The process of degradation into the final stage of simulated growth patterns of the vegetation with a β - value of $\beta = 0.0619864031$ for lower fertility under average water is indicated in Figures 6.21 and 6.22.

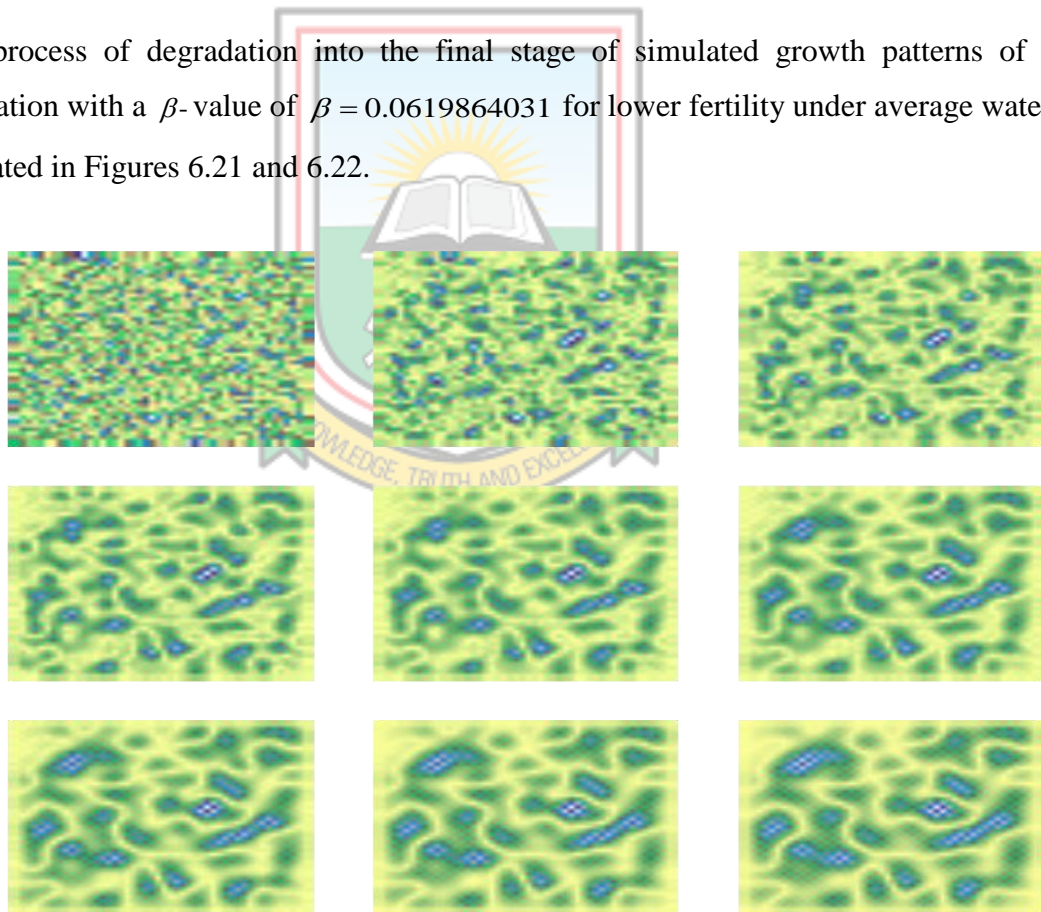


Figure 6.21 Stages of Degradation into the Final Stage of Simulated Patterns of Lower Fertility under Arid Water Condition

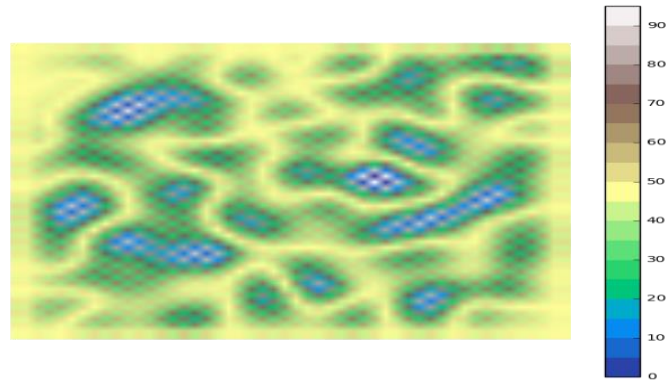


Figure 6.22 Final Vegetation Pattern of Lower Fertility under Arid Water with a β - Value of $\beta = 0.0619864031$

Vegetation Pattern of Middle Fertility under Arid Condition

The process of degradation into the final stage of simulated patterns of the vegetation with a β -value of $\beta = 0.0812833722$ for middle fertility under arid condition is indicated in Figures 6.23 and 6.24.

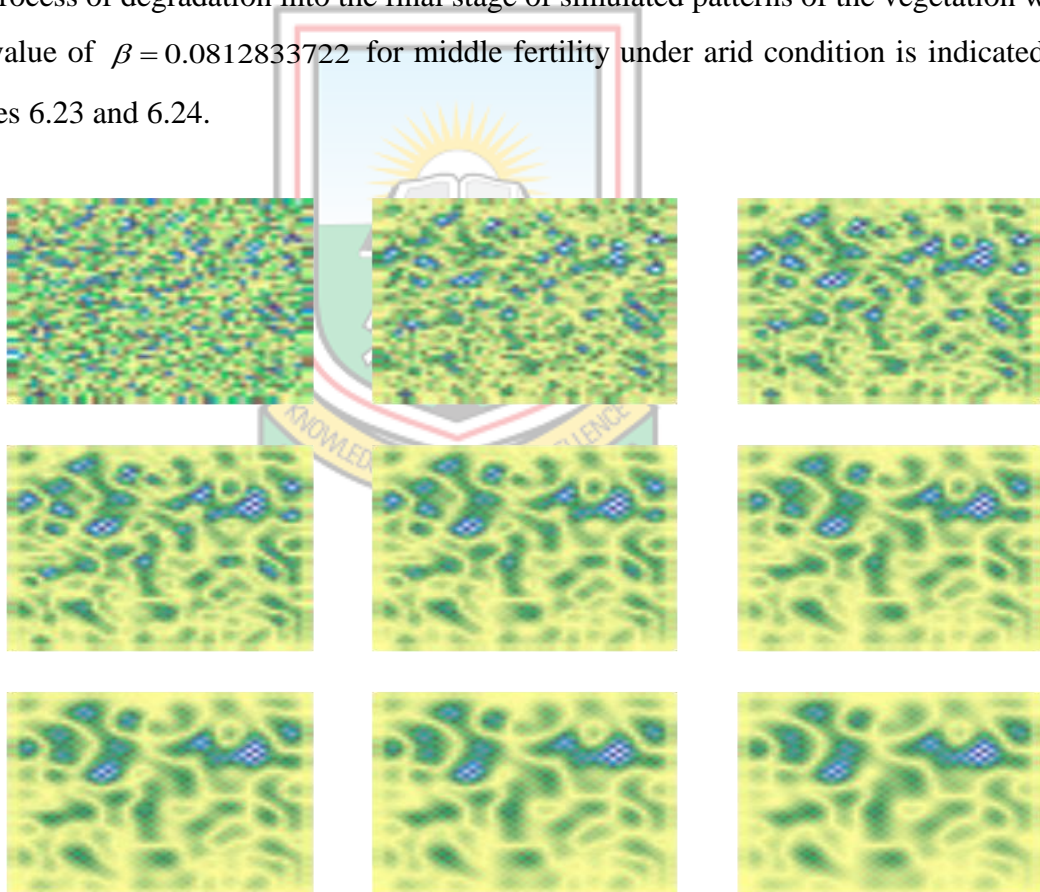


Figure 6.23 Stages of Degradation into the Final Stage of Simulated Patterns of Middle Fertility under Arid Water Condition

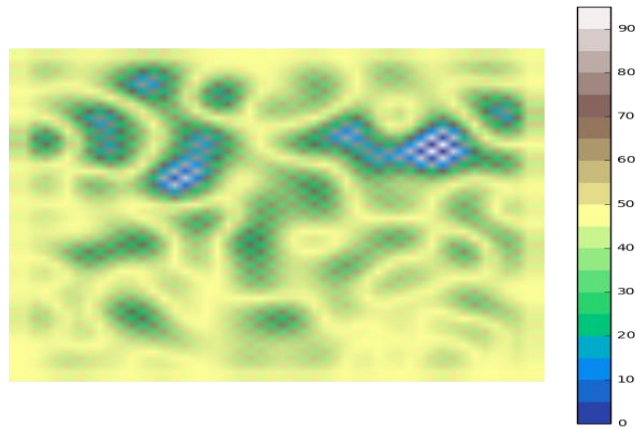


Figure 6.24 Final Vegetation Pattern of Middle Fertility under Arid Water with a β - Value of $\beta = 0.0812833722$

Vegetation Pattern of Higher Fertility under Aridity

The process of degradation into the final stage of simulated patterns of the vegetation with a β -value of $\beta = 0.711112388$ for higher fertility under arid condition is also shown in Figures 6.25 and 6.26

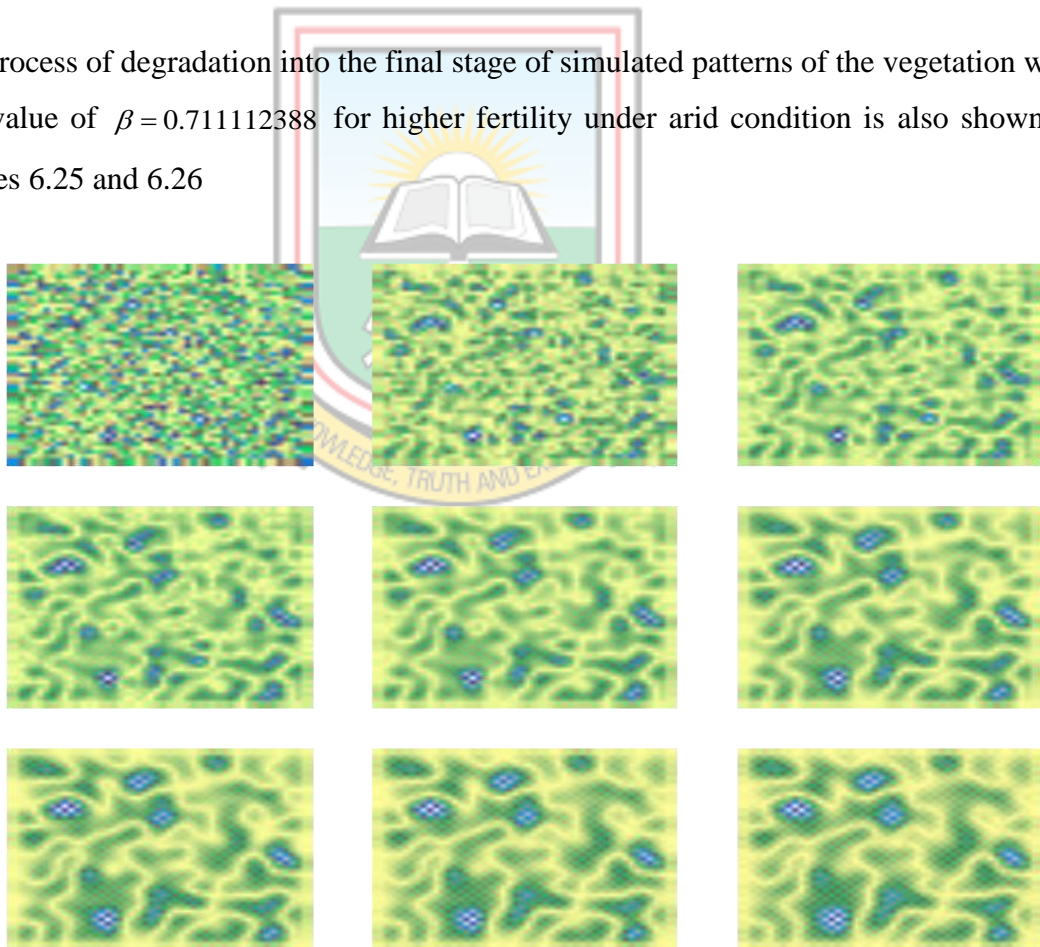


Figure 6.25 Stages of Degradation into the Final Stage of Simulated Patterns of Higher Fertility under Arid Condition

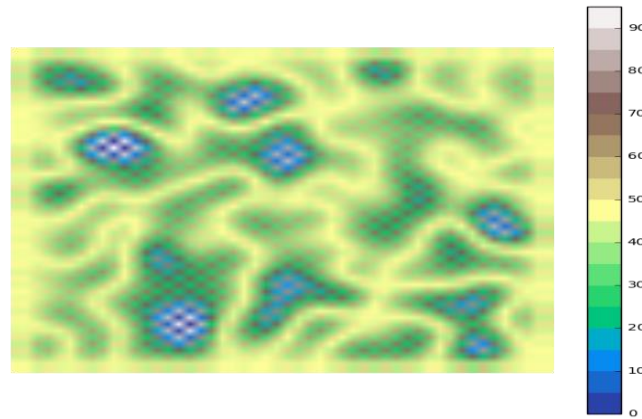


Figure 6.26 Final Vegetation Pattern of Higher Fertility under Arid Water with a β - Value of $\beta = 0.711112388$

The level of degradation for various β - values for control fertility, lower fertility, middle fertility and higher fertility under Arid condition were compared. This is shown in Figure 6.27.

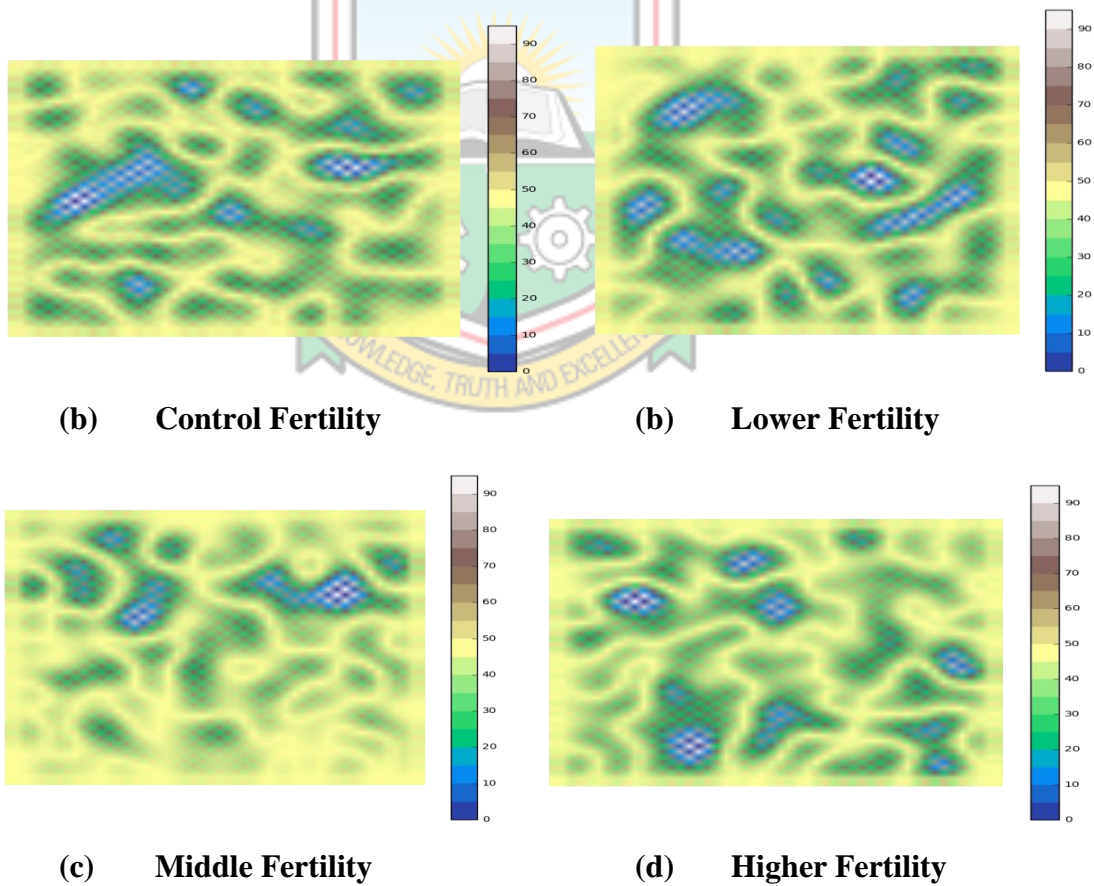


Figure 6.27 Spatial Patterns for Control Fertility, Lower Fertility, Middle Fertility and Higher Fertility of the Soil under Arid Condition

The spatial patterns on evenly flat ground that are generated by the proposed model are again revealed in a two-dimensional domain of a numerical simulations. Different levels of soil fertility namely control fertility, lower fertility, middle fertility and higher fertility based on the state transition parameters, utilisation coefficients and measure indices determined for Arid condition were then compared.

Again, the effects of different fertility levels on the patterns formed by the vegetation under Arid condition were examined. Thus, just as the various fertility levels were determined analytically under rich water and average conditions, the same was done for the arid condition and the effects of β on the vegetation as predicted by the model Equation (5.2).

For a β -value of 0.0560530255 representing the Control fertility under Arid condition, the vegetation shows a pattern with numerous and wider patches of bare or almost bare land compared to patterns exhibited by the other fertility levels. This is shown by Figure 6.27a. For a β -value of $\beta = 0.0619864031$ representing lower fertility, the number of patches of bare or almost bare land formed by the ecosystem reduces. Some of the areas covered by these patches are equally wide and labyrinth in nature, however some few show spottily nature. This is shown in Figure 6.27b. The simulations show a drastic decrease in the number of patches of bare or almost bare land in the case of $\beta = 0.0812833722$ for middle fertility. Nonetheless, these few patches are wider and labyrinth in nature. This is equally represented by Figure 6.27c. When the β -value is at $\beta = 0.0711112388$ representing higher fertility, more patches of bare or almost bare land were generated than in the case of middle fertility though fewer patches of bare land was expected in the higher fertility than the middle fertility. However, the sizes of the patches of bare land or almost bare land were considerably dwindled compared with situations in the control, lower and middle fertilities. This is shown in Figure 6.27d.

6.5 Discussions of the Results

The discussions of results of this research are focused on model formulation which involves two main aspects namely: the theoretical and empirical aspects of growth, spread and vegetation pattern formation; the analysis of the results obtained from the dynamics of the models and the simulation run on the results.

The theoretical aspect of model formulation consists of the mathematical model development techniques of forest growth, spread and vegetation pattern formation as discussed in Chapter 4 of this thesis. The mathematical model development deals with surface water, soil water and biomass dynamics constructed by mimicking the biomass and water dynamics of Klausmeier (1999) model of regular and irregular patterns in semiarid vegetation. Although in the Klausmeier model the water dynamics was considered as a single entity, in the proposed models it was considered as two different entities: the surface water and soil water dynamics. However, in the development of the models, the surface water dynamics was linked to soil water dynamics by the surface water infiltration into the soil. The models further show how the soil water uptake by plants was considered as being proportional to plant growth and spread.

According to Li *et al.* (2003), crop growth process is a multi-environment external force action. Thus, the dynamic models were built by adopting the continuous-time Markov process used by Li *et al.* (2003). This was considered as the empirical aspect of the model formulation. A plant growth function β representing a multi-environment external force action was introduced into the model to assess different levels of soil fertility under different water conditions available to the vegetation growth. The different water conditions considered were Rich-water condition, the Average water condition and Arid condition. The soil fertility levels were the control fertility, lower fertility, middle fertility and the higher fertility. The models formed are coupled reaction-diffusion partial differential equation systems.

Linear stability analysis was done to determine whether patterns formation is possible from a homogeneous vegetation. The principle behind this linear stability analysis is to investigate the parameter space that may induce patterns formation. In the trivial case, the linear stability analysis of the study shows that, stability conditions needed for pattern formation is possible provided that $aN_0/[aN_0 + m(rN_0 + l)] \rightarrow 0$, as $a \rightarrow 0$. This implies that the homogeneous plant equilibrium decreases with decreasing rainfall until plants become extinct. Based on this condition, the trace and determinant criteria the trace and determinant criteria for stability were obtained as $-(m + u)$ and mu respectively. This allows for homogeneous equilibrium of surface water, soil water and plant density. Again, as N_0 increases or decreases, $aN_0/[aN_0 + m(rN_0 + l)]$ also increases or decreases

irrespective of the values of the other parameters. Thus, the results suggest that N_0 which is a surrogate for a dimensionless infiltration capacity prohibits pattern formation at high levels. Hence, one may not expect vegetation patterns to exist when the soil fertility level is high and under rich water condition. Thus, the observation of vegetation patterns on higher fertility level in a given area of rich water condition suggests that, in that area, other environment factors other than increased infiltration with increasing vegetation biomass, high fertility and rich-water condition are operating and responsible for pattern formation. This is consistent with the findings of D'Odorico *et al.* (2007).

In the non-trivial case, the linear stability analysis of the study shows that the conditions needed for pattern formation to be satisfied is that $rmu < a - lw_s$ and $w_s > gu$. Thus, based on these conditions, the trace and determinant criteria are satisfied. Hence, ecologically feasible region of the parameter space that gives rise to Turing regimes in which vegetation patterns continuously evolve in space is such that $gu < w_s < (a - rmu)/l$. Regardless of the parameter space, as precipitation rate decreases the vegetation cover shifts from uniform to gaps, labyrinths, spots, and finally, bare soil. This behavior is consistent with the simulation results reported in the findings of Gilad *et al.* (2007a); Kéfi *et al.* (2010); Meron *et al.* (2004); Meron (2011); and Rietkerk *et al.* (2002).

The linear instability situations are influenced by two main inequalities given by the following $(u + D_{PW}Q^2) < aN_0/[aN_0 + m(rN_0 + l)]$ and

$(m + D_{NW}Q^2 + u + D_{PW}Q^2) < aN_0/[aN_0 + m(rN_0 + l)]$. This gives an indication of the principle of pattern formation outlined by Turing. The models show positive relationship between plant density and water infiltration.

In order to corroborate the theoretical analysis in Chapter 5, a numerical simulation of system Equation (5.2) was carried out based on different soil fertility levels, under different water conditions as indicated in the first part of chapter 6. The computations were performed on a two-dimensional grid of size 200×200 with $\Delta x = 0.01$, $\Delta y = 0.02$ and time step $\Delta t = 2$ and zero flux boundary conditions. Simulations run on these models resulted into the emergence of vegetation patterns as a result of nonlinear dynamical interactions between biomass, available soil water, and surface water. These patterns that emerged for

control fertility, lower fertility, middle fertility and higher fertility under rich water, average water and arid conditions were compared.

It was observed that under rich water condition, the fertility level gradually increased, as the number of patches of bare or almost bare land formed by the vegetation decreased together with the sizes of area covered by these patches of bare land. These observations were clearly seen for control and lower fertilities with β -value of 0.114652458 and 0.1275087323 respectively. Unexpectedly, there was a slight variation in the case of middle fertility. Though, the number of patches of bare or almost bare land were expected to be fewer in the case of middle fertility with β -value of 0.1402957524, they turned out to be more. However, the intensity of the patches of vegetation was high as compared to that of lower fertility and the corresponding patches of bare land were narrower. At higher fertility under the same rich water condition with β -value of 0.1576053443, though patches of bare land were not wholly absent they were barely insignificant compared to other fertility levels shown in Figures 6.5a, 6.5b and 6.5c. Again, the intensity of the vegetation is very high as compared to all the others.

In the case of Average water condition, the vegetation shows a pattern with quite a number of patches of bare or almost bare land of which some are labyrinth in nature and comparatively covers wider areas. This represents the Control fertility with a β -value of 0.0780268371. For lower fertility represented by a β -value of 0.1113796509, the number of patches of bare or almost bare land formed by the vegetation are more compared with the case of control fertility. However, the areas covered by these patches are comparatively dwindled. The number of patches of bare or almost bare land decreased with a corresponding dwindling of these patches of bare land at a β -value of 0.1363325869 for middle fertility. When the β -value is at 0.137662054 representing higher fertility, there was a considerable reduction in the number of patches of bare or almost bare land and the intensity of the patches of the vegetation was quite high compared to all the others. The nature of vegetation patterns developed from these models is an indication that formation of patterns does not only depend on the level of fertility but could be as a result of other factors that can equally compensate for the fertility level and water condition.

Finally, the effects of different fertility levels on the patterns formed by the vegetation under Arid condition depict the following: for a β -value of 0.0560530255 representing the

Control fertility, the vegetation shows a pattern which is labyrinth in nature. In the case of lower fertility with a β -value of 0.0619864031, the number of patches of bare or almost bare land formed by the ecosystem reduces. However, some of the areas covered by these patches are equally wide and labyrinth in nature, yet some few show spottily nature. The simulations show a drastic decrease in the number of patches of bare or almost bare land in the case of $\beta = 0.0812833722$ for middle fertility. Nonetheless, these very few patches are wider and labyrinth in nature. Its homogeneous vegetation cover is higher comparatively to that of higher fertility with a β -value of 0.0711112388. There are more patches of bare or almost bare land generated in the higher fertility than in the case of middle fertility though fewer patches of bare land were expected than in the middle fertility. The few patches of bare land and high intensity of uniform vegetation exhibited in the simulation results is an indication that factors other than fertility level and water condition account for the growth of a vegetation. The results of the simulations also suggest that when these spots, labyrinths and gaps arise from a high intensity and homogeneous vegetation cover, this could be an indication that the ecosystem is approaching desertification. This finding is consistent with other pattern-forming models (von Hardenberg *et al.*, 2001; Gilad *et al.*, 2004; and Rietkerk *et al.*, 2004). Hence, the existence of these vegetation patterns associated with these fertility levels in the simulations of these models indicates imminent catastrophic shifts. The results of the simulations suggest that high N_0 which is a surrogate for a dimensionless infiltration capacity prohibits pattern formation. Hence, one may not expect vegetation patterns to exist on high fertility level and rich water condition. The observation of vegetation patterns on higher fertility in a given area may suggest that, mechanisms other than increased infiltration with increasing vegetation biomass, fertility and water condition are operating and therefore responsible for pattern formation. This is consistent with the report in the findings of D'Odorico *et al.* (2007).

CHAPTER 7

CONCLUSIONS AND RECOMMENDATIONS

7.1 Conclusions

The study was conducted purposely to develop two mathematical models that take into account surface water, soil water and biomass dynamics to investigate the dynamics of forest growth and vegetation pattern formation. From the findings of the research, the following conclusions were made in relation to the objectives of the study.

- a. A system of nonlinear partial differential equations models that takes into account the interactions among external force action of multi environment factors such as light, water, temperature and nutrients on the growth, spread and vegetation pattern formation using Continuous-time Markov (CTM) approach has been established.
- b. The dynamics of the forest reserves using the system of partial differential equations models for growth rate and pattern formation have been explored. These nonlinear models were linearised using Taylor Series expansion method. Applying stability analysis and suitable numerical simulations, the turing parameter space, the associated pattern type and the conditions for pattern formation were identified. The results provided clear evidence indicated below:
 - (i) The linear stability analysis of homogeneous steady-state solutions provided a reliable predictor of the beginning and nature of pattern formation in the reaction–diffusion systems. The stability conditions needed for pattern formation to be satisfied were that $aN_0/[aN_0 + m(rN_0 + l)] \rightarrow 0$, as $a \rightarrow 0$. Thus, the homogeneous plant equilibrium decreases with decreasing rainfall until plant become extinct and as N_0 increases or decreases $aN_0/[aN_0 + m(rN_0 + l)]$ also increases or decreases respectively. The results further suggest that high N_0 which is a surrogate for a dimensionless infiltration capacity prohibits pattern formation. Hence, one may not expect vegetation patterns to exist on high fertility level and rich water condition. However, this was not the case. In the non-trivial case, the linear stability analysis of the study

shows that the conditions needed for pattern formation to be satisfied was that $rmu < a - lw_s$ and $w_s > gu$. Hence, ecologically feasible region of the parameter space that gives rise to turing regimes in which vegetation patterns continuously evolve in space was such that $gu < w_s < (a - rmu)/l$.

- (ii) The linear instability situations are influenced by two main inequalities given by the following

$$(u + D_{PW}Q^2) < aN_0/[aN_0 + m(rN_0 + l)] \text{ and}$$

$$(m + D_{NW}Q^2 + u + D_{PW}Q^2) < aN_0/[aN_0 + m(rN_0 + l)].$$

This gives an indication of the principle of pattern formation outlined by Turing.

- c. Finally, in order to validate the proposed models, numerical simulations of the models were carried out based on different soil fertility levels under different water conditions. Thus, regardless of the parameter space, it was realized that, no matter the level of precipitation, the shift of vegetation cover from uniform pattern to either gaps, labyrinths, spots, and bare soil or almost bare soil is possible.

7.2 Contributions to Knowledge

The contributions of this research to knowledge have been presented in Chapters 4, 5 and 6. The contributions to knowledge are summarised as follows:

- (i) Two systems of nonlinear partial differential equations models that take into account the influence of the interactions among multiple resources such as light, water, temperature and nutrients on the growth, spread and vegetation pattern formation has been formulated and analysed. The plant growth function β representing a multi-environment external force action introduced into the model provides a reference base for conditions to the vegetation growth and pattern formation.
- (ii) A heterogeneous analysis of three dimensional model has been established as against most previous modelling analysis which only considered homogeneous aspect and are mostly two-dimensional.

7.3 Recommendations for Future Research work

The following recommendations based on the challenges of the work are made for future research:

- a. The proposed model derived in the study could be applied to any vegetation type. The model could be used to further analyse the conditions for the development of dynamic patterns and their occurrence in different biological systems.
- b. The topography of a land is not completely perfectly horizontal terrain but includes portions with slope lengths (the horizontal distance from the point of origin of overland flow to the point where either the slope gradient decreases enough to allow deposition to begin or the flow is concentrated in a defined channel). The surface water dynamics component of the proposed model could be modified to include the topographic factor (LS) which represents the ratio of soil loss on a given slope length (L) and steepness (S) to soil loss from a slope that has a length of 72.6 feet and steepness of 9 percent.
- c. The dynamics of a vegetation should be investigated into based on the topography of the land with the procedure for converting the slope length (L) and slope steepness (S) into the topographic factor (LS). This should be done by use of the modified proposed model varied depending on whether the slope is uniform, irregular or segmented.

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APPENDICES

APPENDIX A1 THE DIMENSIONLESS FORM OF THE FIRST PROPOSED MODEL

$$\begin{aligned}
 \underbrace{\frac{\partial W}{\partial T}}_{\text{Rate of change of surface water}} &= \underbrace{A}_{\text{Rainfall}} - \underbrace{LW}_{\text{water loss due to evaporation}} - \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{surface water infiltration into the soil}} + \underbrace{V \frac{\partial W}{\partial X}}_{\text{water movement at uniform speed}} \\
 \underbrace{\frac{\partial N}{\partial T}}_{\text{Rate of change of soil water}} &= \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{infiltration into the soil from surface water}} - \underbrace{MN}_{\text{evaporation and drainage}} - \underbrace{J \times \left(\frac{N}{N + s_1} \right) P}_{\text{Soil water loss by plants uptake}} + \underbrace{D_N \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right)}_{\text{Soil water movement}} \\
 \underbrace{\frac{\partial P}{\partial T}}_{\text{Rate of change of plant density}} &= \underbrace{(\beta + J) \times \left(\frac{N}{N + s_1} \right) P}_{\text{soil water uptake by plants / growth}} - \underbrace{UP}_{\text{Plant loss as a result of mortality}} + \underbrace{D_p \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right)}_{\text{plant dispersal}}
 \end{aligned}$$

The variables are: W , N , P , T , X and Y

The parameters are: A , L , R , V , J , M , s_1 , s_2 , D_N , D_p , N_0 , U and β

From the variables, let $W = \bar{W} \cdot w$, $N = \bar{N} \cdot n$, $P = \bar{P} \cdot p$, $T = \bar{T} \cdot t$, $X = \bar{X} \cdot x$ and $Y = \bar{Y} \cdot y$

$$\begin{aligned}
 \frac{\partial(\bar{W} \cdot w)}{\partial(\bar{T} \cdot t)} &= A - L(\bar{W} \cdot w) - R(\bar{W} \cdot w) \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] + V \frac{\partial(\bar{W} \cdot w)}{\partial(\bar{X} \cdot x)} \\
 \frac{\partial(\bar{N} \cdot n)}{\partial(\bar{T} \cdot t)} &= R(\bar{W} \cdot w) \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] - M(\bar{N} \cdot n) - J \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] (\bar{P} \cdot p) \\
 &\quad + D_N \left(\frac{\partial^2(\bar{N} \cdot n)}{\partial(\bar{X} \cdot x)^2} + \frac{\partial^2(\bar{N} \cdot n)}{\partial(\bar{Y} \cdot y)^2} \right) \\
 \frac{\partial(\bar{P} \cdot p)}{\partial(\bar{T} \cdot t)} &= (J + \beta) \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] (\bar{P} \cdot p) - U(\bar{P} \cdot p) + D_p \left(\frac{\partial^2(\bar{P} \cdot p)}{\partial(\bar{X} \cdot x)^2} + \frac{\partial^2(\bar{P} \cdot p)}{\partial(\bar{Y} \cdot y)^2} \right)
 \end{aligned}$$

$$\left. \begin{aligned} \frac{\bar{W}}{\bar{T}} \cdot \frac{\partial w}{\partial t} &= A - L\bar{W}w - R\bar{W} \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w + \frac{V\bar{W}}{\bar{X}} \cdot \frac{\partial w}{\partial x} \\ \frac{\bar{N}}{\bar{T}} \cdot \frac{\partial n}{\partial t} &= R\bar{W} \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w - M\bar{N}n - J\bar{P} \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p + D_N \bar{N} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\bar{P}}{\bar{T}} \cdot \frac{\partial p}{\partial t} &= (J + \beta) \bar{P} \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p - U\bar{P}p + D_P \bar{P} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w + \frac{V\bar{T}}{\bar{X}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{\bar{N}} \cdot \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w - M\bar{T}n - \frac{J\bar{P}\bar{T}}{\bar{N}} \cdot \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J + \beta) \bar{T} \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p - U\bar{T}p + D_P \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

Let the possible values of \bar{P} and \bar{N} be represented as: $\bar{P} = s_2$, and $\bar{N} = s_1$.

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{s_2 p + s_2 N_0}{s_2 p + s_2} \right] w + \frac{V\bar{T}}{\bar{X}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{s_1} \cdot \left[\frac{s_2 p + s_2 N_0}{s_2 p + s_2} \right] w - M\bar{T}n - \frac{J\bar{T}s_2}{s_1} \cdot \left[\frac{s_1 n}{s_1 n + s_1} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J + \beta) \bar{T} \left[\frac{s_1 n}{s_1 n + s_1} \right] p - U\bar{T}p + D_P \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{s_2 (p + N_0)}{s_2 (p + 1)} \right] w + \frac{V\bar{T}}{\bar{X}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{s_1} \cdot \left[\frac{s_2 (p + N_0)}{s_2 (p + 1)} \right] w - M\bar{T}n - \frac{J\bar{T}s_2}{s_1} \cdot \left[\frac{s_1 n}{s_1 (n + 1)} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J + \beta) \bar{T} \left[\frac{s_1 n}{s_1 (n + 1)} \right] p - U\bar{T}p + D_P \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{V\bar{T}}{\bar{X}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - M\bar{T}n - \frac{J\bar{T}s_2}{s_1} \cdot \left[\frac{n}{(n+1)} \right] p + D_N\bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J+\beta)\bar{T} \left[\frac{n}{(n+1)} \right] p - U\bar{T}p + D_p\bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

The possible values of \bar{T} are: $\bar{T} = 1/(J+\beta)$, $\bar{T} = 1/M$, $\bar{T} = 1/L$ and $\bar{T} = 1/U$. Taking $\bar{T} = 1/(J+\beta)$:

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)\bar{W}} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{V}{(J+\beta)\bar{X}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{W}}{(J+\beta)s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p \\ &\quad + \frac{D_N}{(J+\beta)} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{(J+\beta)} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

The possible values of \bar{X} and \bar{Y} are: $\bar{X} = (D_w/\{J+\beta\})^{1/2}$, $\bar{Y} = (D_w/\{J+\beta\})^{1/2}$ and $\bar{X} = 1/(J+\beta)$. When $\bar{X} = (D_w/\{J+\beta\})^{1/2}$ and $\bar{Y} = (D_w/\{J+\beta\})^{1/2}$:

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)\bar{W}} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{V}{(J+\beta)} \cdot \left(\frac{J+\beta}{D_N} \right)^{1/2} \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{W}}{(J+\beta)s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p \\ &\quad + \frac{D_N}{(J+\beta)} \cdot \left(\frac{J+\beta}{D_N} \right) \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{(J+\beta)} \cdot \left(\frac{J+\beta}{D_N} \right) \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)\bar{W}} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{V}{[D_N(J+\beta)]^{1/2}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R\bar{W}}{(J+\beta)s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{D_N} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

Let the possible value of \bar{W} be represented as: $\bar{W} = (J+\beta)s_1/R$:

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)} \cdot \frac{R}{(J+\beta)s_1} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{V}{[D_w(J+\beta)]^{1/2}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \frac{R}{(J+\beta)s_1} \cdot \frac{(J+\beta)s_1}{R} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{D_N} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{AR}{(J+\beta)^2 s_1} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{V}{[D_w(J+\beta)]^{1/2}} \cdot \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{D_N} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} a &= \frac{AR}{(\beta+J)^2 s_1}, \quad l = \frac{L}{(\beta+J)}, \quad r = \frac{R}{(\beta+J)}, \quad m = \frac{M}{(\beta+J)}, \quad g = \frac{Js_2}{(\beta+J)s_1}, \\ u &= \frac{U}{(\beta+J)}, \quad y = \left(\frac{(\beta+J)}{D_N} \right)^{1/2} Y, \quad x = \left(\frac{(\beta+J)}{D_N} \right)^{1/2} X, \quad D_{PN} = \frac{D_p}{D_N}, \\ w &= \frac{WR}{(\beta+J)s_1}, \quad t = (\beta+J)T, \quad n = \frac{N}{s_1}, \quad p = \frac{P}{s_2}, \quad v = \frac{V}{[D_N(\beta+J)]^{1/2}} \end{aligned} \right\}$$

Substituting into the above equation reduces to the form

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - lw - r \left(\frac{p + N_0}{p + 1} \right) w + v \frac{\partial w}{\partial x} \\ \frac{\partial n}{\partial t} &= \left(\frac{p + N_0}{p + 1} \right) w - mn - g \cdot \left(\frac{n}{n + 1} \right) p + \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left(\frac{n}{n + 1} \right) p - up + D_{PN} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$



APPENDIX A2 THE DIMENSIONLESS FORM OF THE SECOND PROPOSED MODEL

$$\left. \begin{aligned}
 \underbrace{\frac{\partial W}{\partial T}}_{\text{Rate of change of surface water}} &= \underbrace{A}_{\text{Rainfall}} - \underbrace{LW}_{\text{water loss due to evaporation}} - \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{water infiltration into the soil}} + \underbrace{D_W \left(\frac{\partial^2 W}{\partial X^2} + \frac{\partial^2 W}{\partial Y^2} \right)}_{\text{Surface water movements}} \\
 \underbrace{\frac{\partial N}{\partial T}}_{\text{Rate of change of soil water}} &= \underbrace{RW \left(\frac{P + s_2 N_0}{P + s_2} \right)}_{\text{infiltration into the soil from surface water}} - \underbrace{MN}_{\text{evaporation and drainage}} - \underbrace{J \times \left(\frac{N}{N + s_1} \right) P}_{\text{Soil water loss by plants uptake}} + \underbrace{D_N \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right)}_{\text{Soil water movement}} \\
 \underbrace{\frac{\partial P}{\partial T}}_{\text{Rate of change of plant density}} &= \underbrace{(\beta + J) \times \left(\frac{N}{N + s_1} \right) P}_{\text{soil water uptake by plants / growth}} - \underbrace{UP}_{\text{Plant loss as a result of mortality}} + \underbrace{D_P \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right)}_{\text{plant dispersal}}
 \end{aligned} \right\}$$

The variables are: W , N , P , T , X and Y

The parameters are: A , L , R , J , M , s_1 , s_2 , D_N , D_P , D_W , N_0 , U and β

From the variables, let $W = \bar{W} \cdot w$, $N = \bar{N} \cdot n$, $P = \bar{P} \cdot p$, $T = \bar{T} \cdot t$, $X = \bar{X} \cdot x$ and $Y = \bar{Y} \cdot y$

$$\left. \begin{aligned}
 \frac{\partial(\bar{W} \cdot w)}{\partial(\bar{T} \cdot t)} &= A - L(\bar{W} \cdot w) - R(\bar{W} \cdot w) \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] + D_W \left(\frac{\partial^2(\bar{W} \cdot w)}{\partial(\bar{X} \cdot x)^2} + \frac{\partial^2(\bar{W} \cdot w)}{\partial(\bar{Y} \cdot y)^2} \right) \\
 \frac{\partial(\bar{N} \cdot n)}{\partial(\bar{T} \cdot t)} &= R(\bar{W} \cdot w) \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] - M(\bar{N} \cdot n) - J \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] (\bar{P} \cdot p) \\
 &\quad + D_N \left(\frac{\partial^2(\bar{N} \cdot n)}{\partial(\bar{X} \cdot x)^2} + \frac{\partial^2(\bar{N} \cdot n)}{\partial(\bar{Y} \cdot y)^2} \right) \\
 \frac{\partial(\bar{P} \cdot p)}{\partial(\bar{T} \cdot t)} &= (J + \beta) \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] (\bar{P} \cdot p) - U(\bar{P} \cdot p) + D_P \left(\frac{\partial^2(\bar{P} \cdot p)}{\partial(\bar{X} \cdot x)^2} + \frac{\partial^2(\bar{P} \cdot p)}{\partial(\bar{Y} \cdot y)^2} \right)
 \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\bar{W}}{\bar{T}} \cdot \frac{\partial w}{\partial t} &= A - L\bar{W}w - R\bar{W} \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w + D_w \left(\frac{\bar{W}}{\bar{X}^2} \cdot \frac{\partial^2 w}{\partial x^2} + \frac{\bar{W}}{\bar{Y}^2} \cdot \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\bar{N}}{\bar{T}} \cdot \frac{\partial n}{\partial t} &= R\bar{W} \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w - M\bar{N}n - J\bar{P} \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p + D_N \left(\frac{\bar{N}}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{\bar{N}}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\bar{P}}{\bar{T}} \cdot \frac{\partial p}{\partial t} &= (J + \beta)\bar{P} \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p - U\bar{P}p + D_P \left(\frac{\bar{P}}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{\bar{P}}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w + D_w \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 w}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{\bar{N}} \cdot \left[\frac{\bar{P} \cdot p + s_2 N_0}{\bar{P} \cdot p + s_2} \right] w - M\bar{T}n - \frac{J\bar{P}\bar{T}}{\bar{N}} \cdot \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J + \beta)\bar{T} \left[\frac{\bar{N} \cdot n}{\bar{N} \cdot n + s_1} \right] p - U\bar{T}p + D_P \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

Let the possible values of \bar{P} and \bar{N} be represented as: $\bar{P} = s_2$, and $\bar{N} = s_1$.

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{s_2 p + s_2 N_0}{s_2 p + s_2} \right] w + D_w \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 w}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{s_1} \cdot \left[\frac{s_2 p + s_2 N_0}{s_2 p + s_2} \right] w - M\bar{T}n - \frac{J\bar{T}s_2}{s_1} \cdot \left[\frac{s_1 n}{s_1 n + s_1} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J + \beta)\bar{T} \left[\frac{s_1 n}{s_1 n + s_1} \right] p - U\bar{T}p + D_P \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{s_2 (p + N_0)}{s_2 (p + 1)} \right] w + D_w \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 w}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{s_1} \cdot \left[\frac{s_2 (p + N_0)}{s_2 (p + 1)} \right] w - M\bar{T}n - \frac{J\bar{T}s_2}{s_1} \cdot \left[\frac{s_1 n}{s_1 (n + 1)} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J + \beta)\bar{T} \left[\frac{s_1 n}{s_1 (n + 1)} \right] p - U\bar{T}p + D_P \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A\bar{T}}{\bar{W}} - L\bar{T}w - R\bar{T} \left[\frac{(p+N_0)}{(p+1)} \right] w + D_w \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 w}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{T}\bar{W}}{s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - M\bar{T}n - \frac{J\bar{T}s_2}{s_1} \cdot \left[\frac{n}{(n+1)} \right] p + D_N \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= (J+\beta)\bar{T} \left[\frac{n}{(n+1)} \right] p - U\bar{T}p + D_p \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

The possible values of \bar{T} are: $\bar{T} = 1/(J+\beta)$, $\bar{T} = 1/M$, $\bar{T} = 1/L$ and $\bar{T} = 1/U$. When $\bar{T} = 1/(J+\beta)$:

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)\bar{W}} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + D_w \bar{T} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 w}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{W}}{(J+\beta)s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p \\ &\quad + \frac{D_N}{(J+\beta)} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 n}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{(J+\beta)} \left(\frac{1}{\bar{X}^2} \cdot \frac{\partial^2 p}{\partial x^2} + \frac{1}{\bar{Y}^2} \cdot \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

The possible values of \bar{X} and \bar{Y} are: $\bar{X} = [D_w/(J+\beta)]^{1/2}$, $\bar{Y} = [D_w/(J+\beta)]^{1/2}$. When $\bar{X} = [D_w/(J+\beta)]^{1/2}$ and $\bar{Y} = [D_w/(J+\beta)]^{1/2}$:

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)\bar{W}} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{D_w}{(J+\beta)} \cdot \left(\frac{J+\beta}{D_w} \right) \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{W}}{(J+\beta)s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p \\ &\quad + \frac{D_N}{(J+\beta)} \cdot \left(\frac{J+\beta}{D_w} \right) \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{(J+\beta)} \cdot \left(\frac{J+\beta}{D_w} \right) \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)\bar{W}} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{D_w}{D_w} \cdot \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R\bar{W}}{(J+\beta)s_1} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p + \frac{D_N}{D_w} \cdot \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{D_w} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

Let the possible value of \bar{W} be represented as: $\bar{W} = (J+\beta)s_1/R$:

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{A}{(J+\beta)} \cdot \frac{R}{(J+\beta)s_1} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{D_N}{D_w} \cdot \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \frac{R}{(J+\beta)s_1} \cdot \frac{(J+\beta)s_1}{R} \cdot \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p + \frac{D_N}{D_w} \cdot \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{D_w} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= \frac{AR}{(J+\beta)^2 s_1} - \frac{Lw}{(J+\beta)} - \frac{R}{(J+\beta)} \left[\frac{(p+N_0)}{(p+1)} \right] w + \frac{D_w}{D_w} \cdot \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \left[\frac{(p+N_0)}{(p+1)} \right] w - \frac{Mn}{(J+\beta)} - \frac{Js_2}{(J+\beta)s_1} \cdot \left[\frac{n}{(n+1)} \right] p + \frac{D_N}{D_w} \cdot \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left[\frac{n}{(n+1)} \right] p - \frac{Up}{(J+\beta)} + \frac{D_p}{D_w} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

$$\left. \begin{aligned} a &= \frac{AR}{(\beta+J)^2 s_1}, \quad l = \frac{L}{(\beta+J)}, \quad r = \frac{R}{(\beta+J)}, \quad m = \frac{M}{(\beta+J)}, \quad g = \frac{Js_2}{(\beta+J)s_1}, \\ u &= \frac{U}{(\beta+J)}, \quad y = \left(\frac{(\beta+J)}{D_w} \right)^{1/2} Y, \quad x = \left(\frac{(\beta+J)}{D_w} \right)^{1/2} X, \quad D_{pw} = \frac{D_p}{D_w}, \\ w &= \frac{WR}{(\beta+J)s_1}, \quad D_{nw} = \frac{D_N}{D_w}, \quad t = (\beta+J)T, \quad n = \frac{N}{s_1}, \quad p = \frac{P}{s_2} \end{aligned} \right\}$$

Substituting into the above equation reduces to the form

$$\left. \begin{aligned} \frac{\partial w}{\partial t} &= a - lw - r \left(\frac{p + N_0}{p+1} \right) w + \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) \\ \frac{\partial n}{\partial t} &= \left(\frac{p + N_0}{p+1} \right) w - mn - g \cdot \left(\frac{n}{n+1} \right) p + D_{nw} \cdot \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) \\ \frac{\partial p}{\partial t} &= \left(\frac{n}{n+1} \right) p - up + D_{pw} \cdot \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} \right) \end{aligned} \right\}$$

