Mathematical Analysis of Plant-Herbivore Interaction: *with Temporal and Spatial Variations in the Ethiopian Climate*

Manalebish Debalike Asfaw

December 2018

Addis Ababa University

Mathematical Analysis of Plant-Herbivore Interaction: *with Temporal and Spatial Variations in the Ethiopian Climate*

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A Dissertation Submitted to the Department of Mathematics in Partial Fulfillment to the Requirements for the Degree Doctor of Philosophy in Mathematics at Addis Ababa University

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Declaration

This dissertation is my original work and has not been presented for a degree in any other university, and that all sources of the materials used for the dissertation have been duly acknowledged.

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Abstract

In ecology, the food chain pyramid suggests that there must be less consumers than their food source. In our case the balance in the population of plants and herbivores should be maintained in the ecosystem. Otherwise, the extinction of one or both population may occur. In the interaction between plants and herbivores that live in the same ecosystem, understanding the conditions in which coexistence equilibrium occurs answers a major question in ecology. In this interaction, plants serve as food for herbivores. Then the livelihood of herbivores highly depend on the availability of plants. Moreover, the abundance of the plant density alone does not guarantee the non-extinction of the herbivore population as they are assumed to reproduce sexually. Plant-herbivore relationship depends also on environmental factors like rainfall, temperature and altitude. Due to global climate change the increase/decrease in temperature and also in rainfall will have an effect on their interaction. Environmental noises both positive (such as putting extra water source for the herbivores, or fencing the land to recover by keeping herbivores away) and negative (such as animal/plant disease) often affect population dynamics.

In this study, threshold conditions are obtained for the non extinction of the herbivore population and a trapping region is obtained to ensure coexistence of the population. Moreover, it has been shown that the dynamics of the population is significantly sensitive to the feeding rate and the harvest rate of the herbivore population. It was also found that the environmental noises added to the herbivore population resulted more change in the dynamics than those added to the plant population (food source). Ignoring the environmental noise could make the land management and wild life conservation difficult to maintain their goals.

Furthermore, considering periodically changing rainfall and temperature, it has been shown that we can find a trapping region for the coexistence of populations. To validate the results of the mathematical model, real data from the Genale-Dawa river basin in the southern part of Ethiopia, is collected and used. The river basin represents the three major climatic zones of the country, the cool zone, temperate zone and hot lowlands. It is also found that if the temperature and rainfall varies with in 10% there is a possibility of extinction of population. This needs the attention of an environmental conservation people and/or those people who are animal farmers.

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1 Introduction

Animals of all kind live together in various ecosystems. Within these natural communities, their diet connects them together in a food chain. Among these diets, creatures that eat only plants exclusively are called herbivores. Animals that feed on meat (other animals) are called carnivores and those that feed on both plants and meet are called omnivores.

Ecology is the science in which the interaction of living things with each other and their natural environment is studied. It addresses the diverse and complex relationships of living organisms from various angles. Ecology provides essential information on how the world works and interdependence between the natural world and people.

1.1 Plant-Herbivore Interaction

All living things get energy for their survival, growth and developments from water, sun light and their various sources of food. The rule of nature for all living things in any ecosystem is based on the battle of survival, and every species act accordingly [HP13]. Different species[1] occupying similar ecosystems and living amongst each other will regularly interact. This interaction is broadly classified into predation and competition. Competition is the issue of organisms fighting for some limited resource in an ecosystem. Predation is a species interaction when one species, the predator eats another species, the prey as a source of food. Plants and herbivores are parts of the food web where plants serve as food sources for herbivores.

All food chain start with energy source that is the sun. These energy is then captured by plants. Thus the living part of the food chain always starts with plant life. Plants are called producers because they are able use light enery from the sun and produce food (sugar) from carbon-dioxide and water. Animals cannot make their own food so they must eat plants and/or other animals. They are called consumers. Herbivores form an important link in the food chain because they consume plants in order to digest the carbohydrates photosynthetically produced by plants. Herbivores are also known as primary consumers because of their ability to survive solely on tough and fibrous plant matter.

[1] species is a grouping of organisms that can interbreed and produce fertile offspring

Plants and herbivores comprise almost 50% of the organisms on earth. They are found at the base of the pyramid of the food chain. The interaction between plants and herbivores powerfully shape communities and ecosystems [Col98]. Many plant-herbivore relationships can be fully described by complex often nonlinear relationships which can lead to a threshold whereby slight and apparently weak changes in processes operating at small scale can result in sudden and dramatic changes at larger scales [CP01; Hol+13]. Consequently understanding the effect of herbivores on whole plants and plant communities require a detailed understanding of the complex relationship that drive small-scale processes and the manner in which they interact to generate dynamics at larger scales [BM11].

Herbivores in general can be classified in to three broad categories these are: Concentrate selectors that feed mostly fruit tree and shrub browsing feeding smaller amount frequently (like Deer and Giraffe). Intermediate feeder are those that are adapted mostly to browsing or grazing and they shift their feeding behavior according to plant availability (like Moose, goat, sheep) and Grazers or Roughage feeders which mostly eat grass and take longest retention time necessary to digest cell-wall (such as Cattle and Buffalo). Herbivores can also be classified according to their sizes: small (insects) and large. The interaction between plants and herbivore is one of the prey-predator system and one such interaction can be considered as grazing.

It has long been considered that the existence of herbivores has a negative impact on plants, both in terms of growth and reproduction. Herbivore not only can decrease leaf area, but also nutrient stocks, photosynthetic capacity [Buc+05; Zan+02], reproductive success or vegetative growth [Leb+14]. Yet, in response to herbivory, plants have evolved different defense strategies, which can be broadly categorized into resistance and tolerance [Aba+12; Leb+14].

On the other hand herbivory also help plants during pollination period by spreading the seeds or pollen. Herbivore grazing is advantageous towards the soil and grasses, promoting nutrient dense soil and stimulating the growth of plant varieties. Furthermore, the animal's urine and feces " recycle nitrogen, phosphorus, potassium and other plant nutrients and return them to the soil" [Kan+08]. It also acts as rations for insects and organisms found within the soil. These organisms within the soil "aid in carbon sequestration and water filtration ". The dung of herbivores help the soil to rehabilitate and serve as a fertilizer. Therefore, the interaction of plants and herbivore is mutualistic [Leb+14].

Herbivore diet differ due to availability, for example in a study done by Lyons et al [Lyo+]shows that goat prefer forbs, but browse is probably a more readily available food source during tough times. Herbivore diet also vary from season to season for example cattle eat more grass in winter and less in spring; more forbs in spring and

less in fall and winter; and more browse in fall and less in spring. In Ethiopia the four seasons are Summer - June, July and August are the summer season. Heavy rain falls in these three months. Autumn - September, October and November are the spring season sometime known as the harvest season. Winter - December, January and February are the dry season with frost in morning specially in January. Spring - March, April and May are the autumn season with occasional showers. May is the hottest month in Ethiopia.

Herbivore impacts are highly spatially and temporally variable [Fen+09; Moo+10] : which means understanding the underlying relationship at one scale, outcomes at larger scale may vary due to difference in context or inherent stochasticity in the system.

Due to the importance of plant-herbivore interaction, the dynamic relationship between them has long been and continues to be one of the dominant themes in mathematical ecology [Buo+14; Ji+11]. In many circumstances such relations are analyzed using deterministic mathematical models see, for example, [Fen+11; FD17; Hol+13; Kar16; Kan+08; Leb+14; Lev68a; Liu+08; Lim12; Ter15]. However, population dynamics are often affected by environmental noise, and hence there are many benefits to be gained by using stochastic models because they provide some additional degree of realism compared to their deterministic counterparts [Agu+13; Ji+11; Mao+02].

1.2 Mathematical Modeling in Ecology

Mathematical modeling is the means of transforming problems from real world phenomenon into an easy mathematical equation (formula) whose numerical and theoretical analysis provides answers, insight, and useful guidance for solving or describing and forecasting the original real life condition. Mathematical formulas are used to describe the interactions of the various components of the system. Mathematical modeling is preferred technique because we can change different biological scenarios to mathematically solvable equations and this provides direction on how to solve real life problems without performing an experiment. It gives exactness or approximation, it will help us understand the modeled system deeply and thoroughly. This paves the way for a better method of design or management of a system. It allows the proficient use of modern software programs and computer simulations.

Mathematical modeling on ecology basically considers the interrelationship between species and their environment, in such areas as predator-prey, competition interactions, renewable resource management, evolution of pesticide resistant species,

genetically engineered control of pests, multi-species societies or plant herbivore systems, etc. Mathematical models make our assessment and prediction in ecology more objective and reliable.

When species interact the population dynamics of each species is affected. There are three main types of interaction. These are 1) Predator Prey Situation: If the growth rate of one population is decreased and the other increased. 2) Competition: If the growth rate of each population is decreased. 3) Mutualism or Symbiosis:If each population growth rate is enhanced. The balance of an ecosystem depends on the presence of every type of animal. If one type of animal becomes too numerous or scarce, the entire balance of the ecosystem will change.

Differential equations, among other things are used in the analysis of the dynamics of population variation through time. Since rates are expressed as derivatives the variation in time of the population can be expressed in differential equations. In population studies the common assumption is that in the absence of a limiting factor a population will grow at a rate proportional to its size.

$$\frac{dP}{dt} \sim P \qquad \frac{dP}{dt} = rP \tag{1.1}$$

where $P(t)$ is population size at time t, and r is a constant. Solution of this equation by integration gives

$$P(t) = P(0)e^{rt} \tag{1.2}$$

where $P(0)$ is population size at the initial time. The solution of the equation means the population grows at exponential rate. But most natural populations are subject to constraints such as food supply or carrying capacity of the habitat which restricts the range of sustainable population size. There is also migration looking for water and food. In general the rate of change of population is the difference of birth rate and death rate

The theory is well established for a predator prey model. Mathematically we can describe the predators and prey (plant and herbivore) interaction using rates of changes of a population. The rate of change for population of the plant can be written as the difference of the birth rate and the death rate and/or consumption rate. In this study we assume that the birth rate of plant is greater than the sum of the death rate and consumption rate together. Similarly the rate of change for herbivore population can be written as the difference of the rate of emerging of the new herbivore due to consumption on the plant and the death rate of herbivores.

1.3 Modeling Plant-Herbivore Interaction

The interaction between plants and herbivores is one of the most fundamental processes in ecology. This interaction has been the object of scientific observation and theory, but mathematical modeling has been applied to plant-herbivore interactions for only a few generations [Abb+08]. Consequently understanding the interaction between plants and herbivores give information about basic processes of life since plant and herbivore species have been co-evolving synergically ever since they began to occupy the different environments in this world [FD17]. These two types of organisms have developed relationships of mutual dependence at a number of different levels, in particular those related to the feeding behavior of the animal species [BM11; Hol+13].

In plant-herbivore models, the dynamics of vegetation is often modeled using the simple logistic function

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right)$$

where P is the vegetation or plant biomass density (say kilograms per square meter, kgm^2), r is the maximum growth rate (say kilograms per kilogram standing biomass per year,$kgkg^{-1}yr^{-1}$), and K is the equilibrium value that the vegetation can attain [FD17].

For modeling of herbivore population dynamics, it is common to start with the formulation of a functional response of a continuous herbivore feeding. The functional response describes the way the feeding rate of an individual herbivore responds when the density of its food resource changes in amount. Generally, the rate of feeding of the herbivore will increase as more edible plant biomass becomes available, but, of course, there is an upper limit on the rate at which a herbivore can feed. Therefore, a functional response must eventually “saturate "; that is, approach an asymptote as plant biomass increases toward the limit of the herbivore’s ability to consume plant biomass. This asymptote is the maximum rate at which the individual herbivore can feed on the prey.

$$F(P) = \frac{aP}{b + P}$$

where $F(P)$ is the functional response, or rate of feeding, depending on Plant density, P, and a and b are parameters, where a is the maximum rate that the plant population can be consumed by a herbivore and b is the half-saturation constant, which corresponds to the density of plants at which the feeding rate reaches half its maximum [FD17].

Understanding the dynamics between herbivores and plants is extremely important for land management, environmental protection and animal husbandry. The remarkable variety of dynamical behaviors exhibited by plant and herbivore species has stimulated great interest in the development of dynamical system models of populations or ecosystems. There are several theoretical outcomes for mutual dependence between plant and herbivore populations [BM11; Buc+05; Fen+11; Hol+13; Kan+08; Kar16; Liu+08]. Plant herbivore interactions can broadly be categorized as “interactive" which refers to situations where the rate of change of herbivore biomass depend on plant biomass and the rate of change of plant biomass depends on herbivore biomass i.e. there is a feedback loop and “non-interactive" which encompasses situations in which the feeding by herbivore (on fruits, seeds) does not influence vegetation growth [FD17].

Both theory and modeling of plant-herbivore system have extended far beyond the simple interaction of Lotka-Volterra type to encompass a whole range of aspect of such interactions, and these continuous time models have been joined by discrete-time difference equation models [Lea86; Liu+08; O’C+ve; Rey+13]. On the other hand, classical approaches in constructing mathematical models to study the plant-herbivore interaction is also based on predator-prey system (see [Fen+11; Kar16; Lea86; Leb+14; Li11; Liu+08; May01]). In particular, the model of Li in 2011 [Li11] is a system of differential equations with Holling type II functional response, in which the influence of toxic nature of some plants in herbivore population is considered.

Terry [Ter15] presented four predator prey models with component Allee effect for predator reproduction, logistic growth for plants Holling type II functional response and constant mortality rate (Allee effect is a basic ecological mechanism that set lower bounds on population density of species. It is defined as a reduced per capita population growth rate at low densities, has important consequences for population dynamics and persistence). The analysis showed that each of the models has fixed points that represent predator extinction which is always locally stable.

Predator-Prey interaction is one of the basic inter-species relations for ecological and social models and it is also the base block of more complicated food chain, food web and biochemical network structure [Wan+11]. The interaction between plant and herbivore is one of the prey predator system.

Many modeling approaches used to study the plant herbivore interactions must trade off realism with generality [Lev68b]. Many scholars that study models designed to address general questions such as the spread of invasive plant species [Fag+05] or the effect of herbivory on ecosystem [CL81] or plant defenses [Fen+11] tend to consider plants and herbivores in terms of their collective density or biomass, and

primarily give mathematically tractable, theoretical results that are used to generate hypothesis about specific plant herbivore systems.

Different articles show the interrelation of plants and herbivores with grazing interactions. A detailed mathematical model was formulated by Michael B. Coughenour which was subjected to factorial combination of grazing height and frequency and the result was portrayed as the response of plant production. That is, short grasses yield most when grazed at law height and every 24 days while tall grasses respond more favorably to a longer grazing interval of about 55 days [Cou91]. Here the study was confined to the length and frequency of grazing.

Jennifer et al. [Rey+13] have studied the negative impact of herbivore browse on plants such as the rate of leaf consumption derive the impact of herbivores on the whole growth or survival, and subsequent changes in plant population structure. In an another literature Penelope et al [Hol+13] derive a mathematical model to predict annual rate of browse-induced tree mortality and found the thresholds. Lebon et al. [Leb+14] considered a simple two dimensional plant herbivore model where the two dimensions are the response of plants to herbivory through direct dependency of the plant growth rate on the number of herbivores and showed the importance of direct compensation for the presence of plant-herbivore mutualism.

Also about grazing optimization, nutrient cycling, and spatial heterogeneity of Plant-herbivore interactions, Clair De Mazancourt and Michel Loreau [ML00] discuss the interactions in-terms of nutrient concentration. Leah et al [Lea86] also studied about mathematical theory of plant-herbivore mutualism.

1.4 Temperature and Rainfall

Temperature continuously changes during a day, week, month, year or any period and this change is called periodic temperature variation if it is perfectly repeating itself after a year (or some other cycle). Periodic temperature variations are usually considered as the annual temperature variation or annual temperature cycle and the diurnal temperature variation or daily temperature cycle.

The annual temperature variation gives rise to seasons i.e. summer and winter. The annual temperature range varies greatly from place to place. It reflects the daily increase in insulation from mid-winter to mid-summer and decrease in the same structure from mid-summer to mid-winter in the north hemisphere and vice verca in the southern hemisphere. Usually there is a temperature lag of 30 to 40 days after the period of maximum and minimum insulation.

In the northern hemisphere winter's minimum temperature occurs in January and summer's maximum temperature is in July and the opposite time is true for regions in the southern hemisphere. The smaller range occurs near equator and largest in high latitudes. The difference between the highest and lowest temperature for a given period is known as temperature range. In the northern hemisphere the summer time is from 21st of March to 22nd of September and winter from 23rd September to 20th March and just vice-versa in southern hemisphere.

The diurnal temperature variation gives rise to daily maximum and minimum temperatures. From the sunrise, the sun continuously supplies energy and the temperature continuously rises, recording maximum at about 2.00 to 4.00 PM though the maximum amount of solar radiation is received at the solar Noon (i.e. 12.00 hrs). This delay in occurrence of maximum temperature is caused by gradual heating of the air by convective heat transfer from the ground which is known as thermal lag or thermal inertia. Similarly minimum air temperature occurs shortly after sunrise due to lag in transfer of heat from the surface to the air / space [Hug+07].

The rate of change of temperature with a horizontal distance is known as temperature gradient. Maximum solar energy is received in equatorial region and therefore highest temperatures are observed in this region. As the latitude increases the solar energy received on the earth surface correspondingly decreases and also temperature decreases with increase in latitude being lowest on the pole. The sun crosses the equator twice in a year, therefore, two maxima and two minima are observed in annual cycle. Outside this zone only one maxima and one minima is observed. Ethiopia is located in the equatorial region hence, it experiences two maxima and two minima temperatures annually.

Temperature and Rainfall have direct impact on the growth and development of both plants and herbivore population. Plants need water to grow and they get water from rainfall and water bodies. In many areas of Ethiopia seasonal plant growth occurs in a perfect synchronization with the rainy season. In the presence of water and sunlight plants take in more CO_2 during photosynthesis to create glucose and other sugar for building plant structure. The amount and distribution of rainfall have a strong impact on the development of plants.

Temperature influences all plant growth processes such as photosynthesis, respiration, transpiration, breeding of dormant seed, seed germination, protein synthesis and trans-location. At high temperature the trans-location of photosynthetic output is faster so the plants tend to mature earlier. In general, plants can grow in a temperature range of $0°C - 50°C$. The favorable or optimal day and night temperature range for plant growth and maximum yields varies among species.

The response in plants to an increase in temperature varies with the stage of plant growth, heat stress affecting, to a certain extent, all vegetative and reproductive stages. The observed effects depend on species and genotype, with abundant inter- and intra-specific variations of the plant [Cou91]. Various physiological injuries have been observed under elevated temperatures, such as burning of leaves and stems, leaf abscission and senescence, shoot and root growth inhibition or fruit damage. High warming temperatures reduce plant growth by affecting the shoot net absorption rates and thus the total dry weight of the plant. Heat stress induces changes in respiration and photosynthesis and thus leads to a shortened life cycle [Rey+13]. Increased temperature, increase lignification of plant tissues and reduce the digestibility and degradation of plant species which leads to reduced nutrient availability for herbivores [Get14].

Temperature adjusts the metabolism and bodily processes of herbivores; thus, temperature increase or warming can directly affect the development, growth, reproduction, hideaway survival, behavior, and penology of herbivores. Herbivore metabolic rates are highly sensitive to temperature, increasing with an increase of $10°C$ across the full range of regularly experienced temperatures [Hol+13]. Increased metabolic speed leads to higher consumption, growth, and development rates. Faster development, in turn, may lead to population increases via reduced generation time and decreased exposure to natural enemies and shortage of food. Warming-induced population outbreaks have been shown to arise from a combination of accelerated development and reduced overwintering mortality [Hol+13].

Enzyme activity and the rate of most chemical reactions generally increase with rise in temperature. Up to a certain point, there is doubling of enzymatic reaction with every $10°C$ increase in temperature but at excessively high temperature, denaturation of enzymes and other protein occur [O'C+ve].

Excessively low temperature can also cause limiting effects on plant growth and development. For example, water absorption is inhibited when the soil temperature is low because water is more viscous at low temperature and less permeable. At temperature below freezing point of water, there is change in the form of water from liquid to solid [Hol+13].

Generally temperature dependence of plants and herbivores for their growth and reproduction rates suggests potential effects of temperature abundance. Direct extensions of temperature dependent metabolic models to population abundance produce quantitative predictions for how change in temperature (warming) should affect plant and herbivore populations [O'C+ve].

In this study the seasonal variation of temperature and rainfall and their effect on the plant herbivore interaction through time dependent coefficients is considered and discussed.

1.5 Motivation

Among the plant-herbivore interactions the most common one is grazing. Grazing is important for the plants. As well as it is beneficial to the ecosystem. It also helps to promote the growth of native plants and grasses. Often, these indigenous plants are not able to compete with the surrounding plants that utilize the majority of water and nutrients.

By livestock grazing, the non-native grasses are controlled and the native plants can redevelop. As well as using grazing to increase plant growth, the actual hoof action of the livestock also promotes growth. The trampling helps to embed the seeds into the soil so that the plants and grasses can continue to germinate. Additionally, management in many parks makes use of grazing to help lower fire hazards by reducing potential fuel, such as large buildups of forage. When the land is not grazed, dead grasses accumulate. These dead grasses are often causes to large fire hazards in the summer months. On the other hand, grazing can also allow for “accumulation of litter (horizontal residue)” helping to eliminate soil erosion [Hol+13].

Exposing plants to intensive livestock grazing for extended periods of time, or without sufficient recovery periods leads to the occurrence of Overgrazing. It happens when a plant is forced to keep drawing on energy from its roots over and over without a chance to recover and some plants grow horizontally (staying close to the ground to avoid animal mouths) rather than vertically [Rey+13]. This gives a degree of protection as a result. It can be caused by either livestock in poorly managed agricultural applications (by not properly controlling their grazing activity), or by overpopulation (by having too many animals) on the farm of native or non-native wild animals.

Overgrazing reduces plant leaf areas, which prevents sunlight from reaching the plant and affects the plant growth. Plants become weakened and have reduced root length. Overgrazing causes animals to run short of pasture. Overgrazing can also affect livestock performance and condition. Female herbivores having inadequate pasture immediately following weaning (process of gradually introducing a mammal infant to what will be its adult diet and withdrawing the supply of its mother’s milk.), may have poor body condition the following season [Hol+13].

The interaction between herbivores and plants may be both positive and negative depending on the mechanism we choose to utilize nature's gifts. Overgrazing can cause desertification which is a sensitive issue to the world and especially to the developing countries like Ethiopia. Desertification which is the degradation of land in arid, semi arid and dry sub-humid areas are resulting from various climatic variations, but primarily from human activities such as overgrazing. Currently desertification is taking place much faster and usually arises from the demands of increased populations that settle on the land in order to grow crops and graze animals. Overgrazing can increase soil erosion. By pounding the soil with their hooves, livestock press the subsoil into fine soil which can be carried easily by wind and water. Reduced soil depth, soil organic matter, and soil fertility hurt the land's future productivity.

Drivers of global environmental changes such as increasing concentrations of CO_2 and human induced polluted nitrogen (N) can directly increase short-term plant growth rates and alter plant chemistry ($C : N$ ratio and concentration of carbon-based compounds often increase), and these physiological changes can affect a range of biotic interactions involving plants. In contrast, the effects of climate and land use change on interspecific interactions pervade across multiple trophic levels, rather than being mediated solely by plants.

Enrichment of CO_2 and climate change can influence both the quality and quantity of resources that plants return to the soil through a number of mechanisms; some of these have positive effects on plant-derived resources while others have negative effects.

Most of the models that are formulated to study the plant herbivore interaction use constant mortality rate for herbivore. (See for instance, [Ter11; Ter15; Wan+11; Zho+05] and the references therein.) But this common assumption is unrealistic because it ignores the fact that the death rate of herbivore population is dependent on their functional response. In reality, a herbivore needs to consume plants at some minimal rate to avoid death by starvation or by a consequence of weakness brought on by excessive hunger. As its consumption rate increases from a minimum to intermediate value we might expect herbivore to be healthier and therefore less likely to die in a shorter time. Osborne, in the paper [Osb00] stated that during the drought of 1993 in Kenya the number of Buffaloes in Masai Mara reserve declined. It was indicated that 70% of them died of starvation and a high calf mortality was also related to shortage of food supply. Furthermore, the relationship between density of plants and death rate of herbivore, which is developed by Coe et al [Coe+76] also serve to illustrate the importance of food supply in determining herbivore biomass. Similar argument was also used in [Ter15; Ver10] but none of these papers consider

the specific effect of density dependent mortality in their detailed mathematical analysis.

In addition, threshold values that guarantee the co-existence of the two populations were not formulated and studied. Since the Allee effect and environmental noise can interact due to a wide range of biological phenomena, the recognition of their consequences on the reproduction, conservation and behavior of species emerges as an important goal for the population dynamics community.

Furthermore, the effect of changing environment or seasonal variation on the plant herbivore population is not given much attention. Therefore, in this study it is intended to consider the environmental change or the seasonal variation in two separate ways. one is to consider it as a stochastic noise and use stochastic differential equation. The other is using a non-autonomous system but with only those coefficients that are dependent on the seasonal temperature and rainfall to vary. Therefore, using these two methods we believe the model constructed would give additional information for land management officials and animal farming societies.

1.6 Definition of the Problem

We study the plant herbivore interaction, where this interaction is determined by grazing. The effect of taking a plant density-dependent herbivore death rate, Allee effect and harvest rate in a model where the plant population grows logistically and the functional response of herbivores is Holling type II function is of interest to us.

Furthermore since plant herbivore interaction is highly affected by the environmental perturbation we will also use a stochastic differential equation model to get a better insight on the environmental noises. Such noises can be factors that affect plant population only, factors that affect herbivore population only or factors affecting both populations.

We are also interested in the study of the effect of temperature and rainfall variation on the plant herbivore system. That is, its effect on the herbivore feeding, growth, reproduction, on the plant growth and the dynamics as a whole. We also study the effect of temperature variation on the environment and on the dynamics of this interaction.

The environment is under continuous change and desertification and drought are problems in the eastern Africa as a result of the widening of the Sahara desert. The problem of changing climate and environmental factors mainly affect agriculturalists and pastoralists in Ethiopia. Since agriculture in the country mainly depend on the

traditional way (in an unplanned way) and which is done as a routine, that is, plants grow naturally and get water from rainfall; herbivores get food from free grazing on the fields. In a similar manner we investigate the effect of varying rainfall intensity and temperature variation by keeping the altitude constant. Then by choosing different altitudes we study the effect of altitude variation on the plant herbivore interaction.

Although grazing is important for plants, overgrazing can cause desertification which is the degradation of land in arid, semi arid and dry sub-humid areas resulting from various climatic variations, but primarily from human activities. Current desertification is taking place much faster and usually arises from the demands of increased populations that settle on the land in order to grow crops and graze animals. Overgrazing can increase soil erosion. By pounding the soil with their hooves, livestock press the subsoil into fine soil which can be carried easily by wind and water. Reduced soil depth, soil organic matter, and soil fertility hurt the land's future productivity.

Traditional animal production in Ethiopia is highly susceptible to over grazing since it is done intuitively and in an unplanned manner. Therefore studying the interaction of plants and herbivores with various temperature, rainfall intensity, altitude ranges as well as considering the Allee effects and stochasticity would help in understanding the real problem of the agriculturalists and pastoralists. Being able to understand these interactions as a mathematical model, we can do the analysis using numerical and analytical methods and understand each and every part of the process. This would help identify where we can intervene.

There are no abundant literature that study the effects of temperature, rainfall and altitudes altogether and also consider the stochastic model which is a more realistic model. Analyzing this model would result in a practical and effective solution which consider many factors. To validate the model considered we needed to collect data on rainfall, temperature and vegetation from three climatic zones with different altitudes.

1.7 Study Area

Geographically, Ethiopia is the world's 27th-largest country. It lies between latitudes 3° and 15°N, and between longitudes 33° and 48°E. The country is located in the so called Afar triangle, the easternmost part of the African landmass. Its elevation and geographic location produce three climatic zones [Get14] the cool zone above $2,400$ meters $(7,900ft)$ above sea level where temperature ranges from near freezing to $16^\circ C(32-61^\circ F)$; the temperate zone at elevations of $1,500$ to $2,400$ meters

$(4,900 - 7,900 ft)$ above sea level with temperatures from $16°C$ to $30°C(61 - 86°F)$; and the hot zone below $1,500$ meters $(4,900 ft)$ above sea level with both tropical and arid conditions and daytime temperatures ranging from $27°C$ to $50°C(81 - 122°F)$ [Get14].

Ethiopia, because of its geographical position, ranges of altitude, rainfall pattern and soil variability has an immense ecological diversity and a huge wealth of biological resources. This complex topography coupled with environmental heterogeneity offers suitable environments for a wide range of life-forms. Vegetation types in Ethiopia are highly diverse ranging from afro-alpine to desert vegetation [Isc14]. Zemede and Mesfin [AT01] indicated that the number of higher plant types in Ethiopia was over 7000 species from which 12 $\%$ are probably endemic.

For our study, we chose the Genale Dawa basin located in the south eastern part of Ethiopia, the river basin ranges from $4^o N - 7^o 30^{'} N$ and $38^o 00^{'} E - 44^o 00^{'} E$. It represents the three major climatic zones of the country, the cool zone, temperate zone and hot lowlands.

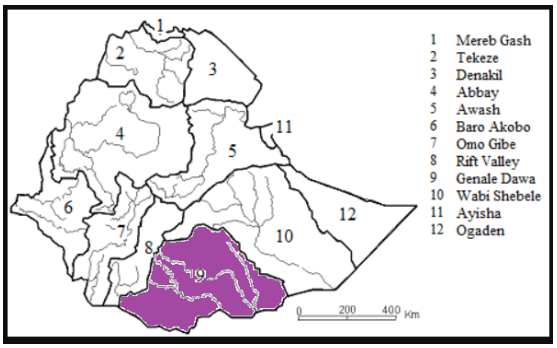

Figure 1.1: River basins of Ethiopia.

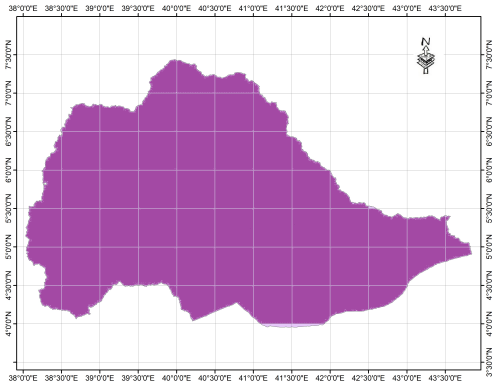

Figure 1.2: Genale-Dawa river basin, southeastern part of Ethiopia

Hence using the rainfall, temperature and vegetation data from these three climatic zones we check the validity of the model and further estimate some unknown parameters. Using the proposed model we study the thresholds for coexistence of plant and herbivore population, stability of these coexistence possible effects of increase or decrease in temperature and rainfall.

1.8 Objectives and Expected outcomes

1.8.1 General Objectives

The general objective of the study is to investigate the environmental factors in the plant herbivore interaction. This was done in two different cases

1. Assuming the environmental effect as a random noise and using Stochastic differential equation.

2. Considering the seasonal effect of the environmental noise such as the temperature and rainfall, a model with time dependent coefficients is analyzed and discussed.

1.8.2 Specific Objectives

At the end of these Dissertation we will be able:

1. To study a Plant herbivore model with constant coefficients for threshold values of coexistence of both population and study the dynamics of this interaction over a long period of time.

2. To discuss the environmental influence on the plant herbivore interaction by using stochastic differential equations.

3. To analyze a model which considers the temperature and rainfall effects on the interaction of plants and Herbivores ,like the feeding rate herbivores and growth rate of plants and as a result the effect of these interactions on the surrounding environment.

4. To study these effects at different altitudes or Spatial variation of the vegetation in the altitude.

5. To find the relationship of the plant herbivore interaction with the surrounding environment clearly.

6. to find threshold values for coexistence of both populations and their stability.

7. to check the sensitivity of the coefficients considered on the threshold.

1.9 The Structure

Chapter 2

The development of a plant herbivore model and its development through time is discussed. We recall the story and development of the predator prey and how it is related to and plant herbivore models.

Chapter 3

This chapter is dedicated to define a mathematical model with constant coefficients

and describe how plant herbivore interaction is represented in the model. we state what is considered and what is ignored by the model used. The formulated model is analyzed using the theories of dynamical systems. The existence and stability of equilibrium points is established. The sensitivity analysis of the parameters with respect to the reproduction number is discussed.

Chapter 4

we propose and describe the stochastic plant herbivore model to be studied. The simplified model is first analyzed for global Lipschitz continuity, positivity existence and uniqueness of solutions. Numerical simulations are presented for the simplified model and is then extended for model proposed stochastic model. Numerical simulations are presented and discussed for model The Allee effect on the plant herbivore dynamics is discussed.

Chapter 5

we propose and describe a general model with periodic plant growth and herbivore feeding rates to be studied. We discuss the general effect of temperature and rainfall on the plant herbivore interaction and describe the study area. Mathematical analysis of existence and uniqueness of periodic solution are discussed. Numerical simulations are presented for plant herbivore interaction for the three different climatic zones.

Chapter 6

In this chapter, we give the conclusion about the different models we considered in this study.Discuss their possible limitations and give direction about future work

Lotka-Volterra and its Extensions

2

2.1 The Classical Lotka-Volterra Model

Many scholarly articles study the different dynamics of the plant herbivore interactions, the direct and indirect impacts of one another [Fag+05; Fen+11; Leb+14; Wan+11],using the most widely known prey-predator(Lokta-Volterra) equations.

In 1926, the Italian mathematician Vito Volterra proposed a differential equation model to explain the observed increase in predatory fish and the corresponding decrease in prey fish after the first world war which was much abundant than before the war in the Adriatic sea. Around the same time (1925) the American Alfred Lotka [Lot25] derived the equation independently to describe a hypothetical chemical reaction in which the chemical concentration oscillate.

The first differential equation model and the simplest of predator prey type, called Lotka-Volterra equation, was formulated when attempts were first made to find ecological laws of nature. Both discrete and continuous predator-prey models have formed a fundamental part of ecological theory.

This Lotka-Volterra equations are a pair of first order, nonlinear differential equations frequently used to describe the dynamics of biological systems in which two species interact one as predator and the other as prey. The population change through time according to the pair of equations

$$\begin{aligned} \frac{dP}{dt} &= \alpha P - \beta PH \\ \frac{dH}{dt} &= c\beta PH - \gamma H, \end{aligned} \tag{2.1}$$

where P is the number (population density) of prey (for example, plants), H is the number (population density) of the predator (for example, herbivores), $\frac{dP}{dt}$ and $\frac{dH}{dt}$ represent the growth rate of the prey and predator population over time, t represents time. α, β, c, γ are positive real parameters describing the interaction.α growth rate, β rate of predation, $c$conversion rate of what is consumed into a new born herbivore γ-the loss rate of the predators due to either natural death or emigration.

This Lotka-Volterra model makes a number of assumptions about the environment and evolution of the predator and prey population. These are:

- The prey population find ample food at all times and reproduce exponentially unless experienced a predation. That is, density-independent exponential growth of the prey population in the absence of predators with intrinsic rate of increase α.

- The food supply of the predator population depends entirely on the size of the prey population. That is, a constant predation rate β (a fraction of the prey population eaten per predator). So, the total predation is proportional to the abundance of prey and the abundance of predators. There is no slowing of predation rate at high abundance and no interference among predators.

- The rate of change of population is proportional to its size.

- During the process, the environment does not change in favor of one species and genetic adaptation is inconsequential.

- Predators have limitless appetite.

- A constant conversion rate c of the eaten prey is used into new predator abundance.

- A constant per capita mortality rate of predators γ is considered.

The first equation of the system (2.1)

$$\frac{dP}{dt} = \alpha P - \beta PH$$

can be interpreted as *the change in the prey's number (density) is given by its own growth minus the rate at which it is preyed upon*.

The second equation of the system (2.1)

$$\frac{dH}{dt} = c\beta PH - \gamma H$$

can be considered as the growth of the predator population minus the loss rate of the predator due to either natural death or emigration and can be interpreted as *the change in the predator population as growth fueled by the food supply minus natural death*.

Having the above assumptions the Lotka voltera model describes the dynamics of predator prey interactions as the predator thrive, when there are plentiful prey but ultimately outstrip their food supply and decline. As the predator population is low the prey population will increase again and these dynamics continue in a cycle. From

the model one can also find stationary points trivial and nontrivial and study the stability of these stationary points.

To find equilibrium points of equation system (2.1), we put right hand side equations to zero hence we have the trivial $(0,0)$ and the nontrivial $\left(\frac{\gamma}{c\beta}, \frac{\alpha}{\beta}\right)$

$(0,0)$ represent the extinction of both species. If both species are at zero then they will continue to be so indefinitely. The nontrivial $\left(\frac{\gamma}{c\beta}, \frac{\alpha}{\beta}\right)$ represent a fixed point at which both populations sustain their current, nonzero numbers,and do so indefinitely. The levels of population at which this equilibrium is achieved depend on the chosen values of the parameters α, β, c, γ Linearizing using the corresponding Jacobean matrix is

$$J_{(P,H)} = \begin{pmatrix} \alpha - \beta H & -\beta P \\ c\beta H & c\beta P - \gamma \end{pmatrix} \tag{2.2}$$

Evaluating at the trivial steady state and computing the eigenvalues we have

$$J_{(0,0)} = \begin{pmatrix} \alpha - \beta\,(0) & -\beta\,(0) \\ c\beta\,(0) & c\beta\,(0) - \gamma \end{pmatrix} \tag{2.3}$$

$$= \begin{pmatrix} \alpha & 0 \\ 0 & \gamma \end{pmatrix} \tag{2.4}$$

computing the eigenvalue by $\det(Jac_{(0,0)} - \lambda I_2) = 0$ we have $(\lambda - \alpha)(\lambda - \gamma) = 0 \Rightarrow \lambda = \alpha$ and $\lambda = -\gamma$ since the parameters $\alpha > 0$, $\gamma > 0$ and as result the eigenvalues will always differ in sign. Hence the fixed point is a saddle point. That is $(0,0)$ unstable. It follows that the extinction of both specious is difficult in the model.

Evaluating at the nontrivial steady state and computing the eigenvalue we have

$$J_{\left(\frac{\gamma}{c\beta}, \frac{\alpha}{\beta}\right)} = \begin{pmatrix} \alpha - \beta\left(\frac{\alpha}{\beta}\right) & -\beta\left(\frac{\gamma}{c\beta}\right) \\ c\beta\left(\frac{\alpha}{\beta}\right) & c\beta\left(\frac{\gamma}{c\beta}\right) - \gamma \end{pmatrix} \tag{2.5}$$

$$= \begin{pmatrix} 0 & -\frac{\gamma}{c} \\ c\alpha & 0 \end{pmatrix} \tag{2.6}$$

computing the eigenvalue $\lambda^2 + \alpha\gamma = 0 \Rightarrow \lambda = i\sqrt{\alpha\gamma}$ and $\lambda = -i\sqrt{\alpha\gamma}$ purely imaginary and conjugates of each other hence this fixed point is elliptic. So we have periodic solution oscilating on a small ellipse around the fixed point, with a period $\omega = \sqrt{\alpha\gamma}$.

One can simulate the time series as follows using the the parameter values of $r = 0.25, a = 0.025, c = 0.250, \mu = 0.3$ with initial population $P(0) = 40$ and $H(0) = 15$.

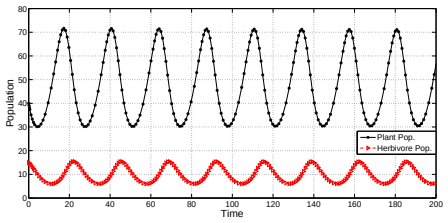

Figure 2.1: plant herbivore dynamics over time

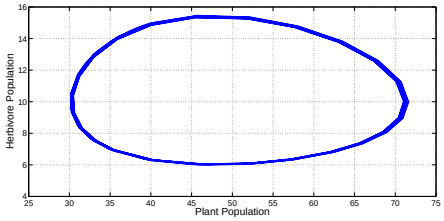

Figure 2.2: phase portrait of plant herbivore population

This figure indicates that a stable limit cycle meaning the plant population coexist with the herbivore population with oscillator balance behavior.

Sketching the vector field to study the flow direction we have the black vertical line is $P = \frac{\mu}{ca}$ and $H = \frac{r}{a}$ and the cycles are for different initial values of plants and herbivores the starting point is indicated in blue circle and the end is indicated in black squares.

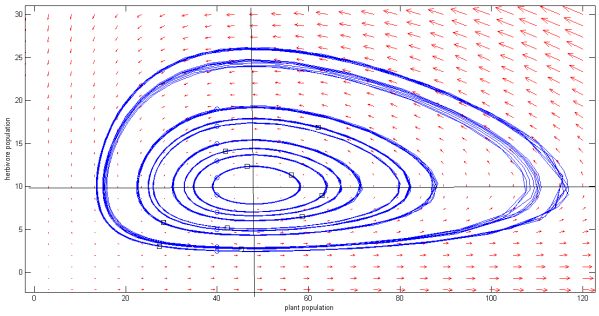

Figure 2.3: vector field of the plant-herbivore population dynamics

Although the Lotka-Volterra predator prey model is often criticized because of its single positive equilibrium point is a center (i.e. a “neutrally stable” equilibrium surrounded by a family of periodic orbits whose amplitudes depend on the initial population sizes), the slightest change to the model structure typically results in qualitatively different behavior [Wan+11].

This Lotka-Volterra model does not describe actual behavior observed in nature. Some of these are (a) prey population may grow infinitely without any resource limit, (b) predators have no saturation that is the consumption rate is unlimited. (c) the

model ignores variation among individuals and assumes infinite size population with perfect mixing. One of the biggest problem of the model is that the prey population is not self-limiting and therefore it can be arbitrarily large which is not the case in reality.

2.2 Lotka-Volterra Model with Logistic Growth

In the population models, the rate limiting feedback terms are often modeled as function of the predator itself. These models are called Carrying Capacity models. The carrying capacity is the density or concentration above which the growth rate of the consumer becomes negative.

The carrying capacity formulation is an approximation of processes not explicitly included in the model. These processes may be resource limitation, competition for space and so on. A simple example of a population growth model with a carrying capacity formulation is the logistic equation sometimes known as Verhulst model [SMH08].

$$\frac{dN}{dt} = rN\left[1 - \frac{N}{K}\right] \tag{2.7}$$

where N is population density, $\frac{dN}{dt}$ is the rate of change, r is the maximal net growth rate, K is carrying capacity, that is, the maximum population size that can be supported by the environment; K has the same unit as N. This equation has been so influential in ecological modelling. Clearly, N is the compartment that is growing and r is the maximal net growth rate while $\left[1 - \frac{N}{K}\right]$ is the rate limiting term.

- At very low densities $(N << K)$, the limitation term $\left[1 - \frac{N}{K}\right]$ will be ≈ 1 and the population grows exponentially.

- In the neighborhood of the carrying capacity K, the limitation term approaches 0, therefore the rate of change becomes very small and density will remain quasi-constant.

- At densities much higher than the carrying capacity, the limitation term $\left[1 - \frac{N}{K}\right]$ will be negative and the population density will decrease quasi-exponentially towards K.

In 1930, A new version of Lotka-Volterra model was introduced with modification. This model was modified by substituting the exponential growth (which is usually

assumed) of the prey species by a logistic type growth with a carrying capacity K, while a linear mortality rate is assumed for predator[Wan+11].

$$\begin{aligned} \frac{dP}{dt} &= \alpha P\left(1-\frac{P}{K}\right)-\beta PH \\ \frac{dH}{dt} &= c\beta PH-\gamma H \end{aligned} \tag{2.8}$$

This logistic growth guarantees that the prey population is self-limiting and it can grow only up to a certain saturation level. This logistic equation was originally derived by Piere Francois Verhulst. Alfred J. Lotka [Lot25] utilized the equation to analyze predator-prey interactions in his book on Bio-mathematics .

The change brought upon by introducing the logistic growth was significant in the analysis of the system. With this model a third equilibrium point is found which is at the carrying capacity of the environment. But still this model assumes a constant predation rate β which again lucks reality.

2.3 Rosenweig-MacArthur Model

In the models discussed above the predators appetite was impossible to satisfy that is they eat as long as there is food but this is not the case all consumer animals have a saturation level. As indicated in the previous section, there are many examples in nature which demonstrate that predators can control the numbers (or density) of their prey. When predators are faced with increasing local density of their prey, they often respond by changing their consumption rate. This relationship of an individual predators' rate of food consumption to prey density was termed by C.S. Holling in 1959 [CS59] as the functional response.

A functional response is the predation rate described as a function of the prey density. It is generally classified in to three types:-

Type I

This functional response is mathematically the simplest. It assumes a linear increase in intake rate with prey density either for all food densities, or only for food density up to a maximum beyond which the intake rate is constant. The linear increase assumes that the time needed by the consumer to process a food item is negligible, or that consuming food does not interfere with searching for food. This functional response of type I is used in the classical Lotka-Volterra predator-prey model.

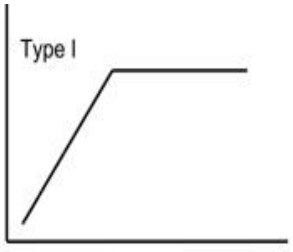

Figure 2.4: Hollying Type I function response

Type II

A more complex functional response is one in which the predation rate increase very rapidly with initial increase in prey density, and thereafter increased more slowly approaching a certain fixed level [CS59]. The fraction of prey consumed/killed become progressively less as prey density increases. This typically is caused by predators having to spend time capturing and consuming each prey, and perhaps from predators becoming satiated and ceasing to forage. On the graph of prey killed versus prey density, a type II functional response increased initially nearly in linear fashion. But gradually slows down and eventually asymptotes at a maximum feeding rate.

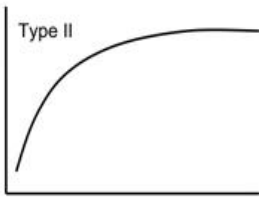

Figure 2.5: Holling type II function response on a prey versus predator

A common model for a Type II functional response replaces the constant predation rate parameter β of the Lotka-Volterra model with the function

$$\frac{\beta}{1+\beta T_h P}$$

in which T_h is the handling time

Type III

The third functional response is S shaped so that the rate of predation at first increase with an increase of prey density and then decrease [CS59]. Similar to

functional response of Type II in that at high level of prey density saturation occurs but now at low prey density level the graphical relationship of the number of prey consumed/killed versus prey density is more than linear increase of prey consumed by predator.

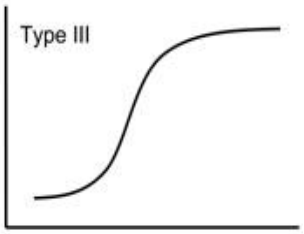

Figure 2.6: Holling type III

This acceleration function is large, descriptive and often justified by learning time, prey switching or combination of both phenomena. But Type III function response lacks the rigorous theoretical understanding of the Type II functional response.

All three functions approach a maximum corresponding to the maximum number of prey population the predator can consume within a certain time unit. Holling's motivation for this maximum was the "handling time": even at an infinite prey density the predator cannot consume the prey infinitely fast because of the time required to eat and digest the prey. The Holling Type II and Type III responses are conventional called Hill functions.

The Holling Type II function response describes a situation in which the number of prey consumed per predator initially rises quickly as the density of prey increases but then levels off with further increase in prey density. In 1963,Rosemweig and MacArtur [RM63] extended the Lotka-Volterra equation with logistic growth equation to include the density dependent growth and a functional response.This has made Lotka-Volterra system to describe more realistic phenomena.

Rosenzweig-MacArthur model uses Holling Type II functional response and is given by the equation

$$\begin{aligned} \frac{dP}{dt} &= rP\left(1-\frac{P}{K}\right)-\left(\frac{a}{b+P}\right)PH \\ \frac{dH}{dt} &= c\left(\frac{a}{b+P}\right)PH - mH \end{aligned} \tag{2.9}$$

The parameter b is the density of prey (plant) at which the predator consumption rate reaches half its maximum. This model assumed the predators' food handling time as "after killing a prey, predator eats its captured food". This process consists

of eating and digesting the meal portion. This was not the case in the original Lotka-Volterra model in which the predation rate was linearly proportional to the prey density.

In the Lotka-Volterra the dynamics posses a periodic orbit (see Figure 2.3). The Rosenweig-MacArthur model dynamics, however, has only a single attracting equilibrium (has a steady state attractor). The model have sustained oscillations but it is difficult to fit models of this sort to a real data. This difficulty is due to the over assumption that the surrounding environment remains constant which is not realistic.

Further Rosenzweig-MacArthur's model was developed in a more generalized form in 2013 by Feng Rao [Rao13] where the function response was modified to include the time of eating and processing food which resulted in the saturation constant of processing time.

$$\begin{aligned} \frac{dP}{dt} &= \alpha P\left(1-\frac{P}{K}\right)-\left(\frac{\beta}{1+\beta T_h P}\right)PH \\ \frac{dH}{dt} &= c\left(\frac{\beta}{1+\beta T_h P}\right)PH-\gamma H \end{aligned} \tag{2.10}$$

This generalization resulted in two similar and two significantly different nullclines as in the Rosenzweig-MacArthur's model and it also results in the coexistence of equilibria. Nullclines, sometimes called zero-growth isoclines, are sets of points in the phase plane so that $\frac{dP}{dt} = 0$ and $\frac{dH}{dt} = 0$. Geometrically, these are the points where the vectors are either straight up or straight down. Algebraically, we find the nullcline by solving the right hand side equal to zero

But this model was done under the assumption that the birth rate of the prey (plants) $\alpha = 1$. But in reality it actually depends on the surrounding condition mostly on temperature and rain fall.

2.4 Predator-Prey Models with Allee Effects

Among the many processes that the Lokta -Volterra model ignores, is the Allee effect which is the most important [Zho+05]. An American ecologist Warder Clyde Allee,[All31] in his book in 1931, answered the question "what minimal numbers are neccessary if a species is to maintain itself in nature?". He discussed the evidence for the effect of crowding on the demographic and life history traits of population. Hence the growth rate is not always positive for small density and it may not be decreasing as in the logistic model either. Generally speaking a population is said to have an Allee effect, if the growth rate per capita is initially an increasing function

for the low density. Moreover, it is called a srtong Allee effect if the per capita growth rate in the limits of low density is negative, and a weak Allee effect means that the per capita growth rate is positive at zero density [Wan+11].

An individual organism is said to be fit in its environment, if it has successful reproduction and efficient in terms of chances of survival. Hence, with short future time the smaller the risk of death or the greater the chance of successful reproduction, the greater the fitness of the organism. The average fitness of the individual in a population can be defined as the per capita growth rate of the population [Cou+08]. The core concept in the study of Allee effect is fitness, especially a demographic Allee effect refers to the per capita population growth rate (the positive correlation between size or density of a population and the average fitness of the individual in it). The greatest the size of the population the greater the average fitness. In other words the lower the size of the population the lower the average fitness [Ter15].

If a population has a sufficiently high density over a sufficiently large range, then competition for food and other resources will be so fierce that further increase to the population will only intensify this competition and thereby reduce individual fitness thus a demographic Allee effect does not hold for a population with sufficiently high density over a sufficiently large range [Ter15].

Small sized population may be subject to a demographic Allee effect in a number of ways. For instance, an increase in size or density of a population may increase the chance of its members deriving benefits from group protection or co-operation [BB02; Cou+99; Ter15]. Another example is if a population is reproducing sexually then an increase in its size or density will allow individuals to find a mate more easily and will reduce the risk of inbreeding [Cou+99; McC97; Ter15]. This also increases the competition over access to a mate or to optimal breeding sites.

Another type of Allee effect is the component Allee effect which refers to the positive correlation between size or density of a population and any measurable component of individual fitness such as juvenile survival or adult reproduction [Cou+08]. Component Allee effect are at the level of components of individual fitness while demographic Allee effect are at the level of over all individual fitness practically always viewed through the demography of the whole population at the per capita population growth rate [Cou+08].

There are different literature which study the predator prey system with strong Allee effect in prey. Wang et al. in [Wan+11] considered the global dynamics of a prototypical predator prey interaction model with an increasing bounded functional

response and the prey satisfies a strong Allee effect growth, that is, the predator prey system under a very general condition.

$$\begin{aligned} \frac{dP}{dt} &= g(P)(f(P) - H) \\ \frac{dH}{dt} &= H(g(P) - \gamma) \end{aligned} \tag{2.11}$$

A1 f is continuously differentiable function, $f(b) = f(1) = 0$ where $0 < b < 1; f(P)$ is positive for $b < P < 1$ and $f(P)$ is negative otherwise

A2 g is continuously differentiable function, $g(0) = 0; g(P) > 0$ for $P > 0$ and $g'(P) > 0$ for $P > 0$, and there exists $\lambda > 0$ such that $g(\lambda) = \gamma$

Here $g(P)$ is the predator functional response, and $g(P)f(P)$ is the net growth rate of the prey. The graph of $H = f(P)$ is the prey nullcline on the phase portrait. In the absence of the predator, the prey P has a strong Allee effect growth which is reflected from the assumptions (A1). The carrying capacity of the prey is rescaled into 1 here, while b is the survival threshold or sparsity constant of the prey. The predator nullcline is a vertical line $P = \lambda$ solved from $g(\lambda) = \gamma$. The condition (A2) on the functional response $g(P)$ includes the commonly used Holling types II as well as the linear one ($g(P) = P$ as Lotka-Volterra). The parameter γ is the mortality rate of predator; the number λ can also be thought as a measure of the predator mortality as λ increases with γ, and λ is also the stationary prey population density coexisting with predator.

Moreover, they carried out the phase plane analysis. From the stability analysis of this model and properties of the stable manifold and unstable manifold of equilibrium points it was also shown in the paper that the existence and uniqueness of point-to-point heteroclinic[1] orbit loop. The Hopf[2] bifurcation from the coexistence equilibrium point was analyzed. The oscillatory behavior in predator prey has been an important topic in population dynamics. In this article the global bifurcation of a class of general predator prey system with prey growth satisfying a strong Allee effect type growth pattern was rigorously established [Wan+11].

The Allee effect greatly increases the likelihood of local and global extinction, a phenomena that has received considerable attention. But there have been few papers discussing its stabilizing or destabilizing effect on the predator prey system (except for [Ken+03]). By modeling the case of resource subsidy and phase plane analysis, Kent et al.[Ken+03] concluded that the predator prey system is stabilized by an

[1] is a path in phase space which joins two different equilibrium points.
[2] is the appearance or the disappearance of a periodic orbit through a local change in the stability properties of a steady point.

influx of prey in the form of a rescue effect and destabilized by an outflux of an Allee effect.

Zhou et al. [Zho+05] studied the different Allee effects on the basic Lotka-Volterra Model namely Allee effect I which denotes an Allee effect that may increase the intrinsic death rate or decrease the intrinsic birth rate of the prey population, causing the per capita growth rate of prey to be decreased at low population density [Den89; Zho+05]. These may occur under social thermo-regulation, reduction of inbreeding and genetic drift. Allee effect II is the second effect caused by anti predator defense, like anti-predator vigilance and aggression [Den89].

In [Zho+05] Zhou et al. have shown by introducing these effects that the equilibrium of the system may otherwise be changed from asymptotically stable or neutral stable to unstable, to neutral stable or the system will take much longer time to reach the stable stage.

Significant number of literature can also be found on the mathematical modeling of Allee effects in recent years [Cou+08; Wan+11; ZM10; Voo+07; Zu+10; Ter09; Ter11]. There remains considerable scope for exploring this area. such as considering the environmental perturbation as a random noise and applying stochastic differential equation and/or considering the seasonal effects and using non-autonomous differential equations.

2.5 Stochastic Predator-Prey Model with Allee Effect

In reality, there are many benefits to be gained in using stochastic models because real life is full of randomness and stochasticity. A large number of stochastic differential equation models are considered as they provide some additional degree of realism compared to their deterministic counterpart [Agu+13; Mao+02; Rao13]. The environment factors are time dependent randomly varying and should be taken as stochastic.

In stochastic differential equations, environmental randomness is represented by noise terms affecting each population. More specifically, it considers a term that expresses the variability of the growth rate of species due to external, unpredictable events [Agu+13]. Adding stochasticity to a deterministic model means studying the stability of the system if some perturbation has occurred in the environment or on the specious involved.

Aguirre et al [Agu+13] studied a predator-prey model with the Allee effect on prey and whose dynamics is described by a system of stochastic differential equations

assuming environmental randomness is represented by noise terms affecting each population. More specifically they considered a term that express the variability of the growth rate of both species due to external and unpredictable events.

$$\mathrm{d}x = \left[\left[r\left(1-\frac{x}{K}\right)-\frac{m}{x+b}\right]x-\frac{qxy}{x^2+a}\right]dt+\sigma_1 x dW_1(t) \tag{2.12}$$

$$\mathrm{d}y = \left[sy\left(1-\frac{y}{nx}\right)\right]dt+\sigma_2 y dW_2(t) \tag{2.13}$$

where $(x(t), y(t)) \in A = \{(x, y) \setminus x > 0, y > 0\}$ denote prey and predator densities respectively. $\mu = \{r, a, b, K, m, n, q, s\} \in \mathbb{R}^8_+$ are parameters. $W(t) = (W_1(t), W_2(t) \setminus t \geq 0)$ is two dimensional Brownian motion and parameters $(\sigma_1, \sigma_2) \in \mathbb{R}^2_+$ represent intensities of perturbation.

The intensities of the perturbations were proportional to the population size of each species. The authors prove the solutions of the system have sample pathwise uniqueness and bounded moments.

Using the random noise as a Brownian motion the stochastic model predict the breaking of limit cycles that are present in its deterministic counter part for low random perturbations. On the other hand for high noise intensity they have observed the orbit either converges to the origin causing extinction, or fluctuate around a point which was an attracting equilibrium in the deterministic version. However, If the environmental randomness affects each population with different intensities then the stochastic model predics that there may be extinction of both species.

In 2013, Feng Rao [Rao13] argued that most natural phenomena do not follow stricly deterministic laws but rather oscillate randomly about some average values so that the population density never attains a fixed value with advancement of time. In predator prey model, the random fluctuations are also undeniably arising from either environmental variability or internal species like the birth and death processes of individuals are intrinsically stochastic fluctuations which become especially pronounced when the number of individuals is small.

In the study cited above Feng Rao presented a Holling Type II predator-prey model that includes some important factors such as an Allee effect on prey population, density dependence of predator population and environmental noise. Assuming that the random factors in the environment would display themselves mainly as fluctuations on the intrinsic growth rates of prey and predator.

The modified stochastic Holling type II predation model is given by:

$$\begin{aligned} dP &= P\left(1 - P - \frac{m}{b+P} - \frac{wH}{a+P}\right)(rdt + \sigma d\eta_1(t)) \\ dH &= H\left(\frac{P}{a+P} - d - cH\right)(sdt + \phi d\eta_2(t)) \\ P(0) &= P_0 > 0, H(0) = H_0 > 0 \end{aligned} \tag{2.14}$$

where $r(>0)$ is the intrinsic growth rates of prey and $s(>0)$ is the intrinsic growth rate of predator which are corrected by

$$r \longrightarrow r + \sigma\eta_1'(t) \qquad s \longrightarrow s + \phi\eta_2'(t) \tag{2.15}$$

As in the above models P and H represent the prey and the predator population densities at time t, respectively, $\frac{m}{b+P}$ is the term of additive Allee effect and $m \in (0,1)$ and $b \in (0,1)$ are Allee effect constants. If $m < b$ then it has week Allee effect and if $m > b$ then it has a strong Allee effect cH stands for density dependence of predator population and $c > 0$.

$w(>0)$ is a predation rate, $a(>0)$ the half saturation density of Holling Type II functional response, and $d(>0)$ the predator death rate. The positive constants σ and ϕ respectively are the coefficients of the effect of the environmental stochastic perturbation on the prey and on the predator population. $\eta_i'(t)(i = 1, 2)$ is a standard white noise.

Having these assumptions on the model and by constructing suitable Lyapunov functions and applying Ito formula and numerical simulations Feng formulated some properties like existence of global positive solutions, stochastic boundedness, and stochastic asymptotic stability which means that in the biological point of view the community consisting of both prey and predator species is a stable biotic community where all species will coexist [Rao13]. This is one of the advantages of using stochastic differential equation.

2.6 Predator Prey Models with Temperature

Some climatic factor changes such as temperature and weather changes can have strong effects on species interactions. Temperature-dependent effects on plant-herbivore interactions are a major mechanism through which these effects occur.Since this is where the sun-energy is converted to food through photosynthesis.

D. Vasseur and K. McCann [VM05] provided a modification of the Rosenweig and MacArthur model by including temperature as a parameter in the consumer resource models (predator prey models) and this has increased the ability to explain variabil-

ity in growth, ingestion, and metabolism. Next to body mass, temperature explains the largest residual variation in biological rates. The wide range of temperature experienced by many species influences their growth, foraging, reproduction and metabolism among others via a direct influence on enzyme kinetics [VM05]. Making these assumptions the authors found that consumer and prey abundance decrease with warming and they suggest that long term changes in temperature can influence the equilibrium dynamics of species in predictable ways, given the dependence of their rates of growth ingestion and metabolism on temperature. The most straight forward extensions of metabolic theories predict that abundance declines with temperature. However, the authors further argued that these extensions typically ignore biotic feedback, resource supply rates, and how different temperature dependencies of metabolic rates influence species interactions [VM05].

O'Connor et al [O'C+ve] have studied the theoretical prediction for how temperature change affects the dynamics of interacting herbivores and plants . They analyzed a set of consumer prey model that incorporate temperature dependent rates for heterotrophic and autotrophic[3] processes and resource based carrying capacity. Then, their results show that primary producer abundance can be independent of temperature even when primary productivity is temperature dependent contradicting the result of the model by Vassues and MacCann [VM05].

In the presence of herbivores, primary producers (plants) abundance declines at a rate identical to herbivore abundance when herbivore mortality was dependent on density [O'C+ve]. In contrast, in systems where the impact of herbivory is controlled by predation or other factors, excessive warming is likely to have a negative effect on the abundance of primary producers. In the absence of herbivory, excessive warming causes a decline in plant abundance which is inversely proportional to the temperature dependence of primary productivity [O'C+ve]. Hence incorporating temperature-dependent rates in to models alters the prediction from direct effects of a temperature change on population abundance.

There is strong ecological evidence showing that plant population dynamics have more important effects on plant-herbivore interactions than herbivore. We will study the plant herbivore interaction by considering logistic growth rate in the plant population and the Holling type II functional response for the feeding interaction. To analyze this type of model, we take a constant multiple of the feeding relation (efficacy) together with the Allee effect for the birth rate of the herbivore population. This is because for the herbivore population to continue existing in the ecosystem and due to the fact that herbivore reproduce sexually we will need a minimum number to guarantee female herbivore find a mate to reproduce.

[3] Autotrophs are those organisims that are able to make energy-containing organic molecules from inorganic raw material by using basic energy sources such as sunlight. Plants are prime example of autotrophs, using photosynthesis. Those organisms which feed on others are called heterotrophs

3 The Plant-herbivore Mathematical Model with Constant Coefficients

3.1 Analysis of the Plant-Herbivore Mathematical Model with Constant Coefficients

There is strong ecological evidence showing that plant population dynamics have more important effects on plant-herbivore interactions than herbivore population does. We will study the plant herbivore interaction by considering logistic growth rate in the plant population and the Holling type II functional response for the feeding interaction. For the herbivore population we take a constant multiple of the feeding relation (efficacy) together with the Allee effect for the birth rate. Moreover, a variable herbivore mortality rate which is dependent on the plant density is formulated and used in the model.

The basic system we consider in this chapter is the classical predator prey ecological model in the version presented in [Ter15], where the Allee effects for the herbivore are taken into account. We are studying two different populations, plant and herbivore. Therefore, the state variables are given by: Plants density, P, and herbivore density H. The dynamics is represented by the following system of nonlinear ordinary differential equations:

$$\dot{P} = rP\left(1-\frac{P}{K}\right) - HF(P) \tag{3.1}$$

$$\dot{H} = H\left[cF(P)\left(\frac{H}{h+H}\right) - D(F(P)) - \mu\right] \tag{3.2}$$

$$P(0) \geq 0, \qquad H(0) \geq 0.$$

where the upper dot denotes the time derivative. r, K, c, h, μ are positive constants, and $F(P) = \frac{aP}{b+P}$ is a function representing the value of consumption of plants by herbivores with a is feeding rate constants and b is half saturation constant.

It is assumed that $D(F(P)) = D(F)$ is a continuously differentiable function of the variable F, $F \geq 0$; and also, for $F \geq 0$, we have $dD/dF \leq 0$, and

$$0 < d_1 \leq D(F) \leq d_2 < 1, \tag{3.3}$$

for some constants d_1 and d_2.$d_2 < 1$ because it is a death rate.

The first term of equation (3.1) represents the idea that, the plant population grows logistically in the absence of herbivore. That is, when $H = 0$, initially it seems to grow exponentially but eventually it grows only up to the carrying capacity of the environment. This is biologically observable because the plant population in a certain land with enough water resource and nutrients in the soil and without herbivore interference can grow only as much as the land can hold.

The first term of equation (3.2) represents the average herbivore reproduction rate, and is equal to $cF(P)\left(\frac{H}{h+H}\right)$. This reflects that individual herbivore reproduces more if it eats more. In addition, in the absence of plants we have, $cF(0)\left(\frac{H}{h+H}\right) = 0$ which represents that individual herbivore will be unable to reproduce if they could not find plants to consume. Moreover, to reproduce or to give birth to a new herbivore, existence of enough herbivore population is crucial and this is taken care of by the term $\frac{H}{h+H}$ due to the fact that $cF(P)\left(\frac{H}{h+H}\right)$ vanishes as H goes to extinction. That is, individual herbivore will struggle to reproduce as the herbivore density falls to zero, either because they cannot find a mate or because of a greater risk of inbreeding. (For further discussion in this see [Ter13]).

Mortality on herbivore, plants or on both may be caused by various events, example include scarcity of food or nutrients and water, the occurrence of drought, floods, grass/forest fires. For the ease of understanding let us define mortality event for a plant herbivore system to be an event which changes the environmental condition and which results in the mortality to at least one of the populations, plant or herbivore. A mortality event may be unique (such as fire) or periodic (such as floods in the rainy season). The other effect of mortality events on the plant herbivore system is an event that may cause herbivore to die out while plants do not. In this case, since there will be no influence from the herbivore, the plant population may then increase to the carrying capacity of the environment and we usually say in this case that the land "recovers".

Realistically, considering a constant death rate for the herbivore population ignores the fact that mortality of herbivores (predators) is dependent on the availability of food source, the plant biomass (prey density) as well. However, the life process of a herbivore is fueled by consuming plants and this includes most fundamentally staying alive. If a herbivore finds only little to consume, it will be more likely for the animal to starve and die. In difficult conditions, the mortality rate of the herbivore population could reach its maximum value, say $d_2 < 1$.

On the other hand, if there are sufficiently large amount of plant biomass for the herbivore to feed on, starvation will not occur. Hence, herbivore mortality should

be a decreasing function of consumption $F(P)$ whose rate of change is very small when the feeding rate is sufficiently large. Moreover, regardless of particular factors affecting herbivore mortality no animal lives forever, so it is sensible to assume that herbivore mortality is always bounded below by some positive constant, say $d_1 > 0$. In this paper, the death rate of herbivores is taken to be a non constant function of the plant density, by taking in to account the idea that herbivore survival mainly depends on availability of food.

The term $D(F(P))$ satisfying the conditions : $D(F(P)) = D(F)$ and we have the condition $0 < d_1 \leq D(F) \leq d_2 < 1$ Since $D(F)$ is assumed to be a positive decreasing function of F, let us consider the following form to describe it:

$$D(F) = d_2 - \frac{F}{g+F} \qquad \text{for some parameter } g. \tag{3.4}$$

Then for, $P = 0$ we have $F(0) = \dfrac{a(0)}{b+(0)} = 0$ and we also have

$D(F(0)) = d_2 - \dfrac{F(0)}{g+F(0)} = d_2$ But on the other hand since

$\lim_{P\to K} F(P) = \lim_{P\to K} \dfrac{aP}{b+P} = \dfrac{aK}{b+K}$ Including this value in (3.4) and noting that the minimum value that $D(F(P))$ can take is d_1, we get $D(F) = d_2 - \dfrac{F}{g+F}$

$\implies d_1 = D\left(\dfrac{aK}{b+K}\right) = d_2 - \dfrac{\dfrac{aK}{b+K}}{g+\dfrac{aK}{b+K}}$ Hence, solving for g gives us

$$g = \frac{aK(1-d_2+d_1)}{(d_2-d_1)(b+K)} \tag{3.5}$$

Therefore, for $0 < d_1 < d_2 < 1$, let us define the density dependent death rate function to be

$$D(F(P)) \quad = \quad \frac{d_2K(1+d_1-d_2)(b+P)+P(b+K)(d_2-d_1)(d_2-1)}{K(1+d_1-d_2)(b+P)+(d_2-d_1)(b+K)P} \tag{3.6}$$

With this definition, the term $D(F(P)) := D(F)$ satisfies a condition that $0 < d_1 \leq D(F) \leq d_2 < 1$.

Moreover, $D(F)$ is a positive decreasing function of $F(P)$ as equation (3.6) can be described as $D(F) = d_2 - \dfrac{F}{g+F}$, for some parameter $g = \dfrac{aK(1-d_2+d_1)}{(d_2-d_1)(b+K)} > 0$. In addition if $d_1 = d_2$, then $D(F)$ reduces to a constant d_2 which is the value considered in the mathematical analysis part of the paper by Terry [Ter15]

The harvest rate μ is considered as a non-negative constant. It represents the human interference on the system by removing herbivores from the system at this constant rate. This rate could be interpreted as the removal rate of the animals through either, hunting (if the herbivore is a wild animal) or culling or selling (if the herbivore is a domestic animal). The system we will study, therefore, takes the following form.

$$\begin{aligned} \frac{dP}{dt} &= rP\left[1-\frac{P}{K}\right]-\left(\frac{a}{b+P}\right)PH \\ \frac{dH}{dt} &= H\left[c\left(\frac{a}{b+P}\right)P\left(\frac{H}{h+H}\right)-D(F(P))-\mu\right], \end{aligned} \tag{3.7}$$

where $D(F(P))$ is described as in (3.6).

3.1.1 Region of Positivity

It is important to show positivity and boundedness of the model system (3.7) as the variables represent biological population densities. Positivity implies survival of the population, and boundedness may be interpreted as a natural restriction to growth as a consequence of limited resources. We will show in this section that all solution for (3.7) that start with positive initial quantity satisfies positivity. That is, for this model to be mathematically and biologically well posed, we need to ensure that for all positive times the state variables $P(t)$ and $H(t)$ must be non-negative for each solution of the system starting with $P(0) \geq 0, H(0) \geq 0$. This is equivalent to saying that the positive quadrant $\mathbb{R}^+_2 = \{(P,H) \in \mathbb{R}_2 : P \geq 0, H \geq 0\}$ is positively invariant. We denote by $\mathbb{R}^+_2$ the non-negative quadrant, and by $int(\mathbb{R}^+_2)$ the positive quadrant.

Lemma 3.1.1 (Positivity). *All solutions of system* (3.7) *starting in* $int(\mathbb{R}^+_2)$*, remain positive.*

Proof: One can see from system (3.7). Using the Cauchy-Lipschitz theorem (see Theorem 2.1 in [Smi08] or Theorem 2.2 in [Tes11]), as the (absence of herbivore population) Horizontal-axis and the (absence of plant population) vertical-axis are orbits, the positive quadrant $int(\mathbb{R}^+_2)$ is positively invariant. □

Lemma 3.1.2 (Boundedness). *For model system* (3.7)*, let* $\widehat{P} := \max\{P(0), K\}$. *Moreover, with* $\eta = \frac{K(r+d_1+\mu)^2}{4r}$*, where* d_1 *satisfies* (3.3)*, let* $\widehat{H} := \max\left\{cP(0)+H(0), \frac{\eta}{d_1+\mu}\right\}$. *Then, for any positive time* $(t>0)$ *we have* $P(t) \leq \widehat{P}$ *and* $H(t) \leq \widehat{H}$.

Proof: We follow the same procedure as in [Ter15]. Let us start by showing the boundedness of $P(t)$ from above by $\widehat{P}$. Note that from Lemma 3.1.1 and Picard-Lindelof Theorem there exists a unique solution for system (3.7) for $t \geq 0$, where

this solution satisfy positivity. We suppose a solution exist on $[0,T]$ for some $T>0$. Then from positivity and first equation of (3.7) we have

$$\frac{dP}{dt} = Pr - \frac{rP^2}{K} - \frac{aPH}{b+P} \leq Pr\left(1-\frac{P}{K}\right) \qquad \text{for } t\in[0,T].$$

Since $P(0)\geq 0$ is given, there exists a function $P_1(t)$ such that, $P(t)\leq P_1(t)$ for $t\in[0,T]$ with $P_1(0)=P(0)\geq 0$ and P_1 is a solution of $\frac{dP_1}{dt} = rP_1\left(1-\frac{P_1}{K}\right)$ for $t\in[0,T]$.

Then, for $P_1\geq \widehat{P}$ where $0\leq \widehat{P}<K$, $\left(1-\frac{P_1}{K}\right)$ is strictly decreasing and $\frac{dP_1}{dt} = rP_1\left(1-\frac{P_1}{K}\right)$ is positive. On the other hand for $P_1>K$, $\frac{dP_1}{dt} = rP_1\left(1-\frac{P_1}{K}\right)$ is negative.

Therefore, using the Intermediate Value Theorem and Mean Value Theorem we must have $P_1(t)\leq \widehat{P}$. Hence, $P(t)\leq P_1(t)\leq \widehat{P}$, *i.e.*, $P(t)$ is bounded from above.

Next, we consider a bound for $H(t)$ from above. From our model we have that the emergence (birth) rate of herbivores is always less than a linear multiple of the functional response. That is, $cF(P)\left(\frac{H}{h+H}\right) < eF(P)$ for some positive constant $e>0$ and also $D(F(P))\geq d_1$ for the positive constant d_1 as given in equation (3.3). From model (3.7) when $P\geq 0$ and $H\geq 0$ finally we have $rP\left(1-\frac{P}{K}\right)$ is bounded above by a positive constant (say Q) for $P\geq 0$. Note that, $rP\left(1-\frac{P}{K}\right)$ is continuous on the interval $[0,K]$ and is, therefore, bounded due to the standard Min-max Theorem in Analysis. Moreover, $rP\left(1-\frac{P}{K}\right)<0$ for $P>K$. Combining these observations, the positivity result (from Lemma 3.1.1) and using equations of the model system (3.7), we have for $t\geq 0$,

$$\begin{aligned}
\frac{d}{dt}(eP+H) &= e\frac{dP}{dt} + \frac{dH}{dt} \\
&= erP\left(1-\frac{P}{K}\right) - eH\left(\frac{aP}{b+P}\right) + H\underbrace{\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)\right]}_{cF(P)(H/(h+H))<eF(P)} - \underbrace{D(F(P))}_{<d_1}H - \mu H \\
&\leq erP\left(1-\frac{P}{K}\right) - eHF(P) + HeF(P) - d_1H - \mu H \\
&= erP\left(1-\frac{P}{K}\right) - (d_1+\mu)H \\
&= erP\left(1-\frac{P}{K}\right) + (d_1+\mu)eP - (d_1+\mu)eP - (d_1+\mu)H \\
&= erP\left(1-\frac{P}{K}\right) + (d_1+\mu)eP - (d_1+\mu)(eP+H).
\end{aligned}$$

Here, we can see that $erP\left(1-\frac{P}{K}\right)+(d_1+\mu)eP = -er\frac{P^2}{K}+e(r+d_1+\mu)P$ is a quadratic expression in P and is easily seen to have a global maximum namely at

$$\frac{-4(-er/K)(0)-(e(r+d_1+\mu))^2}{4\frac{-er}{K}} = \frac{Ke(r+d_1+\mu)^2}{4r}.$$

Hence, $\eta = \dfrac{Ke(r+d_1+\mu)^2}{4r} \geq erP\left(1-\dfrac{P}{K}\right)+(d_1+\mu)eP$

and we have

$$\begin{aligned}\frac{d}{dt}(eP+H) &\leq \frac{Ke(r+d_1+\mu)^2}{4r}-(d_1+\mu)(eP+H)\\ &\leq \eta-(d_1+\mu)(eP+H). \end{aligned} \tag{3.8}$$

Then, it follows from the last step of (3.8) that $eP(t)+H(t)\leq W(t)$ for all $t\geq 0$ where $W(0)=eP(0)+H(0)\geq 0$ and $W(t)$ is a solution of $\dfrac{dW}{dt}=\eta-(d_1+\mu)W$.

Solving for W we have $W=\dfrac{\eta}{d_1+\mu}-\dfrac{K}{(d_1+\mu)}e^{-(d_1+\mu)t}$ and then

$$W(t)\leq \max\left\{W(0),\frac{\eta}{(d_1+\mu)}\right\}=\max\left\{eP(0)+H(0),\frac{\eta}{(d_1+\mu)}\right\}=\widehat{H}.$$

Hence, $eP(t)+H(t)$ is bounded by $\widehat{H}$. Since P satisfies positivity condition and is bounded above by $\widehat{P}=\max\{P(0),K\}$, then H itself must be bounded above by $\widehat{H}$.

Theorem 3.1.1. *The set on which the system* (3.7) *is defined,*

$$\Omega=\left\{(P,H)\in\mathbb{R}_2 : P\geq 0, H\geq 0, P\leq \widehat{P}, H\leq \widehat{H}\right\}$$

is positively invariant, where $\widehat{P}:=\max\{P(0),K\}$ *and* $\widehat{H}:=\max\left\{cP(0)+H(0),\dfrac{(r+d_1+\mu)^2}{4r(d_1+\mu)}K\right\}$.

Proof: From the first equation of the model system (3.7), it is clear that if $P=0$ then $\dfrac{dP}{dt}=0$. Moreover, from the second equation when $H=0$ and $P\geq 0$ we have $\dfrac{dH}{dt}=0$. Therefore, by Theorem 2.1 (on p.81 of [Smi08]) we can conclude that the trajectory of the solution of the system is directed inward on the boundary points of the positive quadrant, *i.e.*, on the set $\partial\mathbb{R}^+_2=\left\{(P,H)\in\mathbb{R}^+_2 | P=0, H=0\right\}$.

Hence, the conclusion of the theorem follows immediately from Lemma 3.1.1 and Lemma 3.1.2 above. □

The above theorem verifies that, for the model system (3.7) with the given non-negative initial conditions there exists a solution to it that remains in the domain for all $t \geq 0$. Thus, the model system is mathematically and biologically well posed.

3.1.2 Dynamics without Herbivores

In the absence of herbivores, the population dynamics for the plant biomass is the net result of population production through growth and it is self limiting by the carrying capacity. That is, for $H = 0$, $rP\left[1 - \frac{P}{K}\right] > 0$ if $0 < P < K$, where r is the growth rate and the loss of biomass by self limitation is given by $\frac{rP}{K}$. Note that, if $P > K$ the plant biomass decays even without herbivory until it saturates back at the carrying capacity K. Such things may happen due to shortage of nutrients, water deficiency and/or soil salinity and competition. But since we want to study only the herbivory effect on the plant population we assume that $0 < P < K$. On the other hand, in the absence of plants the herbivore population cannot grow and decays at a constant rate of d_2.

3.1.3 Plant-Herbivore Interactions (*Existence of Herbivores*)

In the presence of both plant and herbivore populations, the plant biomass will initially decrease due to the functional response of herbivores. On the other hand, since it is assured that the emergence rate, $cF(P)\left(\frac{H}{h+H}\right)$, is dependent on the functional response and the death rate is also dependent on the plant biomass $D(F(P))$, the evolution of the herbivore population is also dictated by the abundance of plants. This will lead for the dynamics of both population to reverse its direction after some times and may oscillate or arrive at some equilibrium point. We will consider this analysis in the next section. Moreover, with the existence of herbivore population there will also be a human interference which is represented in the system as a harvest rate μ. Which means, it is also assumed that humans remove the herbivore population from the system with a constant rate of μ.

3.2 Equilibrium Analysis

3.2.1 Existence of Equilibria and Stability

To find equilibrium points of the model system we put the right hand side of the model system (3.7) to be equal to zero. That is

$$\frac{dP}{dt} = P\left[r\left(1 - \frac{P}{K}\right) - \frac{aH}{b+P}\right] = 0, \tag{3.9}$$

$$\frac{dH}{dt} = H\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right) - D(F(P)) - \mu\right] = 0. \qquad (3.10)$$

From equation (3.9) we have

$$P\left[r\left[1-\frac{P}{K}\right] - \frac{a}{b+P}H\right] = 0. \quad \text{Then, either } P = 0 \text{ or } r - \frac{rP}{K} - \frac{aH}{b+P} = 0,$$

and from equation (3.10) we get

$$H\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right) - D(F(P)) - \mu\right] = 0. \qquad \text{Then, either } H = 0$$
$$\text{or } \frac{caPH}{(b+P)(h+H)} - \frac{d_2K(1+d_1-d_2)(b+P) + P(b+K)(d_2-d_1)(d_2-1)}{K(1+d_1-d_2)(b+P) + (d_2-d_1)(b+K)} - \mu = 0.$$

Next, we have the following cases for the combinations of solutions for equations (3.9) and (3.10).

Case 1: ***Herbivore-Free Equilibria*** :

When there is no herbivore, that is, when $H = 0$, P needs to satisfy $Pr\left(1 - \frac{P}{K}\right) = 0$. Which implies that two equilibria is possible for the system: one is the trivial equilibrium $(P, H) = (0, 0)$ and the other is the herbivore free and maximum plant capacity equilibrium $(P, H) = (K, 0)$.

Local Stability of Herbivore-free Equilibria

The local stability of the equilibrium points is determined by using the Jacobean matrix which linearizes the given model system near the equilibrium points. Let us first calculate the Jacobean matrix of the system:

$$\text{Jac} = \begin{pmatrix} r - \frac{2rP}{K} - \frac{abH}{(b+P)^2} & \frac{-aP}{(b+P)} \\ \left(\frac{cab}{(b+P)^2}\right)\left(\frac{H^2}{h+H}\right) - H\frac{d}{dP}D(F(P)) & \left(\frac{caP}{b+P}\right)\left(\frac{H(H+2h)}{(h+H)^2}\right) - D(F(P)) - \mu \end{pmatrix}$$

Evaluating the Jacobian at the trivial equilibrium point $(P = 0, H = 0)$ we get the eigenvalues of the resulting matrix to be $\lambda_1 = r$ and $\lambda_2 = -d_2 - \mu$ where d_2 is the maximum possible death rate constant with $d_2 > 0$ and μ is the harvesting constant with $\mu > 0$. Since one of the eigenvalues $\lambda = -d_2 - \mu < 0$ is negative and the other $\lambda = r > 0$ is positive then by Poincaré-Lyapunov Theorem the point $(P = 0, H = 0)$ is unstable for all parameter values.

For the stability of the second equilibrium point $(P = K, H = 0)$ (which is the herbivore extinction equilibrium point) we have the following. Evaluating the Jacobean matrix at the second equilibrium point $(P = K, H = 0)$ we have

$$\text{Jac}|_{(K,0)} = \begin{pmatrix} -r & \frac{aK}{b+K} \\ 0 & -d_1 - \mu \end{pmatrix}.$$

The eigenvalues of this matrix are $\lambda_1 = -r < 0$ and $\lambda_2 = -d_1 - \mu < 0$. Then, by Poincaré theorem the herbivore-free equilibrium point $(K, 0)$ is locally asymptotically stable.

Case 2: ***Co-Existence Equilibria*** :

When the herbivore population is always positive, *i.e.*, $H > 0$, from equation (3.10) the term

$$c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)$$

represents the aggregate rate of emergence of herbivore and is an increasing function of P. Similarly, the term $D(F(P)) + \mu$ represents the rate of removal of herbivores and is a decreasing function of P. Moreover, from the assumption that $P \leq K$ we have $\frac{aP}{b+P} \leq \frac{aK}{b+K}$, and $D(F(K)) \geq d_1$.

If $\frac{caK}{(b+K)}\left(\frac{H}{H+h}\right) < d_1 + \mu$ then the rate of herbivore mortality will always be higher than herbivore growth rate. Hence, the herbivore population eventually decays to extinction. Therefore, for the non extinction of herbivores we must always have the condition that $\frac{caK}{(b+K)}\left(\frac{H}{H+h}\right) > d_1 + \mu$.

Thus, define $\mathcal{R}_o = \frac{caK}{(d_1+\mu)(b+K)}$ to be a threshold parameter value for the system, and we shall call it the *reproduction ratio* for the herbivore population. Then, we have the following theorem.

Theorem 3.2.1. *Suppose the model system* (3.7) *is given with positive initial plant population* $(P(0) > 0)$. *If* $\mathcal{R}_o \leq 1$, *then as time goes on, the herbivore population decays to zero whereas the plant population grows to the carrying capacity* K *of the environment i.e.,* $\lim_{t\to\infty}(P(t), H(t)) = (K, 0)$.

Proof: Let us bound the values of $\frac{dH}{dt}$ from above. To do this, we bound the herbivore death rate function from below and the herbivore birth rate from above.

In view of positivity (Lemma 3.1.1), the herbivore death rate function $D(F(P))$ is bounded below by the parameter d_1. Since the herbivore birth rate is

$$c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right),$$

to bound this from above, first, by positivity where $\widehat{H}$ is the maximum value for herbivore population, $H \leq \widehat{H}$ and we have $\dfrac{H}{h+H} \leq \dfrac{\widehat{H}}{h+\widehat{H}}$ for $t \geq 0$, where $\widehat{H} = \max\left\{eP(0)+H(0), \dfrac{\eta}{(d_1+\mu)}\right\}$ is a positive constant defined in Lemma 3.1.2. Second, note that by positivity we have for $t \geq 0$ in the proof of Lemma 3.1.2 we saw that $P(t)$ can be bounded above by a function $P_1(t)$, which when $P(0) > 0$, have the property that $P_1(t) \to K$ as $t \longrightarrow \infty$.

Hence for any $\varepsilon_1 > 0$, there exist $T_1 > 0$ such that $P(t) \leq P_1(t) < K + \varepsilon_1$ for $t \geq T_1$. Using this and the positivity property we can have the relation:

$$\frac{caP}{b+P} \leq \frac{ca(K+\varepsilon_1)}{b+(K+\varepsilon_1)} \qquad \text{for} \qquad t \geq T_1 \qquad \text{for some } T_1 > 0. \tag{3.11}$$

Moreover from Lemma 3.1.1 and the Standard Comparison argument (Theorem 1.1 in [Smi08]) we have $P \leq K$ for $t \geq T_1$, and which implies that $\dfrac{caP}{b+P} \leq \dfrac{caK}{b+K}$ for all $t \leq T_1$.

Combining these observations we get

$$\frac{dH}{dt} \leq H\left[\frac{ca(K+\varepsilon_1)}{b+(K+\varepsilon_1)}\left(\frac{H}{h+H}\right) - d_1 - \mu\right] \leq \widehat{H}\left[\frac{ca(K+\varepsilon_1)}{b+(K+\varepsilon_1)}\left(\frac{\widehat{H}}{h+\widehat{H}}\right) - d_1 - \mu.\right] \tag{3.12}$$

Now, for $\mathcal{R}_0 \leq 1$, $\dfrac{caK}{b+K} \leq d_1 + \mu$, and since $0 < \left(\dfrac{\widehat{H}}{h+\widehat{H}}\right) < 1$, we may choose ε_1 small enough such that the term in the square bracket of equation (3.12) is a negative constant, say $-\alpha$ (where $\alpha > 0$). Then, we have $H(t) \leq H_1(t)$ for $t \geq T_1$ where $H_1(T_1) = H(T_1)$ for $t \leq T_1$, and H_1 is a solution of $\dfrac{dH_1}{dt} = -\alpha H_1$. Since H satisfies positivity (Lemma 3.1.1) and is bounded above (by Lemma 3.1.2) then $H_1(T_1) = H(T_1)$ is non-negative and finite. Hence $H_1(t) \longrightarrow 0$ as $t \longrightarrow \infty$, which implies that $H(t) \longrightarrow 0$ as $t \longrightarrow \infty$, since $0 \leq H(t) \leq H_1(t)$ for $t \geq T_1$.

Finally, we shall show that $P(t) \longrightarrow K$ as $t \longrightarrow \infty$.

To this end, we consider the herbivore emergence rate $c\left(\dfrac{aP}{b+P}\right)\left(\dfrac{H}{h+H}\right)$ in the model system (3.7). To show that this expression is bounded from above, we first note by positivity that $\dfrac{H}{h+H} \leq \dfrac{\widehat{H}}{h+\widehat{H}}$ for $t \geq 0$ where $\widehat{H}$ is a positive constant

defined in Lemma 3.1.2; second note that by positivity we have for $t > 0$, $\frac{caP}{b+P} \leq \frac{caK}{b+K}$. Then for any $\varepsilon_2 > 0$, there exists $T_2 > 0$ such that

$$P(t) < K + \varepsilon_2 \qquad \text{for} \qquad t \geq T_2.$$

Now, choose $\varepsilon_3 > 0$ such that $\varepsilon_3 < \max\left\{\frac{r}{a}, \frac{r\varepsilon_2}{2aK}\right\}$. Then since $H(t) \longrightarrow 0$ as $t \longrightarrow \infty$ we can see that there exists $T_3 > 0$ such that

$$0 < H(t) < \varepsilon_3 \qquad \text{for all} \qquad t \geq T_3.$$

Using this and also positivity we have $\frac{aPH}{b+P} < \frac{a\varepsilon_3 P}{b+P} < a\varepsilon_2 P$, for $t \geq T_3$

Hence by the equation for $\frac{dP}{dt}$ we have for $t \geq T_3$ that $\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - \frac{aPH}{b+P}$. Thus, $\frac{dP}{dt} \geq rP\left(1 - \frac{P}{K}\right) - a\varepsilon_3 P$ or $\frac{dP}{dt} \geq rP\left(1 - \frac{a\varepsilon_3}{r} - \frac{P}{K}\right)$.

We also know that $P(T_3)$ is bounded and positive. Then $P(t) \geq P_2(t)$ for $t > T_3$ where $P_2(T_3) = P(T_3) > 0$, and where, for $t > T_3$, P_2 is a solution of $\frac{dP_2}{dt} = rP_2\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)$.

Since by definition $\varepsilon_3 < \frac{r}{a}$, then $1 - \frac{a\varepsilon_3}{r} > 0$, so that by solving explicitly for $P_2(t)$ we have

$$\frac{dP_2}{dt} = rP_2\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)$$

or

$$\frac{P_2}{\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)} = Ae^{\left(1-\frac{a\varepsilon_3}{r}\right)rt}$$ for some constant A. Now, as $t \longrightarrow \infty$, since $1 - \frac{a\varepsilon_3}{r} > 0$ we have $\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right) \longrightarrow 0$ or $\lim_{t\longrightarrow\infty} P_2 = K\left(1 - \frac{a\varepsilon_3}{r}\right)$.

In particular then, $P_2 > K\left(1 - \frac{2a\varepsilon_3}{r}\right)$ for $t \geq T_4$ and for some constant T_4 such that $T_4 \geq T_3$. But by our choice of ε_3, we have $\varepsilon_3 < \frac{r\varepsilon_2}{2aK}$, so that $1 - \frac{2a\varepsilon_3}{r} > 1 - \frac{\varepsilon_2}{K}$. Hence $P(t) \geq P_2(t) > K\left(1 - \frac{\varepsilon_2}{K}\right) = K - \varepsilon_2$ for $t \geq T_4$.

Finally, letting $T_5 = \max\{T_2, T_4\}$, we see that $K - \varepsilon_2 < P(t) < K + \varepsilon_2$ for $t \geq T_5$. Thus $P(t) \longrightarrow K$ as $t \longrightarrow \infty$, as required. □

This theorem suggests that, if the herbivore emergence rate is less than the aggregate mortality (or removal) rate then more herbivores die compared to their emergence. Therefore, this results in the long run that the plant population grows

up to the carrying capacity of the environment while the herbivore population goes to extinction.

In the case where $\frac{caK}{(b+K)}\left(\frac{H}{H+h}\right)$ is bounded from above, it is relevant to consider the condition that $\frac{caK}{(b+K)}\left(\frac{H}{H+h}\right) < d_1+\mu$. In this case, since herbivore mortality will always be higher than their rate of emergence, the actual growth rate is negative, which implies that the herbivore population eventually decreases until extinction.

Hence, to study the behavior of the system in the existence of the herbivore population we assume for the rest part of the chapter that $\frac{caK}{(b+K)}\left(\frac{H}{H+h}\right) > d_1+\mu$.

Theorem 3.2.2. *Suppose that $\mathcal{R}_o > 1$ and define $H_m = \frac{(d_1+\mu)h(b+K)}{caK-(d_1+\mu)(b+K)}$. Then, the following hold.*

(i) If $H(0) < H_m$ and $P(0) > 0$, then $(P(t), H(t)) \longrightarrow (K, 0)$ as $t \longrightarrow \infty$.

(ii) If $H(0) \geq H_m$ and $0 < P(0) < \frac{1}{(ca\beta e^{r\beta})}$, where $\beta = \left(\frac{2}{d_1+\mu}\right)\left[1+\ln\left(\frac{H(0)}{H_m}\right)\right]$ is a positive constant; then $(P(t), H(t)) \longrightarrow (K, 0)$ as $t \longrightarrow \infty$.

(iii) For $\varepsilon > 0$, $n_0 > b + P$, if $H(0) \geq H_m$ and $P(0) > \frac{n_0}{(\varepsilon ca\gamma e^{-r\gamma})}$ where $\gamma = \left(\frac{1}{2(d_2+\mu)}\right)\left[1+\ln\left(\frac{H(0)}{H_m}\right)\right]$ is a positive constant then $H(t) \not\to 0$ as $t \longrightarrow \infty$.

Proof: From Lemma 3.1.2 we have $P(t) \leq \max\{P(0), K\} = \widehat{P}$ for $t \geq 0$.
Let $\sigma(H) = \left(\frac{caK}{b+K}\right)\left(\frac{H}{h+H}\right) - d_1 - \mu$. Then clearly $\sigma(0) = -d_1 - \mu < 0$. Also $\sigma(H)$ is continuous in $H \geq 0$, and $\sigma(H) > 0$ for all H sufficiently large because $\mathcal{R}_0 > 1$. Therefore, by Intermediate Value Theorem there is a least positive solution H_m to $\sigma(H) = 0$, such that we have $\sigma(H) < 0$ for $0 \leq H < H_m$. Then,

(i) To prove the first part of the theorem, from the proof of Theorem 3.2.1 we find that for $t \geq 0$

$$\begin{aligned}\frac{dH}{dt} &\leq H\left[\frac{caK}{b+K}\left(\frac{\widehat{H}}{h+\widehat{H}}\right) - d_1 - \mu\right] \\ &= H\sigma(H).\end{aligned}$$

Then by the Standard Comparison argument there exists a function H_1 such that $H(t) \leq H_1(t)$ for $t > 0$ where $H_1(0) = H(0) \geq 0$, and H_1 is a solution of $\frac{dH_1}{dt} = H_1\sigma(H_1)$. From the hypothesis we have $H(0) < H_m$ and we have also seen that $\sigma(H) < 0$ for $0 \leq H < H_m$. Therefore, we have $H_1(t) \longrightarrow 0$ as

$t \longrightarrow \infty$. But then $H(t) \longrightarrow 0$ as $t \longrightarrow \infty$ since we have $0 < H(t) \leq H_1(t)$ for $t > 0$.

Next, we will show that $P(t) \longrightarrow K$ as $t \longrightarrow \infty$. In similar manner as in the proof of Theorem 3.2.1 we can show that $P \longrightarrow K$.

For the model system (3.7) the herbivore birth rate is $c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)$. To bound this from above, we first note, by positivity lemma (Lemma 3.1.1) that $\frac{H}{h+H} \leq \frac{\widehat{H}}{h+\widehat{H}}$ for $t \geq 0$ where $\widehat{H}$ is a positive constant defined in Lemma 3.1.2. Second, note that by positivity for $t > 0$we have, $\frac{caP}{b+P} \leq \frac{caK}{b+K}$. And for any $\varepsilon_2 > 0$, there exists $T_2 > 0$ such that

$$P(t) < K + \varepsilon_2 \qquad \text{for} \qquad t \geq T_2.$$

Now, choose $\varepsilon_3 > 0$ such that $\varepsilon_3 < \max\left\{\frac{r}{a}, \frac{r\varepsilon_2}{2aK}\right\}$. Then, since $H(t) \longrightarrow 0$ as $t \longrightarrow \infty$ we can see that there exists $T_3 > 0$ such that

$$0 < H(t) < \varepsilon_3 \qquad \text{for all} \qquad t \geq T_3.$$

Using this and also positivity we have $\frac{aPH}{b+P} < \frac{a\varepsilon_3 P}{b+P} < a\varepsilon_2 P$, for $t \geq T_3$

Hence, by the equation for $\frac{dP}{dt}$ (in equation (3.7)) we have for $t \geq T_3$ that

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - \frac{aPH}{b+P} \geq rP\left(1 - \frac{P}{K}\right) - a\varepsilon_3 P. \qquad \text{Or}$$
$$\frac{dP}{dt} \geq rP\left(1 - \frac{a\varepsilon_3}{r} - \frac{P}{K}\right).$$

We also know that $P(T_3)$ is bounded and positive. Then $P(t) \geq P_2(t)$ for $t > T_3$ where $P_2(T_3) = P(T_3) > 0$ and where, for $t > T_3$, P_2 is a solution of $\frac{dP_2}{dt} = rP_2\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)$.

Since by definition $\varepsilon_3 < \frac{r}{a}$, then $1 - \frac{a\varepsilon_3}{r} > 0$, so that by solving explicitly for $P_2(t)$ we have

$$\frac{dP_2}{dt} = rP_2\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right) \qquad \Rightarrow \frac{dP_2}{P_2\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)} = rdt$$

$$\Rightarrow \frac{1}{\left(1 - \frac{a\varepsilon_3}{r}\right)}\frac{dP_2}{P_2} + \frac{1}{K\left(1 - \frac{a\varepsilon_3}{r}\right)}\frac{dP_2}{\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)} = rdt$$

$$\Rightarrow \frac{dP_2}{P_2} + \frac{1}{K}\frac{dP_2}{\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)} = \left(1 - \frac{a\varepsilon_3}{r}\right)rdt.$$

And hence $\dfrac{P_2}{\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)} = Ae^{\left(1-\frac{a\varepsilon_3}{r}\right)rt}$ for some constant A. Now, as $t \longrightarrow \infty$ we get

$$\frac{P_2}{\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2}{K}\right)} = Ae^{\left(1-\frac{a\varepsilon_3}{r}\right)rt} \longrightarrow \infty, \text{as } 1 - \frac{a\varepsilon_3}{r} > 0.$$

$$\textit{i.e.,} \quad \lim_{t\to\infty}\left(1 - \frac{a\varepsilon_3}{r} - \frac{P_2(t)}{K}\right) = 0.$$

$$\text{Or} \quad \lim_{t\to\infty} P_2(t) = K\left(1 - \frac{a\varepsilon_3}{r}\right).$$

In particular, we have $P_2 > K\left(1 - \dfrac{2a\varepsilon_3}{r}\right)$ for all $t \geq T_4$ where T_4 is some constant such that $T_4 \geq T_3$. But again by our choice of ε_3, we have $\varepsilon_3 < \dfrac{r\varepsilon_2}{2aK}$ so that $1 - \dfrac{2a\varepsilon_3}{r} > 1 - \dfrac{\varepsilon_2}{K}$. Hence, $P(t) \geq P_2(t) > K\left(1 - \dfrac{\varepsilon_2}{K}\right) = K - \varepsilon_2$ for $t \geq T_4$. Finally, letting $T_5 = \max\{T_2, T_4\}$, we see that $K - \varepsilon_2 < P(t) < K + \varepsilon_2$ for $t \geq T_5$. Thus, $P(t) \longrightarrow K$ as $t \longrightarrow \infty$, as required.

(ii) To prove the second part, we suppose $H(0) \geq H_m$. Then since $H_m > 0$, let us define $\beta = \left(\dfrac{2}{d_1 + \mu}\right)\left[1 + \ln\left(\dfrac{H(0)}{H_m}\right)\right]$. Hence, $ca\beta e^{r\beta} > 0$. Let us choose $P(0)$ so that $0 < P(0) < \dfrac{1}{ca\beta e^{r\beta}}$. Now, using the equation for $\dfrac{dP}{dt}$ and positivity we have

$$\frac{dP}{dt} < rP \qquad \text{for} \qquad t \geq 0. \tag{3.13}$$

Or equivalently,

$$P(t) < P(0)e^{rt} \qquad \text{for} \qquad t \geq 0. \tag{3.14}$$

Using our choice of $P(0) < \dfrac{1}{ca\beta e^{r\beta}}$ we get

$$\begin{aligned} P(t) &< \frac{e^{rt}}{ca\beta e^{r\beta}}. \\ \text{Or} \quad P(t) &< \frac{1}{ca\beta} \qquad \text{for} \qquad 0 \le t \le \beta. \end{aligned} \tag{3.15}$$

Now, using the equation for $\dfrac{dH}{dt}$ and positivity we have

$$\begin{aligned} \frac{dH}{dt} &= H\left(\frac{caP}{b+P}\left(\frac{H}{h+H}\right) - D(F(P)) - \mu\right) \\ &\le H\left(\frac{caP}{b+P} - D(F(P)) - \mu\right) \\ &\le H(caP - D(F(P)) - \mu) \\ &< H(caP - d_1 - \mu). \end{aligned}$$

It follows from this inequality that,

$$\frac{dH}{dt} < (caP - d_1 - \mu)H \qquad \text{for} \qquad t \ge 0. \tag{3.16}$$

From (3.15) and (3.16) and using positivity we have that

$$\frac{dH}{dt} < \left(\frac{1}{\beta} - d_1 - \mu\right) H \qquad \text{for} \qquad 0 \le t \le \beta.$$

Separating the variables and integrating from 0 to t we have $H(t) \le H(0)e^{\left(\frac{1}{\beta} - d_1 - \mu\right)t}$ for $0 \le t \le \beta$. Hence $H(\beta) \le H(0)e^{(1-\beta(d_1+\mu))}$. But then from our definition of β we have

$$\begin{aligned} \beta &= \left(\frac{2}{d_1+\mu}\right)\left[1 + \ln\left(\frac{H(0)}{H_m}\right)\right], \\ \text{and clearly we can see that } \beta &> \left(\frac{1}{d_1+\mu}\right)\left[1 + \ln\left(\frac{H(0)}{H_m}\right)\right]. \end{aligned}$$

Therefore, $\beta(d_1+\mu) > \left[1 + \ln\left(\dfrac{H(0)}{H_m}\right)\right]$. Which implies that $\beta(d_1+\mu) - 1 > \ln\left(\dfrac{H(0)}{H_m}\right)$, and equivalently we have

$$H(0)e^{1-\beta(d_1+\mu)} < H_m.$$

Hence $H(\beta) < H_m$.

If we now apply the argument used to prove the first part of the theorem, with the time origin shifted from $t = 0$ to $t = \beta$, this will lead us to the required

result. That is, for $t \geq \beta$, $\frac{dH}{dt} \leq H\left[\frac{caK}{b+K}\left(\frac{\widehat{H}}{h+\widehat{H}}\right) - d_1 - \mu\right] = H\sigma(H)$. Then, $H(t) \leq H_1(t)$ for $t \geq \beta$, where $H_1(\beta) = H(\beta) \geq 0$ and H_1 a solution of $\frac{dH_1}{dt} = H_1\sigma(H_1)$. Now, for $H(\beta) < H_m$ and from $\sigma(H) < 0$ for $0 < H(\beta) < H_m$, by the Standard Comparison argument we have $H_1(t) \to 0$ as $t \to \infty$. Then we have $H(t) \to 0$ as $t \to \infty$ since $0 \leq H(t) \leq H_1(t)$ for $t \geq \beta$. Therefore, we can deduce that $(P(t), H(t)) \longrightarrow (K, 0)$ as $t \longrightarrow \infty$.

(iii) Next, we prove the third part. Suppose $H(0) \geq H_m$. Then since $H_m > 0$, let us define ε to be a very small positive number, n_0 to be a sufficiently large number such that $n_0 > b + P$, and also let
$\gamma = \left(\frac{1}{2(d_2+\mu)}\right)\left[1 + \ln\left(\frac{H(0)}{H_m}\right)\right]$.

Then, $ca\varepsilon\gamma e^{-r\gamma} > 0$. Let us choose $P(0)$ so that $P(0) > \frac{n_0}{ca\varepsilon\gamma e^{-r\gamma}}$. Now, using the equation for $\frac{dP}{dt}$ and Lemma 3.1.1 we have

$$\frac{dP}{dt} > 0,$$

which implies that

$$P(t) > P(0)e^{-rt}.$$

Now for $\varepsilon > 0$, we can set $\frac{H}{h+H} > \varepsilon$ and because of the choice of n_0 with $n_0 > b + P$, we have $\frac{P}{b+P} > \frac{P}{n_0}$; and using our choice of $P(0) > \frac{n_0}{\varepsilon ca\gamma e^{-r\gamma}}$, we get

$$P(t) \geq P(0)e^{-rt} > \frac{n_0 e^{-rt}}{\varepsilon ca\gamma e^{-r\gamma}} > \frac{n_0}{\varepsilon ca\gamma e^{-r(\gamma - t)}}.$$

Hence,

$$P(t) \quad > \quad \frac{n_0}{\varepsilon ca\gamma} \qquad \text{for} \qquad t \geq \gamma. \tag{3.17}$$

Moreover, using the equation for $\frac{dH}{dt}$ and Lemma 3.1.1 since for $\varepsilon > 0$, $\frac{H}{h+H} > \varepsilon$ and for $n_0 > b + P$, $\frac{P}{b+P} > \frac{P}{n_0}$, we have
$\left(c\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right) > \frac{ca\varepsilon P}{n_0}$.

Or $\frac{dH}{dt} \geq \left(c\frac{aP}{b+P}\left(\frac{H}{h+H}\right) - d_2 - \mu\right)H \qquad \text{for} \qquad t \geq \gamma.$

Then, using (3.17) we arrive at

$$\frac{dH}{dt} > \left(\frac{\varepsilon caP}{n_0} - d_2 - \mu\right) H > \left(\frac{1}{\gamma} - d_2 - \mu\right) H \text{ for } t \geq \gamma. \quad (3.18)$$

But then $H(t) \geq H(0)e^{\left(\frac{1}{\gamma} - d_2 - \mu\right)t}$ for $t \geq \gamma$. Hence, $H(\gamma) \geq H(0)e^{(1-\gamma(d_2-\mu))}$.

Again from our definition of γ we have

$$\gamma = \left(\frac{1}{2(d_2+\mu)}\right)\left[1 + \ln\left(\frac{H(0)}{H_m}\right)\right].$$

Therefore, clearly we can see that

$$\begin{aligned} \gamma &< \left(\frac{1}{(d_2+\mu)}\right)\left[1 + \ln\left(\frac{H(0)}{H_m}\right)\right] \\ \implies \gamma(d_2+\mu) - 1 &< \ln\left(\frac{H(0)}{H_m}\right) \\ \implies H(0)e^{1-\gamma(d_2+\mu)} &> H_m. \end{aligned}$$

Hence $H(\gamma) > H_m$.

This implies that the herbivore population will not go to extinction, *i.e.*, $H(t) \not\to 0$ for $t \to \infty$. □

In the absence of Allee effect, that is, with Allee constant $h = 0$, the least number of herbivores needed to guarantee finding of mate for reproduction, H_m becomes zero as well. hence the threshold values in the theorem can be adjusted accordingly.

The above theorem states that when $\mathcal{R}_o > 1$, and the Allee effect is considered for the herbivore population, there is a least minimum value of H which is the corresponding solution of

$$\left(\frac{caK}{b+K}\right)\left(\frac{H}{h+H}\right) = d_1 + \mu,$$

that gives the necessary least possible number of herbivore population for which co-existence is possible. This minimum threshold value is given by

$$H_m = \frac{(d_1+\mu)h(b+K)}{caK - (d_1+\mu)(b+K)}. \quad (3.19)$$

Then, if the initial herbivore population is less than the least number of herbivore population needed to keep the population existing in the system and if the initial plant population is positive then the herbivore population goes to extinction while the plant population grows to the carrying capacity of the environment. In addition,

even if the initial herbivore population is greater than the least number of herbivore population needed to keep the population existing in the system, the herbivore population can still go to extinction if there is no enough plant population to feed on and reproduce. On the other hand, if the initial herbivore population is greater than the least number of herbivore population needed to keep the population existing in the system then the herbivore population would not go to extinction as long as there is sufficient plant population to feed on.

Stable Coexistence

If the reproduction number $\mathcal{R}_o$ is more than unity and if the initial density of the herbivore population is above the minimum threshold H_m defined in Theorem 3.2.2, coexistence of the two population is possible. However, Theorem 3.2.2 does not tell us what happens to the size of the population as time goes on. The answer for this is given in the following theorem.

Theorem 3.2.3. *Let L_P, U_P, L_H and U_H be constants satisfying the following conditions $0 < L_P < U_P$ and $0 < L_H < U_H$. Furthermore, let*

$$L_H F(U_P) > rU_P\left(1 - \frac{U_P}{K}\right), \tag{3.20}$$

$$U_H F(L_P) < rL_P\left(1 - \frac{L_P}{K}\right), \tag{3.21}$$

$$cF(L_P)\left(\frac{L_H}{h + L_H}\right) > D(F(L_P)) + \mu, \tag{3.22}$$

$$cF(U_P)\left(\frac{U_H}{h + U_H}\right) < D(F(U_P)) + \mu. \tag{3.23}$$

Then in model system (3.7)*, if $H(0) \in [L_H, U_H]$ and $P(0) \in [L_P, U_P]$ we have $H(t) \in [L_H, U_H]$ and $P(t) \in [L_P, U_P]$ for all $t \geq 0$. That is, the solution of the system does not go beyond the given region.*

Proof: Assuming the hypothesis of the theorem hold, we need to define

$$\Sigma = \{(P, H) : P \in [L_P, U_P], H \in [L_H, U_H]\},$$

as a trapping region. This trapping region exists if the flow of the system in the phase plane points inwards across all the boundaries of Σ, which is true if:

$$\left.\frac{dP}{dt}\right|_{P=U_P} < 0 \text{ and } \left.\frac{dP}{dt}\right|_{P=L_P} > 0 \text{ for } H \in [L_H, U_H] \tag{3.24}$$

$$\text{and } \left.\frac{dH}{dt}\right|_{H=U_H} < 0 \text{ and } \left.\frac{dH}{dt}\right|_{H=L_H} > 0 \text{ for } P \in [L_P, U_P] \tag{3.25}$$

Using (3.20)-(3.23), let us show that (3.24)-(3.25) are satisfied for $P \in [L_P, U_P]$ and $H \in [L_H, U_H]$.

From (3.20) we have $L_H F(U_P) > rU_P\left(1-\frac{U_P}{K}\right)$ and for $H \in [L_H, U_H]$ since $HF(P)$ is an increasing function in H we have

$$rU_P\left(1-\frac{U_P}{K}\right) < L_H F(U_P) < HF(U_P).$$

Thus, $rU_P\left(1-\frac{U_P}{K}\right) - HF(U_P) < 0$. Or equivalently, $\left.\frac{dP}{dt}\right|_{P=U_P} < 0$ for $H \in [L_H, U_H]$.

Using similar arguments, from (3.21) we have $U_H F(L_P) < rL_P\left(1-\frac{L_P}{K}\right)$ and for $H \in [L_H, U_H]$ since $HF(P)$ is an increasing function in H, we have

$$rL_P\left(1-\frac{L_P}{K}\right) > U_H F(L_P) > HF(L_P).$$

Therefore,

$rL_P\left(1-\frac{L_P}{K}\right) - HF(L_P) > 0$. Or equivalently, $\left.\frac{dP}{dt}\right|_{P=L_P} > 0$ for $H \in [L_H, U_H]$.

Now, from (3.22) we have $cF(L_P)\left(\frac{L_H}{h+L_H}\right) > D(F(L_P)) + \mu$ for $P \in [L_P, U_P]$, and this implies that,

$$D(F(P)) + \mu < D(F(L_P)) + \mu < cF(L_P)\left(\frac{L_H}{h+L_H}\right) < cF(P)\left(\frac{L_H}{h+L_H}\right).$$

This last expression leads to the condition that

$$cF(P)\left(\frac{L_H}{h+L_H}\right) - D(F(P)) - \mu > 0. \tag{3.26}$$

Then, multiplying equation (3.27) by L_H on both sides we get

$$L_H\left[cF(P)\left(\frac{L_H}{h+L_H}\right) - D(F(P)) - \mu\right] > 0. \text{ and } \left.\frac{dH}{dt}\right|_{H=L_H} > 0.$$

Using similar argument from (3.23) we have $cF(U_P)\left(\frac{U_H}{h+U_H}\right) < D(F(U_P)) + \mu$ for $P \in [L_P, U_P]$, and $D(F(P))$ is a decreasing function. This implies that,

$$D(F(P)) + \mu > D(F(U_P)) + \mu > cF(U_P)\left(\frac{U_H}{h+U_H}\right) > cF(P)\left(\frac{U_H}{h+U_H}\right).$$

This last expression leads to the condition that

$$cF(P)\left(\frac{U_H}{h+U_H}\right) - D(F(P)) - \mu < 0. \tag{3.27}$$

Then, multiplying equation (3.27) by U_H on both sides we get

$$U_H\left[cF(P)\left(\frac{U_H}{h+U_H}\right)-D(F(P))-\mu\right]<0 \text{ and } \frac{dH}{dt}\Big|_{H=U_H}<0.$$

□

Biologically, Theorem 3.2.3 means that as long as the initial populations $P(0) \in [L_P, U_P]$ and $H(0) \in [L_H, U_H]$ for all positive time the plant and herbivore population stays in this trapping region. Meaning, when the plant population reaches its maximum U_P we see that the rate of herbivore population $\frac{dH}{dt}$ is positive and the herbivore population increase until it reaches U_H. Then when the herbivore population reaches U_H the rate of plant population $\frac{dP}{dt}$ become negative due to consumption and the plant population starts decreasing until it finally reaches L_P. As a result of limited food supply we can see that the rate of herbivore population $\frac{dH}{dt}$ then becomes negative and the herbivore population decrease until it reaches L_H. This gives a chance for the plant population to regenerate hence $\frac{dP}{dt}$ become positive and the plant population starts increasing until L_P and this cycle repeats itself.

We can also simulate the results of Theorem 3.2.3 using numerical methods. The graph in Figure 3.1 is plotted using the parameter values from Table 3.3 and with the initial values of the population $P(0) = 5000$ and $H(0) = 500$ shows the phase portrait diagram of model system (3.7) for the evolution of the plant and herbivore populations when their initial densities are within the trapping region of Σ. plotting the phase portrait

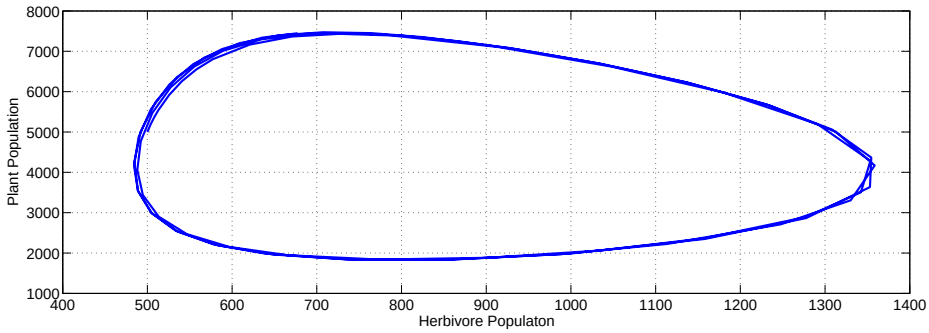

Figure 3.1: Phase portrait of mode system (3.7)

In Figure 3.1 it can be seen that the system has a stable limit cycle and if we start at any point in the trapping region Σ, the system eventually settles at a solution on this orbit. This means that there is no specific coexistence equilibrium point as it keeps appearing and disappearing but the dynamics is always attracted to this stable limit cycle. Co-existence will occur as long as P and H are in Σ.

3.3 Sensitivity Analysis

The objective of sensitivity analysis is to identify critical parameters which significantly affect the evolution of the model system. We examine the partial derivatives of the threshold value $\mathcal{R}_o$ with respect to the input parameters which can easily be computed numerically by performing multiple simulations varying the parameters around estimated normal values.

Note that whether the densities of both population coexist and oscillate or not is determined by the threshold value $\mathcal{R}_o$ which depends on the whole parameter space. For our threshold $\mathcal{R}_o = \frac{caK}{(d_1+\mu)(b+K)}$, the sensitivity analysis is performed by evaluating the partial rank correlation coefficients (PRCCs) for various input parameters against the threshold value $\mathcal{R}_o$, and then the most significant parameters are determined. PRCC measures the influence of uncertainty in estimating the values of the input parameter on the imprecision in predicting the value of the output variable. Uncertainty and sensitivity analysis for all parameters are performed using Latin Hypercube Sampling (LHS) method with 1000 samples. We used the Latin Hypercube sampling/Partial Rank Correlation Coefficient (LHS/PRCC) sensitivity analysis which is an efficient tool in uncertainty analysis to explore the entire parameter space with minimum number of computer simulations.

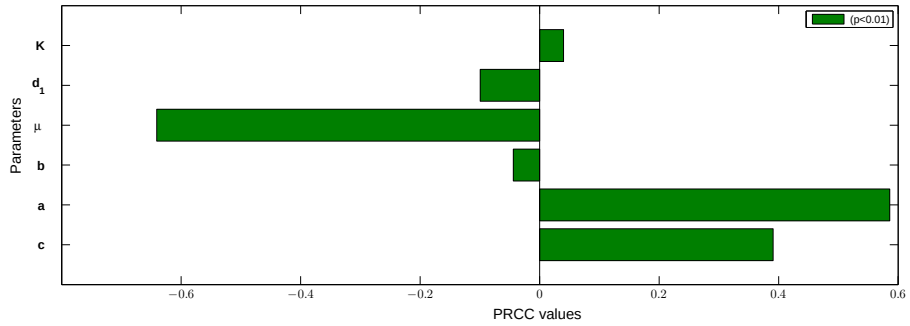

Figure 3.2: sensitivity of parameters using PRCC

The PRCC method suggests that for a sample size of 1000, if the PRCC-value is found to be less than -0.5 or is greater than 0.5 then that parameter is sensitive and is considered as indicating an important correlation, if the values are between 0.2 and 0.4 then this indicates a moderate correlation, and values from 0 to 0.2 are considered to be not significantly different from zero. Therefore, in Figure 3.2 above the PRCC results illustrate the dependence of $\mathcal{R}_o$ on each of the involving parameter values. The positive sign of their PRCCs indicates that if the parameters are increased the value of $\mathcal{R}_o$ increases. The negative sign on the other hand suggests that if the parameters are increased the value of $\mathcal{R}_o$ decreases. Hence from Figure 3.2 we can

see that the feeding rate a is a sensitive parameter in a direct proportional relation and the harvest rate μ is a sensitive parameter in an inverse proportional relation.

Furthermore pairwise PRCC comparison with FDR (false discovery rate) adjusted P-value is produced in Table 3.1.

Table 3.1: Pairwise comparison of PRCC with the FDR.

	c	a	μ	K
c		8.32×10^{-9}	0	0
a			0	0
μ				0
K				

The values in Table 3.1 suggests that all the parameters are sensitive with a p-value zero for every other parameters except for parameter a, which itself is also very close to zero.

The interdependence of parameters is also calculated and is given in Table 3.2. These values represent the independence of Parameters after FDR adjusted.

Table 3.2: Determination of the interdependence of the parameters.

	c	a	μ	K
c		TRUE	TRUE	TRUE
a			TRUE	TRUE
μ				TRUE
K				

The values in Table 3.2 means that, the parameters representing the conversion rate to a new herbivore c, the feeding rate a, and the harvest rate μ are independently sensitive to the reproduction number $\mathcal{R}_o$. Furthermore, the parameters representing the conversion rate to a new herbivore c and the feeding rate a are responsible for increasing $\mathcal{R}_o$ to ensure coexistence.

We can also see that the PRCC values less than 0.2 indicates that the threshold value $\mathcal{R}_o$ is not significantly affected by all such parameters.

3.4 Numerical Illustrations and Discussion

In this section, we perform numerical simulations to illustrate the theoretical results given in section 3, and we will discuss the implications of some of these results.

Table 3.3: Table of parameters and their meaning

Parameter	Description	Units	Value	source
r	plant growth rate	yr^1	0.25	Assumed
a	feeding rate	per hernivore	variable	Assumed
K	carrying capacity(for plant population)		10000	Assumed
b	half saturation constant of herbivore feeding on the plant biomass	per herbivore	1100	Assumed
c	efficiency of converting what is eaten in to a newborn	per herbivore	0.25	Assumed
h	Allee constant	herbivore number	40	Assumed
d_1	minimum death rate	yr^{-1}	0.1	[Ter15]
d_2	maximum death rate	yr^{-1}	0.3	[Ter15]
μ	harvest rate	per total population	0.025	Assumed

The parameter we choose to vary our $\mathcal{R}_o$ value is the feeding rate a. The assumptions we took for the rest of the parameters is summarized in Table 3.3.

To illustrate the results of Theorem 3.2.1 and Theorem 3.2.2, let us draw the graph of the population dynamics over time for both plants and herbivores using the choice of parameters from Table 3.3 and by taking different initial values for the population $P(0)$ and $H(0)$.

From Theorem 3.2.1 we know that for $\mathcal{R}_o \leq 1$ and for any initial plant population $P(0) > 0$ the plant herbivore dynamics will always stabilize to the point $(K, 0)$. That is, if we take the Parameter $a = 0.4$ so that $\mathcal{R}_o = 0.72 < 1$ and if we take two different initial values and plot the population dynamics for both species, we get the graph in Figures 3.3 and 3.4.

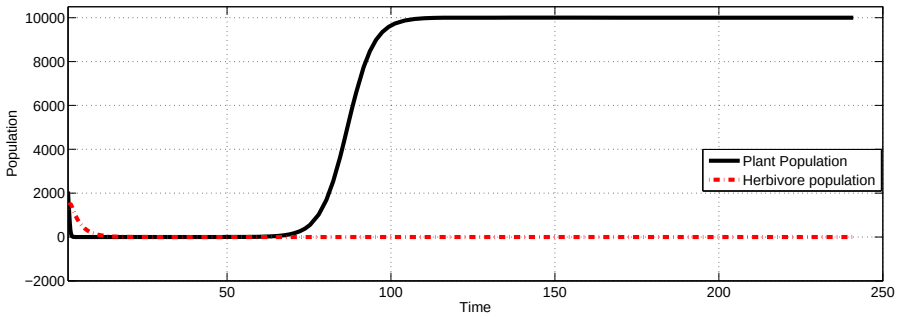

Figure 3.3: Plot of the plant herbivore interaction over time when $\mathcal{R}_o \leq 1$ i.e taking $a = 0.4$ and initial values taken $P(0) = 5000$ and $H(0) = 500$

Figure 3.3 shows that when $\mathcal{R}_o \leq 1$ even if there is enough food, i.e. plant population, the herbivore population will die out because the average number of newly born herbivore is less than one. Plant population will die due to large herbivore population

at first but once the herbivore population dies out it can start growing and eventually reach to the carrying capacity of the environment.

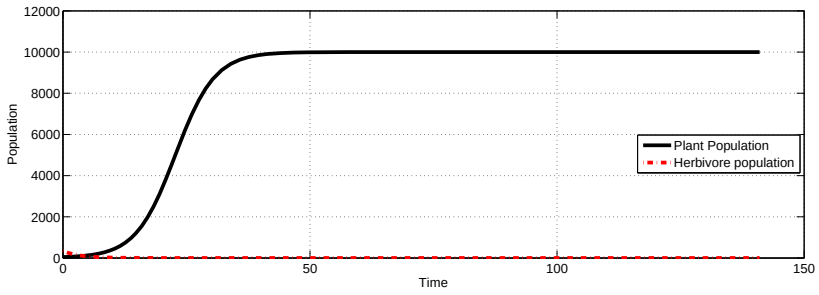

Figure 3.4: Plot of the plant herbivore interaction over time when $\mathcal{R}_o \leq 1$ i.e taking $a = 0.4$ and initial values taken $P(0) = 50$ and $H(0) = 350$

As explained in the results of Theorem 3.2.1, if $\mathcal{R}_o \leq 1$ and if we start with a positive plant population $P(0) > 0$, the plant population will go to the carrying capacity ($P = K$) and the herbivore population vanishes ($H = 0$) regardless of the amount of the initial herbivore population.

However, if we change the parameter value of $a = 0.75$ so that we obtain a value of $\mathcal{R}_o = 1.35 > 1$. Then, from Theorem 3.2.2 (i) given $\mathcal{R}_o > 1$, if $H(0) < H_m$ and $P(0) > 0$ we still have the dynamics evolving to the point $(K, 0)$. Using the parameters in Table 3.3, when we calculate the minimum number of herbivore required, we get $H_m = \dfrac{(d_1 + \mu)h(b + K)}{caK - (d_1 + \mu)(b + K)} = 28.46$. Therefore, the corresponding graph for the dynamics (Figure 3.5) shows that the herbivore population goes to zero when its initial population is below this minimum value.

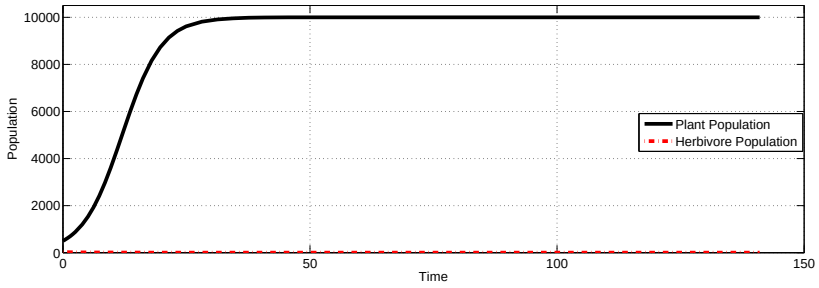

Figure 3.5: Plot of the plant herbivore interaction over time with parameters taken from the Table 3.3 with $\mathcal{R}_o > 1$, initial populations $P(0) = 500$ and $H(0) = 20$

Taking the parameter value $\beta = 1$ and using the remaining parameters as in Table 3.3, we can calculate the threshold for the minimum number of initial population of the plant species required from the formula $\dfrac{1}{(ca\beta e^{r\beta})} = 4.1$.

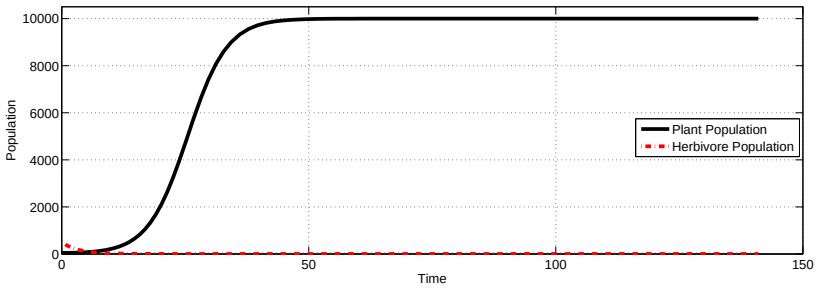

Figure 3.6: Plot of the plant herbivore interaction over time with parameters taken from the Table 3.3 with $\mathcal{R}_o > 1$, initial populations $P(0) = 4$ and $H(0) = 500$

Therefore, Figure 3.6 explains the phenomena in Theorem 3.2.2 (ii) where $H(0) = 35 > H_m \approx 29$ and $0 < P(0) = 4 < \dfrac{1}{(ca\beta e^{r\beta})}$ which can be calculated using values from the table of parameters, Table 3.3, then the population still evolves to the stable point $(K, 0)$.

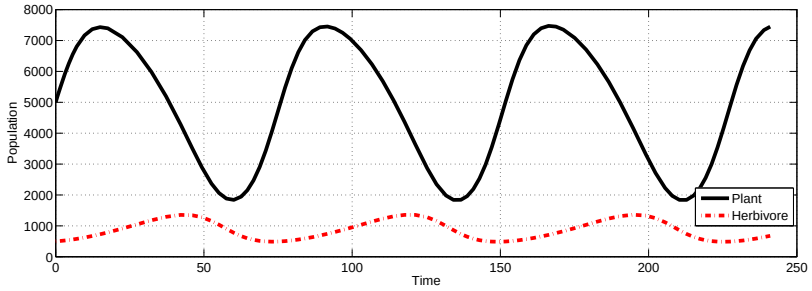

Figure 3.7: Plot of the plant herbivore interaction over time with parameters taken from the Table 3.3 with $\mathcal{R}_o > 1$, initial populations $P(0) = 5000$ and $H(0) = 500$

For the coexistence of the populations under study according to Theorem 3.2.2 (iii) for $\mathcal{R}_o > 1$ if we choose our initial population from the appropriate interval then we would obtain coexistence of both populations. Figure 3.7 is drawn using parameter values from Table 3.3 and with initial values of $P(0) = 5000$ and $H(0) = 500$. This figure shows that plant and herbivore populations coexist without attaining a specific equilibrium point.

Allee effect is am important component for coexistence. In the absence of Allee effect, that is when $h = 0$, and keeping all other parameters the same as in Figure 3.7 the plant herbivore dynamics over time is plotted in Figure 3.8.

In Figure 3.8 it can be seen that the herbivore population increases for some time but once it starts to decreases it goes to zero implying the extinction of the herbivore while the plant population extremely small for some times but regenerates and goes to the carrying capacity after a while when there is no more herbivore interference.

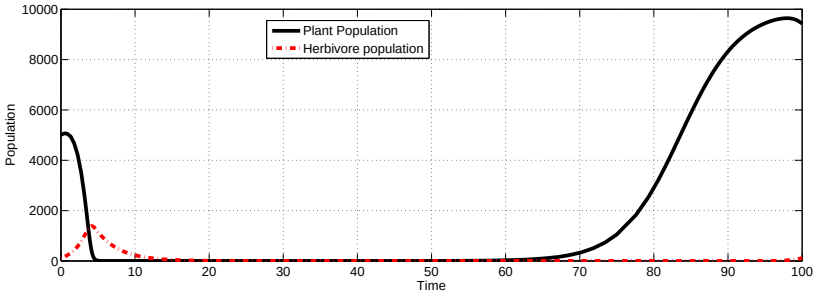

Figure 3.8: Plant Herbivore interaction in the absence of Allee effect

In summary, $\mathcal{R}_o$ represents the average number of newly born herbivore from a single mother. From the formula of $\mathcal{R}_o = \dfrac{caK}{(b+K)(d_1+\mu)}$ in this section the ratio $\frac{1}{d_1+\mu}$ may represent the average survival time for the mother herbivore whereas the term $\dfrac{caK}{(b+K)}$ represents the rate of conversion during this survival time.

If $\mathcal{R}_o < 1$ then the average number of newly emerging herbivore from a mother is less than one which eventually leads to the dying out of the herbivore population regardless of the initial size of the population. Therefore, for coexistence of the two populations first we need $\mathcal{R}_o > 1$. This implies, the average number of newly emerging herbivore from a mother must be more than one for the population to not go to the extinction. In addition, we also need to secure food availability and the chance of finding a mate for the herbivore population to continue existing. That is the reason for the appearance of the threshold value H_m which is the minimum number of required herbivores in the condition.

3.5 Summary

In this chapter a plant-herbivore model with logistic growth rate for the plant population and Holling type II functional response was assumed for the feeding interaction. For herbivore emergence rate a linear multiple of the functional response and the Allee effect were considered since herbivore population is more prone to the Allee effect than plants. Under the assumption that the mortality of herbivores depends on the availability of food source, we used density dependent variable mortality rate which is a decreasing function of the functional response instead of constant death rate which is usually considered in literature. The mortality rate is positive and bounded below since no animal can leave for ever, and we also considered the effect of human interference in terms of the harvest rate μ.

As a result, a multiple equilibrium is obtained similar to the results by Terry [Ter15] and by Verdy [Ver10], in which constant death rate was considered. That means,

two herbivore free equilibrium $(0, 0)$, which is unstable and $(K, 0)$, which is locally asymptotically stable, were found. Furthermore we defined the reproduction number $\mathcal{R}_o$, which can be interpreted as the average rate in which the herbivore population is replacing themselves. Using this threshold value conditions for existence/coexistence of the herbivore population are formulated and analyzed.

Moreover, depending on the initial plant and herbivore population being less or greater than the respective minimum values (that is availability of sufficient food and mate) and due to our newly defined density dependent death rate, we have presented specific conditions that determine the extinction of the herbivore population. Even though $\mathcal{R}_o > 1$, the plant population can grow to the carrying capacity of the environment while herbivore extinction occurs either if the initial herbivore population is less than the least number of herbivore population needed to keep the population existing in the system and the initial plant population is positive, or if the initial herbivore population is greater than the least number of herbivore population needed to keep the population existing in the system but there is no enough plant population to feed on and reproduce. That means, if the initial herbivore population is less than the least number of herbivore population needed to keep the population existing in the system with the initial plant population is positive then the herbivore population goes to extinction irrespective of the value of other parameters. This minimum number of herbivore population is due to the Allee effect. In the absence of Allee effect, $H_m = 0$ and there will be no threshold for the least number of herbivores.

In addition, it is found that if the initial herbivore population is greater than the least number of herbivore population needed to keep the population existing in the system, then the herbivore population can still go to extinction if there is no enough plant population to feed on and reproduce. Furthermore, to guarantee the non-extinction of the herbivore population we need the initial density of herbivore population to be greater than the least number of herbivore population needed to keep the population existing in the system; and the initial plant population must be above the minimum required so that there is sufficient plant population for the herbivore to feed on. This is a new addition as compared to the previous findings, for example see [Ter15].

Moreover, we have found a stable limit cycle for coexistence state inside the trapping region Σ. Numerical simulations for the main results are also discussed using parameter values in Table 3.3 and sample initial values. In this paper the sensitivity of the parameters with respect to the threshold $\mathcal{R}_o$ and with respect to each other is also discussed using the Latin hyper-cube sampling method/ partial rank correlation coefficient (LHS/PRCC) method with P-value < 0.01 and it is found that the feeding rate a has a direct influence independent of any other parameters on the reproduction

number while the harvest rate μ has an inverse influence. Furthermore, even if they appear as a product in the reproduction number, a and c are independently sensitive parameters to $\mathcal{R}_o$.

In this chapter all the parameters are assumed to be constant. However, in reality the plant growth rate r and the feeding rate of the herbivores a are dependent on the availability of food and weather conditions. Therefore, to make the analysis to be more close to the reality, It is important to consider these environmental perturbations. In the following chapter we take the environmental effect on the plant herbivore interaction into consideration. These can be done as a white noise and use a system of stochastic differential equation to study the dynamics or assuming no-autonomous system of differential equations.

The analysis and discussion of such models with the addition of environmental noise as a stochastic white noise is considered in the next chapter.

4 Stochastic Plant-Herbivore Model

4.1 Background

The basic mechanism and factors of population growth like the resources and vital rates such as, births and death rates, change non-deterministically due to randomness in environment factors [Agu+13; Mao+02; Rao13]. Most natural phenomena do not follow strictly deterministic laws but rather oscillate randomly and generally with population densities not attaining fixed values [Mal+04].

In reality, due to continuous fluctuations in the environment, for instance variation in intensity of sunlight, temperature, water level, etc, parameters involved in models are not absolute constants but fluctuate around some average value. As a result the population density never attains a fixed value as time progresses but rather exhibits continuous oscillation around some average value [Ji+11].

Recent advancements in stochastic differential equations have made it possible to introduce stochastic considerations of physical phenomena, such as a random noise in the system of differential equations or environmental fluctuations in parameter values [KK01; Mal+04; Mao+02].

Many recent authors include the idea of environmental noise and have used stochastic differential equation models. For example, [Kog14] used a stochastic model for in-host malaria parasite infection of red blood cells, [Rao13] used a stochastic Predator-Prey Model with an Allee effect on the prey population to analyze the dynamics qualitative properties such as existence of a global solution and stochastic asymptotic stability. [Agu+13] used a stochastic predator prey model with Allee effect on the prey and showed that the solutions of the model system have sample path-wise uniqueness and bounded moments. However, despite the growing interest for including environmental noise in ecology, we could not find sufficient studies that include stochasticity in plant-herbivore models.

This chapter is a sequel to the model of plant- herbivore interaction studied In chapter 3. We consider a plant-herbivore interaction model where the Allee effect on the emergence of herbivore population, a specific density dependent herbivore mortality rate function and a constant harvest rate are included. The effect generated by the random noises that can also affect the environment and consequently on

the growth rate of plants and herbivore population respectively, is studied. Due to the non-linearity of the proposed model, first, the analysis of a simplified model is carried out. Second, for the more complex model the required mathematical analysis is formulated and the model is numerically simulated. The simulation shows the existence and uniqueness of solutions is satisfied as in the simple model. The Euler-Maruyama numerical method is used to simulate the dynamics of the stochastic model for different intensities (ranging from negative to positive) of random noise.

4.2 The Proposed Model

We consider a plant-herbivore model that includes logistic growth for plants and Allee effect, density dependent death and harvest rates for the herbivore population in the presence of environmental noise given below:

$$\begin{aligned} \mathrm{d}P &= \left(rP\left(1-\frac{P}{K}\right)-\frac{aPH}{b+P}\right)\mathrm{d}t+\alpha_1 P\mathrm{d}\beta_1 \\ \mathrm{d}H &= \left(\left(\frac{caPH}{b+P}\right)\left(\frac{H}{H+h}\right)-D(F(P))H-\mu H\right)\mathrm{d}t+\alpha_2 H\mathrm{d}\beta_2 \end{aligned} \tag{4.1}$$

where $P>0, H>0$.

The first equation in (4.1) represents a plant population which grows logistically in the absence of herbivore and which eventually settles at the carrying capacity of the environment, K. This implies that the plant population in an environment with enough water and nutrients in the soil in the absence of herbivore interference can grow only as much as the land can hold. Herbivores consume plants as a food source. In this model the consumption rate (or feeding rate) of herbivore on plants is assumed to be of the Holling type II function $F(P)=\frac{aP}{b+P}$.

The second equation in (4.1) represents the average herbivore reproduction rate, at the rate $c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)$. This reflects the fact that herbivores reproduce more if the food is abundant. In addition, in the absence of plants, this rate becomes zero driving this population to extinction. Lotka-Volterra models in chapter two, ignore some processes in order to maintain simplicity while maintaining the dynamics of the underlying process. Among such processes, that are usually ignored is the Allee effect which is a basic ecological mechanism that sets lower bounds on population densities of species. It is defined as a reduced per capita population growth rate at low densities, and it has important consequences for population dynamics and persistence [Ter15]. Generally speaking a population is said to have an Allee effect, if the growth rate per capita is initially an increasing function for the low density as in Chapter 3. The Allee effect can be caused by difficulties in finding a mate, social interaction and feeding habits are the major ones. In the considered plant herbivore

model Allee effect causes a reduced (but positive) growth rate for the herbivore population. Allee effect also interacts with environment stochastically [Agu+13]. It may cause a population extinction threshold that the population must overcome in order to survive [Agu+13]. Therefore, for herbivore population to reproduce, existence of enough herbivore population is crucial and this is taken care of in the model by the term $\frac{H}{h+H}$ (where h is the Allee constant) in the rate $c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)$ which vanishes as H goes to zero. That is, individual herbivore will struggle to reproduce as the herbivore density declines and raises the possibility of failure to find a mate.

Mortality among herbivores, plants or both may be caused by various events, such as, scarcity of food, nutrients and water, drought, floods, grass/forest fires etc. Mortality for a plant-herbivore system is an event which can change the environmental condition resulting in massive loss to at least one of the populations. A mortality event may be unique (such as fire) or periodic (such as floods in the rainy season). The other effect of mortality events on the plant-herbivore system is an event that can cause herbivore to die out while plants do not as in Chapter 3. In this case, since there will be no or minimum influence from the herbivore, the plant population can then increase to the carrying capacity of the environment and allow the land to recover.

Considering a constant death rate for the herbivore population is tantamount to ignoring the fact that mortality of herbivores is dependent on the availability of a food source. Nevertheless the life process of herbivores is fueled by feeding on plants, such that if a herbivore finds little or no food to consume, it has higher chance to starvation and death. In difficult conditions, the mortality rate of the herbivore population could reach its maximum value, say $d_2 < 1$, as it was assumed in Chapter 3.

On the other hand, if there is a sufficient food source for the herbivore to feed on, starvation will not occur, and herbivore mortality in such a case should be a decreasing function of consumption $\frac{aP}{b+P}$ whose rate of change is very small when the feeding rate is sufficiently large. Moreover, regardless of particular factors affecting herbivore mortality no animal lives forever, so it makes sense to assume that herbivore mortality is always bounded below by some positive constant, say $d_1 > 0$ as in Chapter 3. In this chapter, the death rate of herbivores is taken to be a non constant function of the plant density, by taking into account the idea that herbivore survival mainly depends on availability of food.

Therefore, for $0 < d_1 < d_2 < 1$, we took the density dependent death rate function as in chapter 3,

$$D(F(P)) \quad = \quad \frac{d_2K(1+d_1-d_2)(b+P)+P(b+K)(d_2-d_1)(d_2-1)}{K(1+d_1-d_2)(b+P)+(d_2-d_1)(b+K)P}.$$

With this definition, the term $D(F(P)) := D(F)$ satisfies a condition that $0 < d_1 \leq D(F) \leq d_2 < 1$.

Moreover, $D(F)$ is a positive decreasing function of $F(P)$ as equation (3.6) can be described as $D(F) = d_2 - \dfrac{F}{g+F}$, for some parameter $g = \dfrac{aK(1-d_2+d_1)}{(d_2-d_1)(b+K)} > 0$. In addition if $d_1 = d_2$, then $D(F)$ reduces to a constant d_2 which is the value considered in the paper by [Ter15].

As in the first chapter, we consider the non-negative constant μ to be the harvest rate on the herbivore population. It represents the human interference on the system by removing herbivores from the system by hunting or selling.

The analysis of this proposed model system (4.1) is not straight forward due to the non-linearity of the variables. Therefore instead of analyzing the model (4.1), we first consider a more simplified version to appreciate the dynamics and how stochasticity can alter the results of chapter 3.

4.3 Simplified Model

Let r be the growth rate of the plant population, a the consumption rate of the herbivores on plant population, c the conversion rate of what is consumed to a new born herbivore, and μ the removal rate of herbivores from the system. Consider a stochastic plant-herbivore model given by

$$\begin{aligned} \mathrm{d}P &= (rP - aPH)\,\mathrm{d}t + \alpha_1 P \mathrm{d}\beta_1 \\ \mathrm{d}H &= (caPH - \mu H)\,\mathrm{d}t + \alpha_2 H \mathrm{d}\beta_2 \end{aligned} \tag{4.2}$$

where $P \geq 0, H \geq 0$

$$\beta(t) = (\beta_1(t), \beta_2(t) \setminus t \geq 0)$$

is a two dimensional Brownian motion and parameters $(\alpha_1, \alpha_2) \in \mathbb{R}^2_+$ represent the intensity of the perturbation.

For simplicity of notation let us set $x_t = (x_1(t), x_2(t))^T = (P, H)^T$ and write the system (4.2) in matrix form as

$$\mathrm{d}x_t = f(x_t)\mathrm{d}t + \alpha(x_t)\mathrm{d}\beta, \tag{4.3}$$

where

$$f(x_t) = \begin{pmatrix} rx_1 - ax_1x_2 \\ cax_1x_2 - \mu x_2 \end{pmatrix} = \begin{pmatrix} rP - aPH \\ caPH - \mu H \end{pmatrix},$$

with

$$\alpha(x_t^\epsilon) = \begin{pmatrix} \alpha_1 x_1 & 0 \\ 0 & \alpha_2 x_2 \end{pmatrix} = \begin{pmatrix} \alpha_1 P & 0 \\ 0 & \alpha_2 H \end{pmatrix}.$$

Here the solution of (4.3) is not unique due to the nonlinear term x_1x_2. We want to define under what conditions on $f(x_t)$ the matrix equation (4.3) has unique solutions.

4.3.1 Existence and uniqueness of solution for the simplified model

Let $\Omega = \{(x_1, x_2) = (P, H) \in \mathbb{R}^2_+ \setminus P \geq 0, H \geq 0\}$ be a positive region under study and consider the system (4.3) with initial values

$$x^o = (x_1^o, x_2^o) = (P_o, H_o) \in \mathbb{R}^2_+. \tag{4.4}$$

For technical reasons we modify the system (4.3) by replacing in $f(x_t)$ the nonlinear terms ax_1x_2 by the linearly bounded term $ag_\epsilon(x_1)g_\epsilon(x_2)$ where

$$g_\epsilon(s) = \begin{cases} 0 & \text{if } s < 0 \\ s & \text{if } 0 < s < \frac{1}{\epsilon} \\ \frac{1}{\epsilon} & \text{if } s > \frac{1}{\epsilon} \end{cases}$$

and ϵ is an arbitrary small positive number. We shall denote the modified $f(x_t)$ in system (4.3) by $f^\epsilon(x_t^\epsilon)$ and consider the following stochastic system

$$\mathrm{d}x_t^\epsilon = f^\epsilon(x_t^\epsilon)\mathrm{d}t + \alpha(x_t^\epsilon)\mathrm{d}\beta. \tag{4.5}$$

Consider the following lemma:

Lemma 4.3.1 (Positivity region)**.** *For any finite $T > 0$ the solution x_t^ϵ of the system* (4.5) *with initial condition* (4.4) *remains in $\Omega = \mathbb{R}^2_+$ for all $t < T \wedge \tau_\epsilon$, (where $T \wedge \tau_\epsilon$ denotes the smaller between T and τ_ϵ), so that the components x_t^ϵ satisfy:*

$$x_{t,i}^\epsilon > 0 \qquad \textit{if} \qquad t < T \wedge \tau_\epsilon \qquad \textit{for} \qquad i = 1, 2.$$

Furthermore, the probability that $\tau_\epsilon < T$ is below the value $C_o\tau_\epsilon$, where C_o is a constant independent of ϵ.

proof:- We want to prove first that a non-negative solution does not exit the positive domain Ω. To this end we introduce a Lyapunov type function

$$v(x_1, x_2) = x_1 - k_1 \log x_1 + x_2 - k_2 \log x_2 \qquad x_1, x_2 \geq 0 \tag{4.6}$$

where k_1, k_2 are constants to be determined. Consider the differential

$$d(x_t^\epsilon) = f(x_t^\epsilon), \tag{4.7}$$

If $t < T \wedge \tau_\epsilon$, x_t^ϵ satisfies the function $v(x_{t,T\wedge\tau_\epsilon})$ and we use Ito formula on v to obtain:

$$\begin{aligned}
dv &= \frac{\partial v}{\partial t}dt + \frac{\partial v}{\partial x_i}dx_i + \frac{1}{2}\frac{\partial^2 v}{\partial x_i^2}(dx_i)^2 \\
&= 0 + \frac{\partial v}{\partial x_1}dx_1 + \frac{\partial v}{\partial x_2}dx_2 + \frac{1}{2}\frac{\partial^2 v}{\partial x_1^2}(dx_1)^2 + \frac{1}{2}\frac{\partial^2 v}{\partial x_2^2}(dx_2)^2 \\
&= \left(1 - \frac{k_1}{x_1}\right)\left[(rx_1 - ax_1x_2)\,dt + \alpha_1 x_1 d\beta_1\right] + \left(1 - \frac{k_2}{x_2}\right)\left[(cax_1x_2 - \mu x_2)\,dt + \alpha_2 x_2 d\beta_2\right] \\
&\quad + \frac{1}{2x_1^2}k_1\left[((rx_1 - ax_1x_2))\,dt + \alpha_1 x_1 d\beta_1\right]^2 + \frac{1}{2x_2^2}k_2\left[(cax_1x_2 - \mu x_2)\,dt + \alpha_2 x_2 d\beta_2\right]^2 \\
&= (rx_1 - ax_1x_2 - rk_1 + ak_1x_2)dt + \alpha_1 x_1 d\beta_1 - \alpha_1 k_1 d\beta_1 + (cax_1x_2 - \mu x_2 - cax_1k_2 + \mu k_2)dt \\
&\quad + \alpha_2 x_2 d\beta_2 - \alpha_2 k_2 d\beta_2 + \frac{1}{2}k_1\alpha_1^2 dt + \frac{1}{2}k_2\alpha_2^2 dt.
\end{aligned} \tag{4.8}$$

choose $k_1 = \frac{\mu}{a}$ and $k_2 = \frac{r}{ca}$ so that the linear terms in x_1 and x_2 becomes equal to zero. Then

$$dv = \left[\left(cax_1x_2 - ax_1x_2 - rk_1 + \mu k_2 + \frac{1}{2}k_1\alpha_1^2 + \frac{1}{2}k_2\alpha_2^2\right)dt + \alpha_1(x_1 - k_1)d\beta_1 + \alpha_2(x_2 - k_2)d\beta_2\right] \tag{4.9}$$

In (4.9), let $M = cax_1x_2 + \mu k_2 + \dfrac{k_1\alpha_1^2}{2} + \dfrac{k_2\alpha_2^2}{2}$ and define

$$Lv = Mdt - ax_1x_2 - rk_1dt. \tag{4.10}$$

Then, equation (4.9) can be written as:

$$\begin{aligned}
dv &= Lv + \alpha_1(x_1 - k_1)d\beta_1 + \alpha_2(x_2 - k_2)d\beta_2 \\
&\leq Mdt + c\alpha_1(x_1 - k_1)d\beta_1 + \alpha_2(x_2 - k_2)d\beta_2.
\end{aligned} \tag{4.11}$$

Integrating (4.11) from 0 to $T \wedge \tau_\epsilon$, we get

$$\int_0^{T\wedge\tau_\epsilon} dv \leq \int_0^{T\wedge\tau_\epsilon} Mdt + \int_0^{T\wedge\tau_\epsilon} \alpha_1(x_1 - k_1)d\beta_1 + \alpha_2(x_2 - k_2)d\beta_2.$$

Taking the expectation we have

$$E\left[v(x^{\epsilon}_{T\wedge\tau_{\epsilon}})\right] \leq E\left[v(x^{o}) + MT \wedge \tau_{\epsilon}\right]. \tag{4.12}$$

If a path x^{ϵ}_{t} is such that it exists in $\mathbb{R}^2_+$ at $T \wedge \tau_{\epsilon}$ then by the definition of

$$v := x_1 - k_1 \log x_1 + x_2 - k_2 \log x_2,$$

v becomes ∞ at the exit point.

In view of (4.12) this probability is zero hence x^{ϵ}_{t} does not exit $\mathbb{R}^2_+$. That is, its components are all in $\mathbb{R}^2_+$. In case x^{ϵ}_{t} may exits the set $\mathbb{R}^2_+$ then the $g_{\epsilon}(s)$ term goes from s to $\dfrac{1}{\epsilon}$.

On the other hand, If x^{ϵ}_{t} exits the set $\mathbb{R}^2_+$ then in this case we define a set

$$S_{\frac{1}{\epsilon}} = \{\max_{1\leq i\leq 2} x_i < \frac{1}{\epsilon}\}.$$

In view of (4.12) the probability of this happening is less than $C_o\tau_{\epsilon}$ where C_o is a constant independent of x^{o}. □

Theorem 4.3.1. *The system* (4.3) *with an initial value given in* (4.4) *has a unique solution* $x_t \in \Omega$ *for all* $t > 0$, *and the variance satisfies* $E\left[|x_t|^2\right] \leq Ce^{\eta t}$ *for* $t > 0$, *where* C *and* η *are constants.*

Proof:- The plant population P and the Herbivore population H cannot grow up to infinity due to lack of space (cannot exceed the carrying capacity of the environment) or aging respectively. Therefore we can say that they are bounded.

We denote by τ_{ϵ} the exit time of x^{ϵ}_{t} from the domain $\mathbb{R}^2_+ \cap \left\{\max\limits_{1\leq i\leq 2} x_i < \dfrac{1}{\epsilon}\right\}$ and we may assume that this domain contains the initial point x^{o}. To show that the system (4.5) posses a non-negative solution for $t > 0$, we use Lemma 4.3.1 and show Lipschitz continuity as follows:

Case 1:- $P = x_1 < 0$ and/or $H = x_2 < 0$ then we will have

$$g_{\epsilon}(x_1)g_{\epsilon}(x_2) = 0$$

and also in the case where $P = x_1 > \frac{1}{\epsilon}$ and $H = x_2 > \frac{1}{\epsilon}$ we have

$$g_{\epsilon}(x_1)g_{\epsilon}(x_2) = g_{\epsilon}(\overline{x}_1)g_{\epsilon}(\overline{x}_2) = \frac{1}{\epsilon^2}$$

In either cases, we have

$$\begin{aligned}|f_t^\epsilon(x) - f_t^\epsilon(\overline{x})| &= \left| \begin{pmatrix} rP - ag_\epsilon(P)g_\epsilon(H) \\ cag_\epsilon(P)g_\epsilon(H) - \mu H \end{pmatrix} - \begin{pmatrix} r\overline{P} - ag_\epsilon(\overline{P})g_\epsilon(\overline{H}) \\ cag_\epsilon(\overline{P})g_\epsilon(\overline{H}) - \mu\overline{H} \end{pmatrix} \right| \\ &= \left| \begin{pmatrix} r(P-\overline{P}) \\ -\mu(H-\overline{H}) \end{pmatrix} \right| \\ &= \left| \begin{pmatrix} r & 0 \\ 0 & -\mu \end{pmatrix} \begin{pmatrix} (P-\overline{P}) \\ (H-\overline{H}) \end{pmatrix} \right| \\ &\leq \left\| \begin{pmatrix} r & 0 \\ 0 & -\mu \end{pmatrix} \right\|_F \left| \begin{pmatrix} (P-\overline{P}) \\ (H-\overline{H}) \end{pmatrix} \right| \\ &= \sqrt{r^2+\mu^2}|x-\overline{x}|.\end{aligned}$$

Similarly **Case 2:-** $0 < P < \frac{1}{\epsilon}$ and $H > \frac{1}{\epsilon}$ we have

$$|f_t^\epsilon(x) - f_t^\epsilon(\overline{x})| \leq \sqrt{r^2+\mu^2+2\frac{a}{\epsilon}\left(\frac{a}{\epsilon}-r\right)}|x-\overline{x}|.$$

Case 3:- $0 < H < \frac{1}{\epsilon}$ and $P > \frac{1}{\epsilon}$ we have

$$|f_t^\epsilon(x) - f_t^\epsilon(\overline{x})| \leq \sqrt{r^2+\mu^2+2\frac{a}{\epsilon}\left(\frac{a}{\epsilon}-\mu\right)}|x-\overline{x}|.$$

Case 4:- $0 < P < \frac{1}{\epsilon}$ and $0 < H < \frac{1}{\epsilon}$ using

$$PH - \overline{PH} = (P-\overline{P})\left(\frac{H+\overline{H}}{2}\right) + \left(\frac{P+\overline{P}}{2}\right)(H-\overline{H}),$$

we have

$$\begin{aligned}&|f_t^\epsilon(x) - f_t^\epsilon(\overline{x})| \\ &\leq \sqrt{r^2+\mu^2+\frac{a^2}{2}(1+c^2)((H+\overline{H})^2+(P+\overline{P})^2) - a\left(r(H+\overline{H})+c\mu(P+\overline{P})\right)}|x-\overline{x}|.\end{aligned}$$

To sum up the last four cases, let

$$\begin{aligned}K_\epsilon = \max\Bigg\{&\sqrt{r^2+\mu^2}, \sqrt{r^2+\mu^2+2\frac{a}{\epsilon}\left(\frac{a}{\epsilon}-r\right)}, \sqrt{r^2+\mu^2+2\frac{a}{\epsilon}\left(\frac{a}{\epsilon}-\mu\right)}, \\ &\sqrt{r^2+\mu^2+\frac{a^2}{2}(1+c^2)((H+\overline{H})^2+(P+\overline{P})^2) - a\left(r(H+\overline{H})+c\mu(P+\overline{P})\right)}\Bigg\}\end{aligned}$$

it follows that

$$|f_t^\epsilon(x) - f_t^\epsilon(\overline{x})| \leq K_\epsilon|x-\overline{x}|, \tag{4.13}$$

and for the matrix α of equation system (4.5) we have

$$\alpha(x) - \alpha(\overline{x}) = \left\| \begin{pmatrix} \alpha_1 P & 0 \\ 0 & \alpha_2 H \end{pmatrix} - \begin{pmatrix} \alpha_1 \overline{P} & 0 \\ 0 & \alpha_2 \overline{H} \end{pmatrix} \right\|_F \leq K \left| \begin{pmatrix} (P - \overline{P}) \\ (H - \overline{H}) \end{pmatrix} \right|$$

as $0 \leq K|x - \overline{x}|$ for any positive constant K. Here $x, \overline{x} \in \mathbb{R}^2$ where K_ϵ, K are constants. This implies the functions $f^\epsilon(x_t^\epsilon)$ and $\alpha(x_t^\epsilon)$ satisfy Global Lipschitz continuity conditions.
Hence by Theorem 1.1 in chapter 5 of [Fri75] for any initial value $x_o^\epsilon = x^o \in \mathbb{R}_+^2$ there exists a unique solution x_t^o for system (4.5). Now we define a new variable let

$$y_t = c x_{t,1}^\epsilon + x_{t,2}^\epsilon \tag{4.14}$$

and recall by Lemma 4.3.1, that $x_{t,i}^\epsilon > 0$ for $t < T \wedge \tau_\epsilon$ we have the system

$$\begin{aligned} \dot{P} &= rP - aPH := \mathrm{d}x_{t,1}^\epsilon \\ \dot{H} &= caPH - \mu H := \mathrm{d}x_{t,2}^\epsilon \end{aligned}$$

Using (4.14) and its derivative,

$$\begin{aligned} y_t &= c x_{t,1}^\epsilon + x_{t,2}^\epsilon \\ \mathrm{d}y_{t\wedge\tau_\epsilon} &= c\mathrm{d}x_{t\wedge\tau_\epsilon,1}^\epsilon + \mathrm{d}x_{t\wedge\tau_\epsilon,2}^\epsilon \\ &= crx_{t,1}^\epsilon \mathrm{d}t - cax_{t,1}^\epsilon x_{t,2}^\epsilon \mathrm{d}t + cax_{t,1}^\epsilon x_{t,2}^\epsilon \mathrm{d}t - \mu x_{t,2}^\epsilon \mathrm{d}t + c\alpha_1 x_{t,1}^\epsilon \mathrm{d}\beta_{t,1} + \alpha_2 x_{t,2}^\epsilon \mathrm{d}\beta_{t,2} \\ &= crx_{t,1}^\epsilon \mathrm{d}t - \mu x_{t,2}^\epsilon \mathrm{d}t + c\alpha_1 x_{t,1}^\epsilon \mathrm{d}\beta_{t,1} + \alpha_2 x_{t,2}^\epsilon \mathrm{d}\beta_{t,2} \\ &= Ay_{t\wedge\tau_\epsilon} \mathrm{d}t + c\alpha_1 x_{t,1}^\epsilon \mathrm{d}\beta_{t,1} + \alpha_2 x_{t,2}^\epsilon \mathrm{d}\beta_{t,2} \end{aligned}$$

where A is a constant vector then using the relation

$$\begin{aligned} dy &= Ay\mathrm{d}t + c\alpha_1 y\mathrm{d}\beta_{t,1} + \alpha_2 y\mathrm{d}\beta_{t,2} \\ \frac{dy}{y} &= A\mathrm{d}t + c\alpha_1 \mathrm{d}\beta_{t,1} + \alpha_2 \mathrm{d}\beta_{t,2} \\ \ln y - \ln y_0 &= c\alpha_1 \int_0^t \mathrm{d}\beta_{s,1} + \alpha_2 \int_0^t \mathrm{d}\beta_{s,2} \\ \ln \frac{y_t}{y_0} &= At + c\alpha_1 \int_0^t \mathrm{d}\beta_{s,1} + \alpha_2 \int_0^t \mathrm{d}\beta_{s,2} \\ y_t &= y_0 e^{At} \exp\left\{ c\alpha_1 \int_0^t \mathrm{d}\beta_{s,1} + \alpha_2 \int_0^t \mathrm{d}\beta_{s,2} \right\} \end{aligned}$$

We then calculate the mean $E[y_t]$ and the variance $E\left[(y_t - E[y_t])^2\right]$ from here

$$\begin{aligned} E[y_t] &= E\left[y_0 e^{At} \exp\left\{c\alpha_1 \int_0^t \mathrm{d}\beta_{s,1} + \alpha_2 \int_0^t \mathrm{d}\beta_{s,2}\right\}\right] \\ &= y_0 e^{At} \exp\left\{c\alpha_1 \int_0^t E[\mathrm{d}\beta_{s,1}] + \alpha_2 \int_0^t E\left[\mathrm{d}\beta_{s,2}\right\}\right] \\ E[y_t] &= y_0 e^{At}. \end{aligned} \tag{4.15}$$

and

$$\begin{aligned} \mathrm{Var}(y_t) &= E\left[(y_t - E[y_t])^2\right] \\ &= E\left[(y_0 e^{At} \exp\left\{c\alpha_1 \int_0^t \mathrm{d}\beta_{s,1} + \alpha_2 \int_0^t \mathrm{d}\beta_{s,2}\right\} - y_0 e^{At})^2\right] \\ &= E\left[y_0^2 e^{2At} (\exp\left\{c\alpha_1 \int_0^t \mathrm{d}\beta_{s,1} + \alpha_2 \int_0^t \mathrm{d}\beta_{s,2}\right\} - 1)^2\right] \\ &= y_0^2 e^{2At}\left[\exp\left\{c\alpha_1 \int_0^t E[\mathrm{d}\beta_{s,1}] + \alpha_2 \int_0^t E[\mathrm{d}\beta_{s,2}]\right\} - 1\right]^2 \\ &= y_0^2 e^{2At}\left[e^{2(c\alpha_1 \int_0^t E[\mathrm{d}\beta_{s,1}] + \alpha_2 \int_0^t E[\mathrm{d}\beta_{s,2}])} - 2e^{(c\alpha_1 \int_0^t E[\mathrm{d}\beta_{s,1}] + \alpha_2 \int_0^t E[\mathrm{d}\beta_{s,2}])} + 1\right] \\ &\leq y_0^2 e^{2At} := Ce^{\eta t}. \end{aligned} \tag{4.16}$$

Thus, we can write the variance as

$$E\left[(y_t - E[y_t])^2\right] \leq Ce^{\eta t}. \tag{4.17}$$

This implies uniqueness of solution because we can take the right hand side as small as possible by choosing appropriate values for C and η. This completes the proof of Theorem 4.3.1 □

4.4 Numerical simulation for the simplified model

As more complex mathematical models of the real world phenomena become available, many areas of science are relying on quantitative analysis. Due to the fact that most of these complex models are not amenable to exact solutions, we use numerical simulations to analyze them.

In this section we show the long term dynamics of the deterministic and stochastic versions of the simplified model given in (4.2). We apply the Euler-Maruyama method [Hig11] to the system and we obtain

$$\begin{aligned} P(i+1) &= P(i) + (rP(i) - aP(i)H(i))\mathrm{d}t + \alpha_1 P(i)N(0,1)\sqrt{\mathrm{d}t} \\ H(i+1) &= H(i) + (caP(i)H(i) - muH(i))\mathrm{d}t + \alpha_2 H(i)N(0,1)\sqrt{\mathrm{d}t} \end{aligned} \tag{4.18}$$

for $i = 1 \ldots n$,with $n = 10000$. $N(0, 1)$ is a normal distribution of random numbers with mean zero and a standard deviation 1. We will use the parameter values from the following table.

Table 4.1: Table of parameters for the simplified model

Parameter	Description	Value	Source
r	Growth rate of plant population	0.25	[Ter15]
a	Consumption rate (feeding rate) of herbivores on plant biomass	0.025	assumed
c	conversion rate of what is consumed in to a new born herbivore	0.25	[Ter15]
μ	death rate of herbivore	0.3	assumed

To understand the evolution in time of plant and herbivore population or the dynamics of both plant and herbivore populations over time, we plotted the solutions of the model (4.2) in time using the parameter values given in Table 4.1 with initial populations $P(0) = 40$ and $H(0) = 15$.

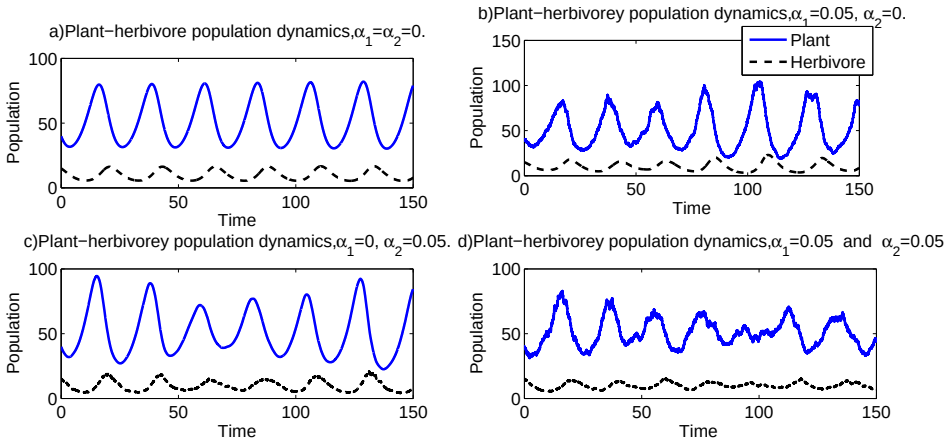

Figure 4.1: The dynamics of plant and herbivore population with a) absence of noise, b) in absence of noise β_2 and with noise β_1 of intensity $\alpha_1 = 0.05$ c) in absence of noise β_1 and with noise β_2 of intensity $\alpha_2 = 0.05$ and finally d) with noises β_1 and β_2 of intensity $\alpha_1 = 0.05$ and $\alpha_2 = 0.05$.

Figure 4.1a) shows the oscillatory behavior of both populations. The peaks for the herbivore population are delayed and follow an increase in the plant population. This is observed among wildlife which will reproduce at the beginning of the rainy season in anticipation of plant growth to increase the survival rate of their young ones. Figure 4.1a) suggests a scenario where the amplitude of peaks remains the same throughout which is unrealistic. Figure 4.1d) shows what can happen in the presence of both noises. The populations may not exhibit characteristics as predicted by the deterministic solution (Figure 4.1a)). This result has implications regarding harvesting from wildlife populations. A deterministic result could suggest higher harvesting levels which could result in the herbivore being driven to extinction.

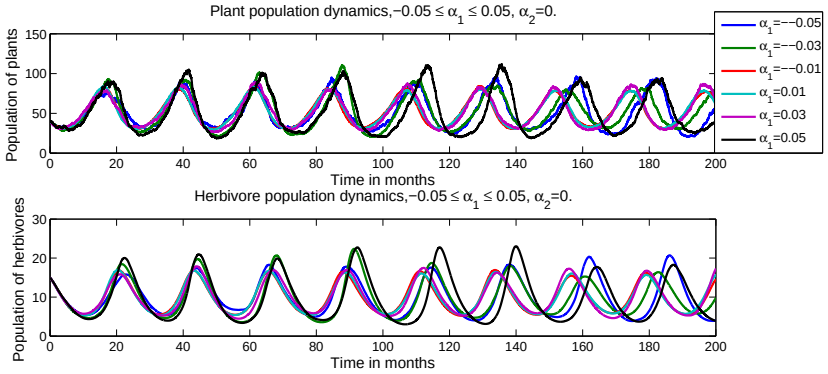

Figure 4.2: Plant population dynamics and herbivore population dynamics in case of noise β_1 with intensity of α_1 varying from -0.05 to 0.05 and $\alpha_2 = 0$ i.e assuming no β_2.

Figure 4.2) shows the effect of assuming deterministic herbivore population on a variable (stochastic) food source. There doesn't seem to be much change in the peak levels as the noise intensity increases.

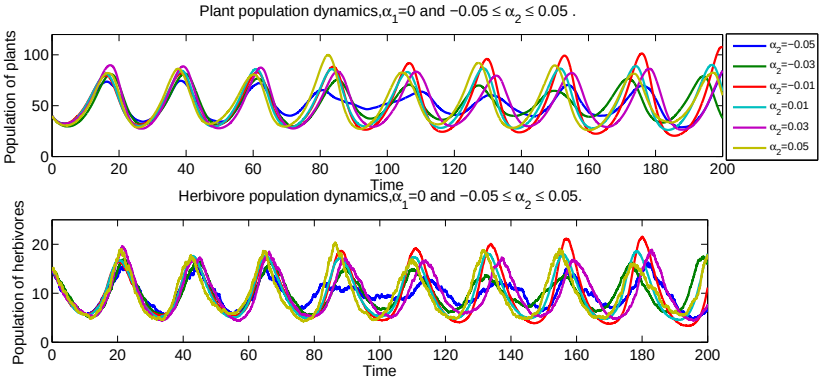

Figure 4.3: Plant population dynamics and herbivore population dynamics with noise β_2 of intensity α_2 varying from -0.05 to 0.05 and $\alpha_1 = 0$ i.e assuming no β_1.

On the other hand Figure 4.3 a) shows that varying the herbivore population randomly but maintaining a deterministic food source can result in significant changes in both plant and herbivore populations.

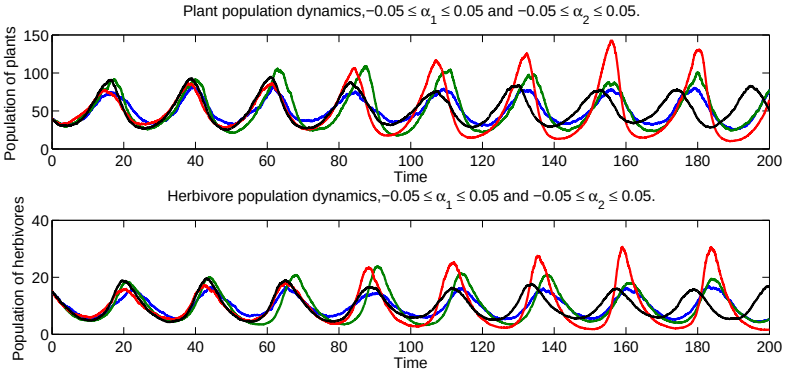

Figure 4.4: Plant population dynamics with noises β_1 and β_2 of intensity α_1 varying from -0.05 to 0.05 and α_2 from -0.05 to 0.05.

Figure 4.4) shows that varying the noise intensity for both plant and herbivore does not result in significant changes in the peak levels or in the variance of the populations in the early stages but there are noticeable changes as time increases. We conclude that changing the noise level of the food source results in significant changes in both species. This result has implications regarding the quality of the environment. Rapidly changing environments due to soil erosion, deforestation, drought etc will have serious consequences on the herbivore population. Figure 4.5) shows how the stability of the two species is altered, especially when $\alpha_1 \neq 0$

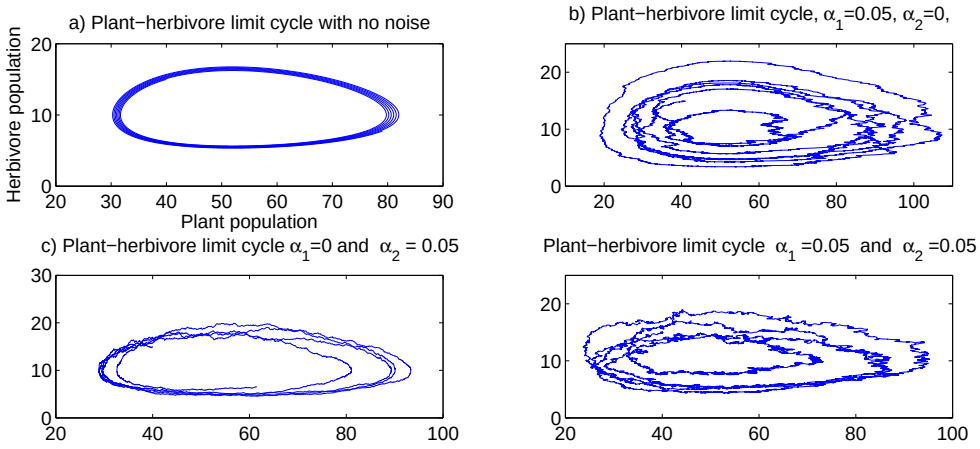

Figure 4.5: Phase portrait of plant-herbivore population model (4.2) with and without noises.

4.5 Analysis of the proposed model

Let us now consider a more realistic model that is proposed in system (4.1) which is given by:

$$\mathrm{d}P = A(P,H) := \left(rP\left(1-\frac{P}{K}\right) - \frac{aPH}{b+P}\right)\mathrm{d}t + \alpha_1 P \mathrm{d}\beta_1$$
$$\mathrm{d}H = B(P,H) := \left(\left(\frac{caPH}{b+P}\right)\left(\frac{H}{H+h}\right) - D(F(P))H - \mu H\right)\mathrm{d}t + \alpha_2 H \mathrm{d}\beta_2$$

We can write this system in matrix form. For simplicity of notation let us write

$$U_t = (U_1(t), U_2(t))^T = (P(t), H(t))^T,$$
$$\mathrm{d}U_t = \mathbf{X}(U_t)dt + \mathbf{Y}(U_t)\mathrm{d}\beta(t) \tag{4.19}$$

with initial conditions

$$U_0 = \begin{pmatrix} P(0) \\ H(0) \end{pmatrix} = \begin{pmatrix} P_0 \\ H_0 \end{pmatrix}. \tag{4.20}$$

Then we can now consider model system (4.1) as an Ito stochastic differential system of equation of type $dU = \mathbf{X}(t, U(t))dt + \mathbf{Y}d\beta(t)$ where

$$U(t) = \begin{pmatrix} P(t) \\ H(t) \end{pmatrix}, \qquad \beta(t) = \begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix},$$

$$\mathbf{X} = \begin{pmatrix} rP\left(1 - \frac{P}{K}\right) - \frac{aPH}{b+P} \\ \left(\frac{caPH}{b+P}\right)\left(\frac{H}{H+h}\right) - D(F(P))H - \mu H \end{pmatrix}, \qquad \mathbf{Y} = \begin{pmatrix} \alpha_1 P & 0 \\ 0 & \alpha_2 H \end{pmatrix},$$

and U_t is the solution, and is an Ito process. $\mathbf{X}$ is a slowly varying drift coefficient and $\mathbf{Y}$ is a rapidly varying continuous random diffusion coefficient.

The effect of the random noise in the model system (4.19) becomes stronger in a sufficiently small neighborhood of the curves $A^{-1}(0) \cup B^{-1}(0)$. In fact in these neighborhoods, by Ito's rule the dynamical system behaves like

$$z(t) \approx Z_0 \exp(\alpha\beta(t)),$$

where Z stands for Por H and $\beta(t)$ is the corresponding Brownian motion with intensity α.

Let $\Omega = \{(P, H) \in \mathbb{R}^2_+ \setminus P \geq 0, H \geq 0\}$ be a positive region under study and consider the system (4.19) with initial values (4.20).

For technical reasons we modify the system (4.19) by replacing in $X(U_t)$ the nonlinear terms $a\frac{P}{b+P}H$ by the linearly bounded term $ag_\epsilon(P)g_\epsilon(H)$ where

$$g_\epsilon(s) = \begin{cases} 0 & \text{if } s < 0 \\ s & \text{if } 0 < s < \frac{1}{\epsilon} \\ \frac{1}{\epsilon} & \text{if } s > \frac{1}{\epsilon} \end{cases}$$

and ϵ is an arbitrary small positive number. We shall denote the modified $X(U_t)$ in system (4.19) by $X^\epsilon(U_t^\epsilon)$ and consider the following stochastic system

$$\mathrm{d}U_t^\epsilon = X^\epsilon(U_t^\epsilon)\mathrm{d}t + \mathbf{Y}(U_t^\epsilon)\mathrm{d}\beta. \tag{4.21}$$

Consider the following lemma:

Lemma 4.5.1 (Region of Positivity). *For any finite $T > 0$ the solution U_t^ϵ of the system* (4.19) *with initial condition* (4.20) *remains in $\Omega = \mathbb{R}^2_+$ for all $t < T \wedge \tau_\epsilon$,(where $T \wedge \tau_\epsilon$ denotes the smaller between T and τ_ϵ), so that the components U_t^ϵ satisfy:*

$$U_{t,i}^\epsilon > 0 \qquad \textit{if} \qquad t < T \wedge \tau_\epsilon \qquad \textit{for} \qquad i = 1, 2.$$

Furthermore, the probability that $\tau_\epsilon < T$ is below the value $C_o\tau_\epsilon$, where C_o is a constant independent of ϵ.

proof:- We want to prove first that a non-negative solution does not exit the positive domain Ω. To this end we introduce a Lyapunov type function

$$v(P,H) = P - k_1 \log P + H - k_2 \log H, \qquad P,H \geq 0, \tag{4.22}$$

where k_1, k_2 are constants to be determined. Consider the differential

$$\mathrm{d}(U_t^\epsilon) = X(U_t^\epsilon). \tag{4.23}$$

If $t < T \wedge \tau_\epsilon$, U_t^ϵ satisfies the function $v(U_{t,T\wedge\tau_\epsilon})$ and we use Ito formula on v to obtain :

$$\begin{aligned}
\mathrm{d}v &= \frac{\partial v}{\partial t}\mathrm{d}t + \frac{\partial v}{\partial P}\mathrm{d}P + \frac{\partial v}{\partial H}\mathrm{d}H + \frac{1}{2}\frac{\partial^2 v}{\partial P^2}(\mathrm{d}P)^2 + \frac{1}{2}\frac{\partial^2 v}{\partial H^2}(\mathrm{d}H)^2 \\
&= \left(1-\frac{k_1}{P}\right)\mathrm{d}P + \frac{k_1}{2P^2}(\mathrm{d}P)^2 + \left(1-\frac{k_2}{H}\right)\mathrm{d}H + \frac{k_2}{2H^2}(\mathrm{d}H)^2 \\
&= \left(1-\frac{k_1}{P}\right)\left[\left(rP - r\frac{P^2}{K} - \frac{aPH}{b+P}\right)dt + \alpha_1 P d\beta_1\right] + \frac{k_1}{2P^2}\left[\left(rP - r\frac{P^2}{K} - \frac{aPH}{b+P}\right)dt + \alpha_1 P d\beta_1\right]^2 \\
&\quad + \left(1-\frac{k_2}{H}\right)\left[\left(c\frac{aPH}{b+P}\frac{H}{h+H} - D(F(P)H - \mu H\right)dt + \alpha_2 H d\beta_2\right] \\
&\quad + \frac{k_2}{2H^2}\left[\left(c\frac{aPH}{b+P}\frac{H}{h+H} - D(F(P)H - \mu H\right)dt + \alpha_2 H d\beta_2\right]^2 \\
&= \left(1-\frac{k_1}{P}\right)\left(rP\left(1-\frac{P}{K}\right) - \frac{aPH}{b+P}\right)dt + \alpha_1 P\left(1-\frac{k_1}{P}\right)d\beta_1 + \frac{k_1}{2P^2}\alpha_1^2 P^2 dt + \frac{k_2}{2H^2}\alpha_2^2 H^2 dt \\
&\quad + \left(1-\frac{k_2}{H}\right)\left(c\frac{aPH}{b+P}\frac{H}{h+H} - D(F(P)H - \mu H\right)dt + \alpha_2 H\left(1-\frac{k_2}{H}\right)d\beta_2 \\
dv &= \left[rP\left(1-\frac{P}{K}\right) - \frac{aPH}{b+P} - rk_1\left(1-\frac{P}{K}\right) + \frac{ak_1 H}{b+P} + \frac{caPH^2}{(b+P)(h+H)} - D(F(P))H - \mu H\right. \\
&\quad \left. - \frac{cak_2 PH}{(b+P)(h+H)} + k_2 D(F(P)) + k_2\mu + \frac{1}{2}k_1\alpha_1^2 + \frac{1}{2}k_2\alpha_2^2\right]dt + \alpha_1(P-k_1)d\beta_1 + \alpha_2(H-k_2)d\beta_2
\end{aligned}$$

$$\begin{aligned}
dv &= \left[2P - r\frac{P^2}{K} - rK_1 - \frac{aPH}{b+P} + \frac{ak_1 H}{b+P} + \frac{caPH^2}{(b+P)(h+H)} - \frac{cak_2 PH}{(b+P)(h+H)}\right. \\
&\quad \left. - D(F(P))H + k_2 D(F(P)) - \mu H + k_2\mu + \frac{1}{2}k_1\alpha_1^2 + \frac{1}{2}k_2\alpha_2^2\right]dt \\
&\quad + \alpha_1(P-k_1)d\beta_1 + \alpha_2(H-k_2)d\beta_2 \\
&= \left[-\frac{r}{k_1}\left(P^2 - 2k_1 P + k_1^2\right) - \frac{aPH}{b+P} + \frac{ak_1 H}{b+P} + \frac{caPH^2}{(b+P)(h+H)} - \frac{cak_2 PH}{(b+P)(h+H)}\right. \\
&\quad \left. - D(F(P))H + k_2 D(F(P)) - \mu H + k_2\mu + \frac{1}{2}k_1\alpha_1^2 + \frac{1}{2}k_2\alpha_2^2\right]dt \\
&\quad + \alpha_1(P-k_1)d\beta_1 + \alpha_2(H-k_2)d\beta_2 \qquad (4.24) \\
dv &\leq \left[\frac{1}{2}k_1\alpha_1^2 + \frac{1}{2}k_2\alpha_2^2 - \frac{r}{k_1}(P-k_1)^2\right]dt + \alpha_1(P-k_1)d\beta_1 + \alpha_2(H-k_2)d\beta_2 \qquad (4.25)
\end{aligned}$$

In (4.25), let $M = \frac{k_1\alpha_1^2}{2} + \frac{k_2\alpha_2^2}{2}$ and then

$$dv \leq Mdt + \alpha_1(P-k_1)d\beta_1 + \alpha_2(H-k_2)d\beta_2. \tag{4.26}$$

Integrating (4.26) from 0 to $T \wedge \tau_\epsilon$, we get

$$\int_0^{T\wedge\tau_\epsilon} dv \leq \int_0^{T\wedge\tau_\epsilon} Mdt + \int_0^{T\wedge\tau_\epsilon} \alpha_1(P-k_1)d\beta_1 + \alpha_2(H-k_2)d\beta_2.$$

Taking the expectation we have

$$E\left[v(U^\epsilon_{T\wedge\tau_\epsilon})\right] \leq E\left[v(U^o) + M(T\wedge\tau_\epsilon)\right]. \tag{4.27}$$

If a path U_t^ϵ is such that it exists in $\mathbb{R}^2_+$ at $T \wedge \tau_\epsilon$ then by the definition of

$$v := P - k_1 \log P + H - k_2 \log H,$$

v becomes ∞ at the exit point.

In view of (4.27) this probability is zero hence U_t^ϵ does not exit $\mathbb{R}^2_+$. That is, its components are all in $\mathbb{R}^2_+$. In case U_t^ϵ may exits the set $\mathbb{R}^2_+$ then the $g_\epsilon(s)$ term goes from s to $\frac{1}{\epsilon}$.

On the other hand, If U_t^ϵ exits the set $\mathbb{R}^2_+$ then in this case we define a set

$$S_{\frac{1}{\epsilon}} = \left\{ \max_{1\leq i\leq 2} U_i < \frac{1}{\epsilon} \right\}.$$

In view of (4.27) the probability of this happening is less than $C_o\tau_\epsilon$ where C_o is a constant independent of U^o. □

Remark 4.5.1. *In order for a stochastic differential equation to have a unique global solution for any given initial value, the coefficients of the equation are generally required to satisfy the linear growth condition and local lipchitz conditions[Rao13].*

The following Lemma shows system (**??**) in the form of system equation (4.19) satisfies the Lipchitz continuity condition.

Lemma 4.5.2. *For the vector field* $\boldsymbol{X}$ *and the matrix* $\boldsymbol{Y}$ *in equation* (4.19) *there exists constants* $\lambda, \nu > 0$ *such that*

$$\langle \boldsymbol{a}-\boldsymbol{b}, \boldsymbol{X}(\boldsymbol{a}) - \boldsymbol{X}(\boldsymbol{b})\rangle \leq \lambda|\boldsymbol{a}-\boldsymbol{b}|^2 \qquad \forall \boldsymbol{a},\boldsymbol{b} \in \Omega \tag{4.28}$$

$$|\boldsymbol{Y}(\boldsymbol{a}) - \boldsymbol{Y}(\boldsymbol{b})|^2 \leq \nu|\boldsymbol{a}-\boldsymbol{b}|^2 \tag{4.29}$$

Proof:- Let $\mathbf{a} = (P_1, H_1), \mathbf{b} = (P_2, H_2) \in \Omega$ and suppose initially the case $P_1 > P_2$. Then, since $A(P, H) \leq rP$ for all $(P, H) \in \Omega$ we have

$$\begin{aligned} (P_1 - P_2)A(P_1, H_1) &\leq (P_1 - P_2)rP_1 \quad (4.30) \\ (P_1 - P_2)A(P_2, H_2) &\leq (P_1 - P_2)rP_2 \quad (4.31) \end{aligned}$$

Subtracting equation (4.31) from equation (4.30) gives

$$(P_1 - P_2)\left[A(P_1, H_1) - A(P_2, H_2)\right] \leq r(P_1 - P_2)^2 \quad (4.32)$$

Similarly for the case $P_1 \leq P_2$. Then, since $A(P, H) \leq rP$ for all $(P, H) \in \Omega$ we have

$$\begin{aligned} (P_2 - P_1)A(P_2, H_2) &\leq (P_2 - P_1)rP_2 \\ (P_2 - P_1)A(P_1, H_1) &\leq (P_2 - P_1)rP_1 \end{aligned}$$

Subtracting these equation gives (4.32). Analogously, since $B(P, H) \leq caH$ for all $(P, H) \in \Omega$ (for $\frac{P}{b+P} < 1$ and $\frac{H}{h+H} < 1$) we have for the case $H_1 > H_2$.

$$\begin{aligned} (H_1 - H_2)B(P_1, H_1) &\leq (H_1 - H_2)caH_1 \\ (H_1 - H_2)B(P_2, H_2) &\leq (H_1 - H_2)caH_2 \end{aligned}$$

Subtracting equation (4.33) from equation (4.33) gives

$$(H_1 - H_2)\left[B(P_1, H_1) - B(P_2, H_2)\right] \leq ca(H_1 - H_2)^2 \quad (4.33)$$

Adding (4.32) and (4.33) we get inequality (4.28) with $\lambda = \max\{r, ca\}$. Finally, inequality (4.29) is immediate because the terms of $\mathbf{Y}$ are constants and so globally Lipschitz functions $\square$.

Once we have checked the Lipschitz continuity of the functions we can show existence and uniqueness of solution for such system (4.19) using the following Lemma.

Lemma 4.5.3. *For any initial conditions $X_0 \in \Omega$ system* (4.19) *has a unique solution $X(t)$ such that $X(0) = X_0$*

Proof:-Consider the mapping given by

$$\mathbb{T} : \mathbb{R}^2 \longrightarrow \mathbb{R}^2 \text{ such that } (P, H) \longrightarrow (P - P_0, H - H_0) \quad (4.34)$$

with $(P_o, H_0) \in \Omega$

Let $\tilde{\mathbf{X}}$ be a new vector field $C^\infty-$conjugated to F. Notice that $\mathbb{T}$ translates the point (P_0, H_0) onto the origin of the new coordinates and the equivalent vector field satisfies

$\tilde{\mathbf{X}}(P,H) = \mathbf{X}(P+P_0, H+H_0)$ for all $(P,H) \in \tilde{\Omega} := \mathbb{T}^{-1}(\Omega)$

If $0 := (0,0) \in \tilde{\Omega}$, then from Lemma 4.5.2 for all $\mathbf{a} \in \tilde{\Omega}$ we have

$$\begin{aligned} \langle \tilde{\mathbf{X}}(\mathbf{a}), \mathbf{a} \rangle &= \langle \tilde{\mathbf{X}}(\mathbf{a}) - \tilde{\mathbf{X}}(0), \mathbf{a} \rangle + \langle \tilde{\mathbf{X}}(0), \mathbf{a} \rangle & (4.35) \\ &\leq \lambda |\mathbf{a}|^2 + |\tilde{\mathbf{X}}(0)||\mathbf{a}| & (4.36) \\ &\leq \frac{1}{2}|\tilde{\mathbf{X}}(0)|^2 + \left(\lambda + \frac{1}{2}\right)|\mathbf{a}|^2 & (4.37) \end{aligned}$$

and similarly $|\tilde{\mathbf{Y}}(\mathbf{a})|^2 \leq 2|\tilde{\mathbf{Y}}(\mathbf{0})|^2 + 2|\tilde{\mathbf{Y}}(\mathbf{a}) - \tilde{\mathbf{Y}}(\mathbf{0})|^2 \leq 2|\tilde{\mathbf{Y}}(\mathbf{0})|^2 + 2\nu|\mathbf{a}|^2$ where $\tilde{\mathbf{Y}}(P,H) = \mathbf{Y}(P+P_0, H+H_0)$, with $(P,H) \in \tilde{\Omega}$.

Hence

$$\max\{\langle \tilde{\mathbf{X}}(\mathbf{a}), \mathbf{a} \rangle, |\tilde{\mathbf{Y}}(\mathbf{a})|^2\} \leq \alpha + \beta|\mathbf{a}|^2, \qquad \forall \mathbf{a} \in \tilde{\Omega}, \tag{4.38}$$

where $\alpha = \max\{\frac{1}{2}|\tilde{\mathbf{X}}(0)|^2, 2|\tilde{\mathbf{Y}}(\mathbf{0})|^2\}$ and $\beta = \max\{\left(\lambda + \frac{1}{2}\right), 2\nu\}$. In this way, the existence and uniqueness of solutions of system (4.19) follow directly from Lemma 2 in [Agu+13] the $C^{\infty}-$ conjugacy (4.34) and the inequality (4.38). $\square$.

Let us recall Theorem 1.1 in the 5th chapter of the book by Friedman [Fri75]. It is stated as follows

Suppose $\mathbf{X}(U,t), \mathbf{Y}(U,t)$ are measurable in $(u,t) \in \mathbb{R}^2 \times [0,T]$ and

$$\begin{aligned} |\mathbf{X}(U,t) - \mathbf{X}(\overline{U},t)| \leq K_*|U-\overline{U}|, \qquad |\mathbf{Y}(U,t) - \mathbf{Y}(\overline{U},t)| \leq K_*|U-\overline{U}|, \\ |\mathbf{X}(U,t)| \leq K(1+|U|), \qquad |\mathbf{Y}(U,t)| \leq K(1+|U|) \end{aligned}$$

where K_*, K are constants. Let U_0 be any 2-dimensional random vector such that $E|U_0|^2 < \infty$. Then there exists a unique solution of (4.19).

Once we showed the Lipschitz continuity, Lemma 4.3.1 and Theorem 4.3.1 can also be extended to the model system (4.19). Hence by Theorem 4.5 existence and uniqueness of global positive solution in a bounded positive region follow. Finally we have the main Theorem:

Theorem 4.5.1. *The system* (4.19) *with an initial value given as in* (4.20) *has a unique solution* $x_t \in \Omega$ *for all* $t > 0$, *and the variance satisfy* $E\left[|x_t|^2\right] \leq Ce^{\eta t}$ *for* $t > 0$, *where* C *and* η *are constants.*

Proof:- The proof follows from Lipschitz continuity Lemma 4.5.2,and the results of Lemma 4.3.1 and Theorem 4.3.1.

4.6 Numerical Simulations for the proposed model

As an extension of what is done for the simplified model in Section 4, we use the Euler-Maruyama method [Hig11; Hig+02] on our model system (**??**). The procedure follows by setting

$$\begin{aligned} P(i+1) &= P(i) + \left(rP(i)\left(1 - \frac{P(i)}{K}\right) - \frac{aP(i)H(i)}{P(i)+b} \right) \mathrm{d}t + \alpha_1 P(i) N(0,1)\sqrt{\mathrm{d}t} \\ H(i+1) &= H(i) + \left(H(i)ca\left(\frac{P(i)}{(P(i)+b)}\frac{H(i)}{H(i)+h}\right) - H(i)D(F(P(i))) \right. \\ &\quad \left. -\mu H(i)\right) \mathrm{d}t + \alpha_2 H(i) N(0,1)\sqrt{\mathrm{d}t} \end{aligned} \tag{4.39}$$

Where $D(F(P(i))) = \dfrac{(d_2 K(1+d_1-d_2)(b+P(i)) + P(i)(b+K)(d_2-d_1)(d_2-1)}{(K(1+d_1-d_2)(b+P(i)) + (d_2-d_1)(b+K)P(i))}$ for $i = 1 \ldots n$.

For the simulation purpose we took and $n = 10000$. Here, $N(0,1)$ is a normal distribution of random numbers with mean zero and standard deviation 1, and the Brownian motion is assumed to take the values $d\beta_t = N(0,1)\sqrt{dt}$.

In this section, we show some numerical simulations for model system (**??**) using parameter values from Table 3.3.

Table 4.2: Table of parameters for the proposed model and their meaning

Parameter	Description	Value	Source
r	plant growth rate	0.25	Assumed
a	consumption/feeding rate of herbivores	0.75	Assumed
K	carrying capacity(for plant population)	10000	[Ter15]
b	half saturation constant of herbivore feeding on the plant biomass	1100	[Ter15]
c	efficiency of converting what is eaten in to a newborn herbivore	0.25	[Ter15]
h	Allee constant	40	Assumed
d_1	minimum herbivore death rate	0.1	[Ter15]
d_2	maximum herbivore death rate	0.3	[Ter15]
μ	harvest rate	0.025	Assumed

We first simulate the population dynamics over time series without noise (deterministic). Next the dynamics with noise β_1 affecting only plant population with intensity $\alpha_1 \neq 0$. This noise could be because of the effect of plant disease which has no influence on herbivore. Then the simulation is done for the dynamics including noise β_2 affecting only herbivore population with intensity $\alpha_2 \neq 0$. Such a noise could be

due to the effect of animal disease which has no influence on plants. Finally it is simulated for the case where the noises $\beta_1$and β_2 affecting both plant and herbivore populations with intensities $\alpha_1 \neq 0, \alpha_2 \neq 0$,respectively. The noise of this kind could be due to environmental changes like drought or fluid which affects both plant and herbivore populations.

The parameter values for the plots is used from Table 5.1 and initial population values $P(0) = 5000$ for plants and $H(0) = 155$ for herbivores are assumed.

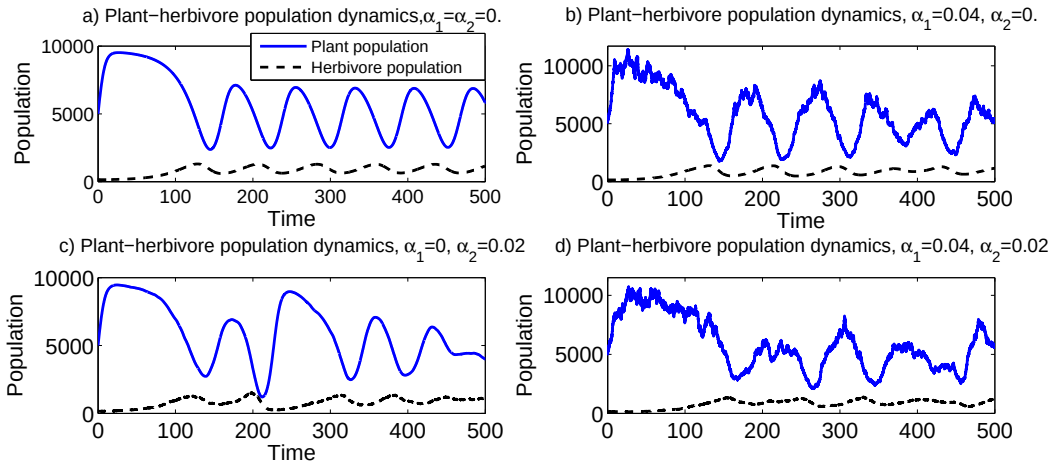

Figure 4.6: Plant herbivore dynamics over time with a) no noise b) positive noise intensity $\alpha_1 = 0.04$ and $\alpha_2 = 0$, c) $\alpha_1 = 0$ and positive noise intensity $\alpha_2 = 0.02$ and d) both positive noise intensities $\alpha_1 = 0.04$ and $\alpha_2 = 0.02$.

Figure 4.6 a) displays different characteristics from Figure 4.1a) since we are now assuming logistic growth for Plants and Holling type II feeding response for herbivores, Allee effect on herbivore birth rate and the plant density dependent death rate and harvest rate for herbivores. The difference is visible on the amplitude peaks and on the phase angles. This means that real life phenomenon is different from the simplified model. Even though they have differences they also show similar characteristics in that they have constant period of oscillation. Figure 4.6 b) displays similar characteristics as Figure 4.1 b) where adding a noise with intensity on the plant population affects the whole population dynamics after sometime. This means the effect on plant biomass result in changing the dynamics after sometime which means the damage is observed at a later date.

On the other hand, Figure 4.6 c) displays similar characteristics as Figure 4.1 c) where adding a noise with intensity on the herbivore population affects the whole population dynamics. This means the effect on herbivore biomass result in changing the dynamics immediately. But now we can see that varying both noises Figure 4.6d) has less dramatic effects as that displayed by the simpler model Figure 4.1d). This is

due to (1) Allee effect which decreases the conversion rate of food source into new herbivores (2) plant density dependent death rate of herbivores, (3) Hollying type II feeding response of herbivores.

Figure 4.6) displays the same characteristics as Figure 4.1a) but now we can see that varying both noises (Figure 4.6d) has less dramatic effects as that displayed by the simpler model Figure (4.1d). This is due to the inclusion of Hollying type II feeding rate of herbivores and the Allee effect which takes into account finding a mate to reproduce that affect conversion rate of food source into new herbivores see equation (4.1).

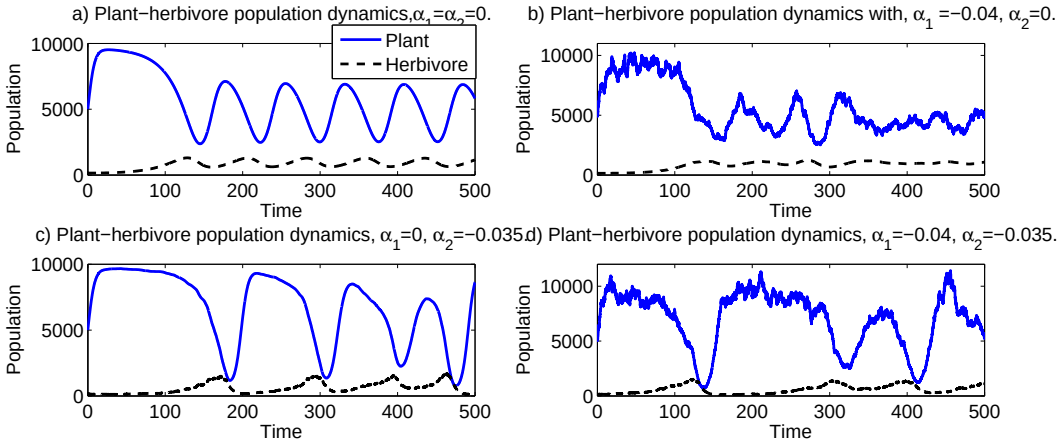

Figure 4.7: Plant herbivore dynamics over time with a)no noise b)negative noise intensity $\alpha_1 = -0.04$ and $\alpha_2 = 0$, c)$\alpha_1 = 0$ and negative noise intensity $\alpha_2 = -0.035$ and d)both negative noise intensities $\alpha_1 = -0.04$ and $\alpha_2 = -0.035$.

Figure 4.7) shows a departure of the stochastic solution from the deterministic solution in terms of peak levels and periods between peaks. The irregularity of the periods in the food source makes it difficult to accurately quantify the herbivore population levels. This result would have serious implications regarding conservation of both plant and herbivore populations.

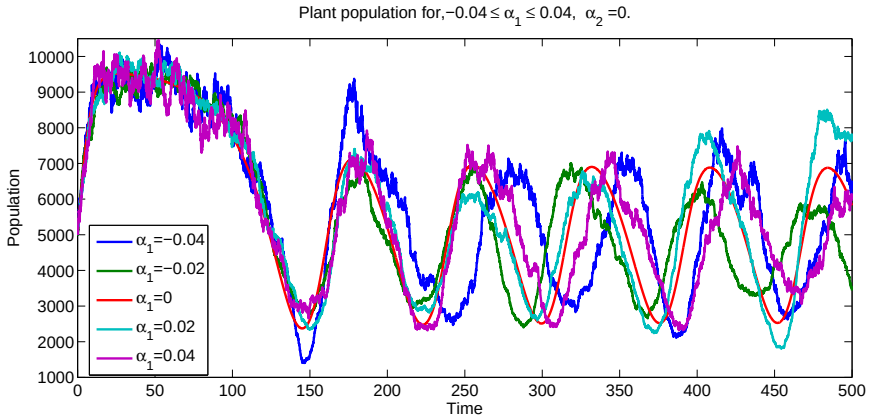

Figure 4.8: Plant population dynamics in time with noise only β_1 on the rate of plant.

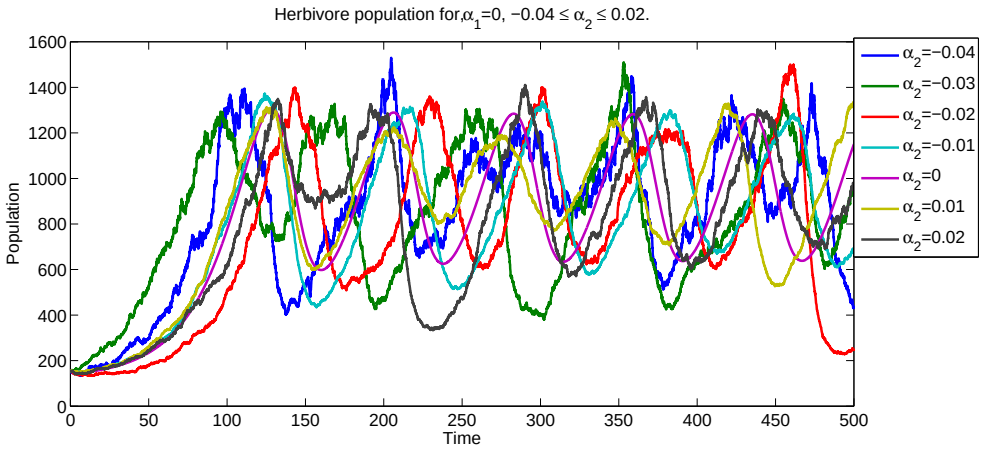

Figure 4.9: Herbivore population dynamics in time with noise β_2 on the rate of herbivores.

Figures 4.8) and 4.9) when compared to Figures 4.2) and 4.3) for the simpler model show significantly different results especially in the herbivore population. The Phase portraits, (Figure 4.10)) show how the stability of the solution is altered when the stochastic intensities are varied. Figure 4.10a), when there is no noise it predicts stable coexistence between the two species. Figure 4.10d), when there are noise terms, predicts an unstable coexistence. Figures 4.11) and 4.12) demonstrate the Allee effect. Clearly, the Allee effect has the potential to smooth out the stochasticities when both α_1 and α_2 are varied although the phase portraits in Figures 4.13) and 4.14) show that in the presence of the Allee effect the solution is gradually degraded (Figure 4.13d).

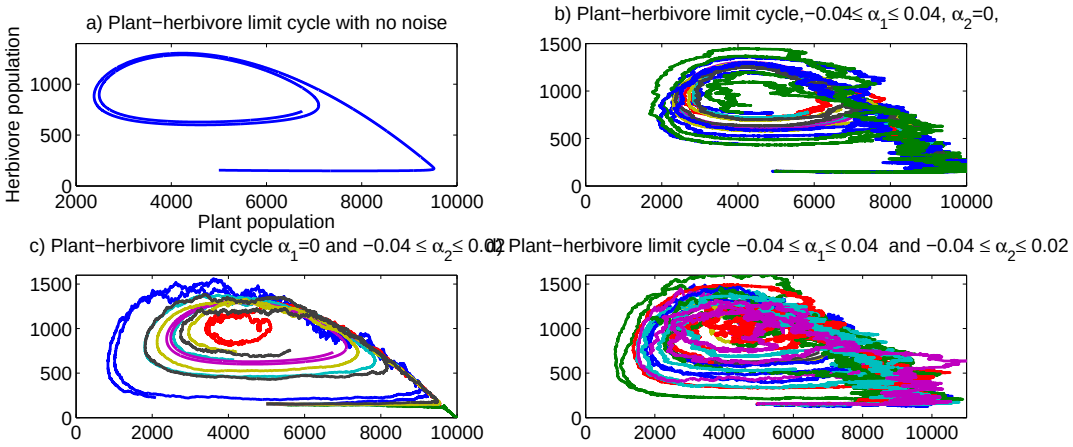

Figure 4.10: Phase portrait of plant herbivore population a) without noise, b) with noise β_1 only c) with noise β_2 only and d) with noise β_1 and β_2

4.7 Allee effect on the Dynamics of Stochastic Plant-Herbivore Model

In the current model (4.1), the individual effect and the combined effect effect of noises on a plant herbivore interaction model with Alle effect and without Allee effect is plotted in Figure 4.11 and Figure 4.12 respectively.

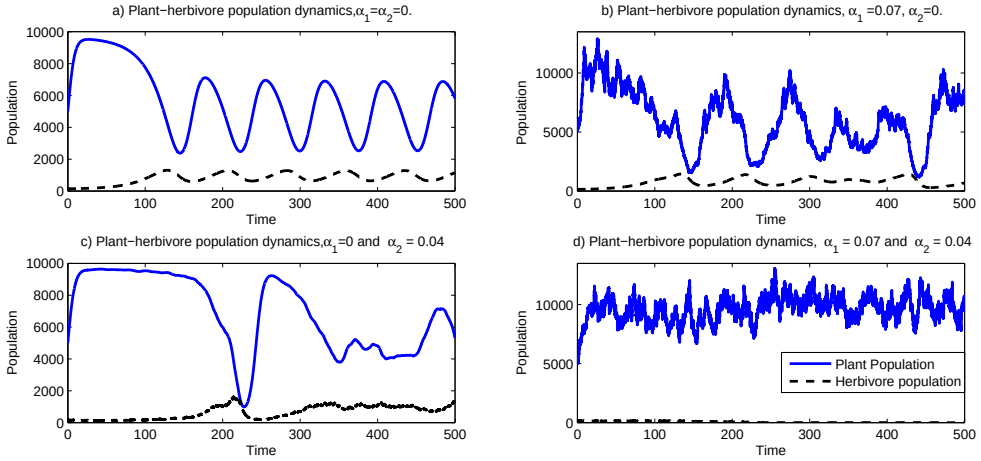

Figure 4.11: Population dynamics with Allee effect and positive noise intensities.

In the case we consider we can see that there is a possibility of extinction of herbivore population.

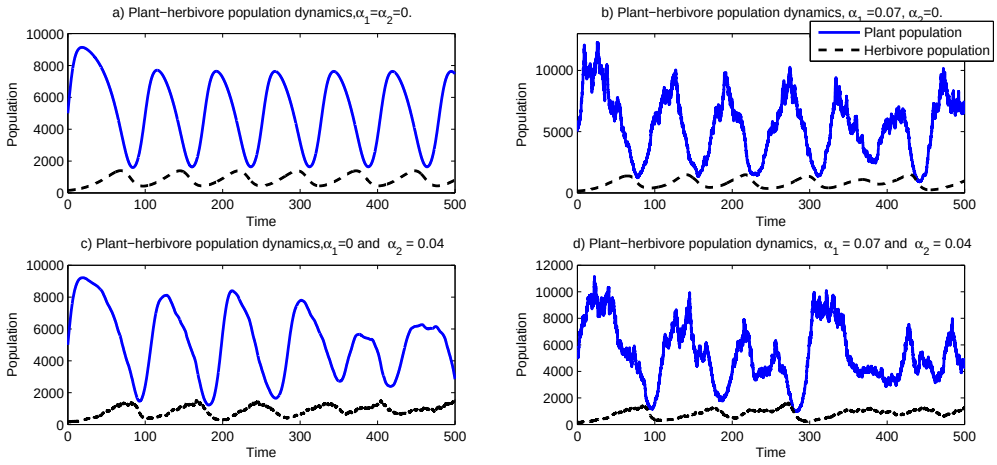

Figure 4.12: Population dynamics without Allee effect and positive noise intensities.

The phase portrait of plants against herbivores in a dynamics with and without Allee effect is plotted in Figure 4.13 and Figure 4.14.

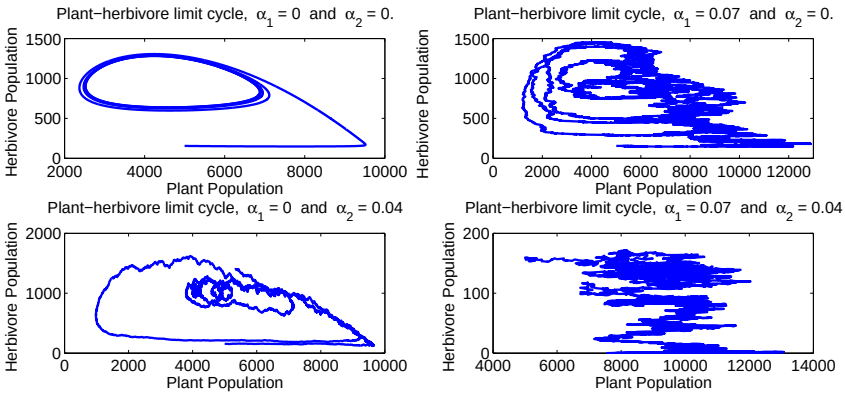

Figure 4.13: Phase portrait for plant herbivore interaction with Alee effect and Positive noise intensities.

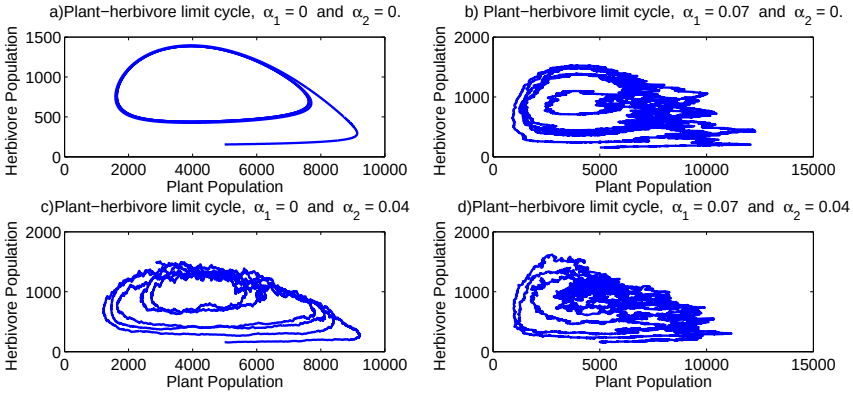

Figure 4.14: Phase portrait for plant herbivore interaction without Allee effect and positive noise intensities.

The comparison of the behavior of the dynamics for the deterministic model (ODE) system and for the Stochastic model (SDE) system can also be seen from Table 4.3

Table 4.3: Table of comparison between the deterministic and stochastic dynamics

	Deterministic model	Stochastic model
stability of herbivore free equilibrium	stable	stability degraded by diffusion term
dynamics with Allee	coexistence limit cycle	possibility of herbivore extinction
phase dynamics	smooth	non-smooth path
stability	stable coexistence	unstable coexistence due to noise
harvesting	suggest higher harvesting leads to herbivore extinction	suggest lower harvesting

4.8 Discussion and Summary

In this study we extended the model in Chapter 3 to include the randomness of the environment by including noise terms. We analyzed the effect of noise in the model (4.2) for two different scenarios when environmental noises β_1 and β_2 influence the rate of change of plant and herbivore populations, respectively. First, we analyzed the simplified model (4.2) for positivity, existence and uniqueness of solution in a bounded set and then extended the idea to the proposed model (4.1). We obtained an insight into the complicated effect and consequence of the stochastic noise on the behavior of both populations. Adding noises of different intensities the stability of the deterministic state becomes quasi stable around the deterministic steady state. By increasing the noise intensity of the food source β_1 the effect on both species is slow and is only significant in the long run. The effect is manifested more visibly in the plant population than the herbivore population. On the other hand, increasing the noise term in the herbivore population, β_2, results in an immediate and more significant change in both species. The effect of both noises β_1 and β_2 can significantly affect the co-existence of both species including the possibility of extinction of the herbivore population. Therefore ignoring environmental noises would affect the quality of the environment, this in turn could lead to extinction of both population to smaller number of the herbivore population such that they cannot overcome the Allee effect. This results have implications for game parks where the park area is confined but the herbivore population is allowed to increase and culling takes place at irregular intervals. The herbivore population could affect the quality of the park. We can give two examples in support of our model revelations. First, the elephant population is increasing rapidly in the Chobe National Park, North Botswana, due to introduction of water supplementation and better than average rainfall in certain years resulting in good vegetation which have provided a conducive environment for the elephant population. However, the increase in the population has fluctuated depending on food availability. On the other hand, the antelope number has been reduced due to frequent droughts, increased predation by lions and loss of habitat due to human invasion. The provision of artificial water-points within the antelope's range also resulted in extensive habitat degradation and competition with other herbivores.

In the next chapter, instead of a system of stochastic differential equation we consider only the growth rate of plants and the feeding rate of herbivores to be periodic function of temperature and rainfall. Thus we analyze a deterministic plant herbivore interaction model with periodic plant growth and herbivore feeding rate coefficients.

5 Plant-herbivore Model with Periodic Coefficient

5.1 General Model with Time Dependent Growth and Feeding Rates $r(t)$ and $a(t)$.

Based on interaction of plants and herbivores, we make the following assumptions

A_1 Environmental changes and weather factors (for example temperature, rainfall etc) have many effects on the growth of plants. Therefore, we assume that the growth rate of the plant $r(t)$ is governed by the logistic equation in which the coefficients are periodic functions on account of seasonal effects.

A_2 Based on assumption A_1 due to the periodic growth rate of plants we assume that the feeding or consumption rate of herbivores on plants $a(t)$ is also a periodic and continuous function of time.

Under these assumptions let us consider the following predator-prey model for the plant herbivore interaction.

$$\begin{aligned} \frac{dP}{dt} &= P\left[r(t) - \frac{r(t)}{K}P - \frac{a(t)}{b+P}H\right] \\ \frac{dH}{dt} &= H\left[-\mu + c\left(\frac{a(t)P}{b+P}\right)\left(\frac{H}{h+H}\right) - D(F(P))\right] \\ P(0) &\geq 0, \qquad H(0) \geq 0. \end{aligned} \tag{5.1}$$

Here, $P(t)$- represents plant biomass, $H(t)$- represents Herbivore biomass, $r(t)$ represents the intrinsic growth rate for plant population and $a(t)$- represents herbivore feeding rate on plant population. Assume that these functions are continuous,and periodic functions of time. The other parameters are positive constants independent of time representing carrying capacity of the environment K, half saturation constant of herbivores b, conversion rate of the consumed plant into herbivore c, Allee constant h and harvest rate μ. We take these parameters as constants because the effect of temperature and rainfall on them is very insignificant to the level that it can be ignored.

The feeding rate have the expression $F(P) = \dfrac{a(t)P}{b+P}$ which is a Holling type II functional response. In the second equation of the model system (5.1) the term $D(F(P))$ represents the density dependent death rate which is a decreasing function of the feeding response and is bounded by the minimum and the maximum death rates d_1 and d_2 as shown in Chapter 3. It is given by:

$$D(F(P)) = \frac{d_2K(1+d_1-d_2)(b+P)+P(b+K)(d_2-d_1)(d_2-1)}{K(1+d_1-d_2)(b+P)+(d_2-d_1)(b+K)P}$$

$D(F(0)) = d_2$ and $D(F(K)) = d_1$ hence we say $d_1 < D(F(P)) \leq d_2$ as in Chapter 3. This plant density dependent herbivore death rate also contain in it the idea that since it depends on the availability of plants the herbivore dynamics follows the plant dynamics hence it will never reach its own carrying capacity.

Moreover, herbivore population reproduces sexually hence existence of enough number of herbivore population is crucial for them to reproduce. This fact is taken care of by the term $\frac{H}{h+H}$ in the model, where h is the Allee constant, due to the fact that $cF(P)\left(\frac{H}{h+H}\right)$ vanishes as H goes to extinction [Ter15]. That is, individual female herbivore will struggle to reproduce as the herbivore density falls to zero, either because they cannot find a mate or because of a greater risk of inbreeding.

5.1.1 Well Posedness

For the system to be mathematically and biologically meaningful, we need to work on positive quantities for population or biomass variables. Hence, we define the domain space by $\Omega = \{(P,H) \in \mathbb{R}^2_+ P \geq 0, H \geq 0\}$ where the population of both plants and herbivores takes values only from the first quadrant.

Lemma 5.1.1. *$int(\Omega) = \{(P,H)|P>0, H>0\}$ is the positive invariant set of the system* (5.1).

Proof: For a time period of ω we have

$$\begin{aligned} P(t) &= P(0)\exp\left\{\int_0^\omega \left(r(t)\left[1-\frac{P}{K}\right]-\frac{a(t)}{b+P}H\right)dt\right\} \\ H(t) &= H(0)\exp\left\{\int_0^\omega \left(c\left(\frac{a(t)P}{b+P}\right)\left(\frac{H}{h+H}\right)-D(F(P))-\mu\right)dt\right\} \end{aligned}$$

Clearly, exponential functions are always positive. Therefore if $P(0) > 0$ and $H(0) > 0$ are positive we have the whole dynamics in the first quadrant. That is, $P(t) > 0, H(t) > 0$ □

Positivity indicates population survival on the system, and boundedness may be interpreted as a natural restriction to growth rates as a consequence of limited

resources. We have shown in the Lemma 5.1.1 that all solutions for (5.1) that start with positive initial quantity satisfies positivity.

To find the lower and upper bounds of the plant population let us consider the system in the absence of herbivore population. Then, we obtain

$$\frac{dP}{dt} = r(t)P\left(1 - \frac{P}{K}\right) = P\left(r(t) - \frac{r(t)}{K}P\right). \tag{5.2}$$

Equating the above rate to zero and solving for P we get $P = 0$ and $P = K$. Hence the plant population is bounded $0 < P \leq K$. The boundedness of the herbivore population follows same procedure as in Chapter3 That is, the model is mathematically and biologically well posed. So, $int(\Omega) = \{(P, H)|P > 0, H > 0\}$ is the positive invariant set of the system (5.1).

5.1.2 Existence of Periodic Solution and Stability

Lemma 5.1.2. *If $r(t) \geq 0$ for all $t \in \mathbb{R}$ and $\int_0^\omega r(t)dt > 0$ then equation (5.2) has a unique positive ω-periodic solution $P^*(t)$ which is globally asymptotically stable. That is, $P(t) - P^*(t) \longrightarrow 0$ as $t \longrightarrow \infty$ for any positive solution $P(t)$ of equation (5.2).*

Proof:- by the condition $\int_0^\omega r(t)dt > 0$ there exist constants $s > u > 0$ such that

$$\int_0^\omega \left(r(t) - \frac{r(t)}{K}s\right)dt < 0, \text{ and } \int_0^\omega \left(r(t) - \frac{r(t)}{K}u\right)dt > 0. \tag{5.3}$$

For any solution $P(t)$ of equation (5.2) with $P(0) > 0$ we have two cases,
Case 1:- Let $P(t) \geq s$ for all $t \geq 0$. Then, since from Equation (5.2) we have

$$P(t) = P(0)\exp\int_0^\omega \left(r(t) - \frac{r(t)}{K}P(t)\right)dt \tag{5.4}$$

$$\leq P(0)\exp\int_0^\omega \left(r(t) - \frac{r(t)}{K}s\right)dt \text{for all } t \geq 0 \tag{5.5}$$

We obtain $P(t) \leq P(0)\exp(M\omega)$ for all $t \geq 0$ where

$$M = \max\left\{0, \max_{0\leq t\leq\omega}\left(r - \frac{r}{K}s\right)\right\}.$$

Then because of the inequality (5.3) , $M = 0$.
Case 2:- There exists $t_1 > 0$ such that $P(t_1) < s$. In this case we can prove that $P(t) \leq s\exp(M\omega)$ for all $t \geq t_1$. In fact, if there exists $t_2 > t_1$ such that

$P(t_2) > s\exp(M\omega)$, then there is $t_3 \in (t_1, t_2)$ such that $P(t_3) = s$ and $P(t) > s$ for all $t \in (t_3, t_2]$, hence

$$\begin{aligned} s\exp(M\omega) &< P(t_2) && (5.6)\\ &= P(t_3)\exp\int_{t_3}^{t_2}\left(r(t) - \frac{r(t)}{K}P(t)\right)dt && (5.7)\\ &\leq P(t_3)\exp\int_{t_3}^{t_2}\left(r(t) - \frac{r(t)}{K}s\right)dt && (5.8)\\ &\leq s\exp(M\omega). && (5.9) \end{aligned}$$

The last expression says that, if $P(t_2) > s\exp(M\omega)$, then $s\exp(M\omega) < s\exp(M\omega)$ This is a contradiction. Therefore, $P(t) \leq s\exp(M\omega)$ is true for the second case.

From **cases 1** and **2** we see that the solution $P(t)$ is bounded for all $t \geq 0$ and the existence interval of $P(t)$ is $[0, \infty)$. From inequality (5.3)

$$\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt < 0,$$

we have

$$\begin{aligned} \int_0^{\infty}\left(r(t) - \frac{r(t)}{K}s\right)dt &= \int_0^{\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt + \int_{\omega}^{2\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt + \ldots + \int_{n\omega}^{\infty}\left(r(t) - \frac{r(t)}{K}s\right)dt\\ &= \lim_{n\to\infty} n\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt = -\infty. \end{aligned}$$

If $P(t) \geq s$ for all $t \in [0, \infty)$ and from **case 1** $P(t) \leq P(0)\exp\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt$ for all $t \in [0, \infty)$. Then

$$\begin{aligned} P(0)\exp\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt &\geq P(t) \geq s\\ s &\leq P(0)\exp\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}s\right)dt \end{aligned}$$

letting $t \longrightarrow \infty$, we obtain $s \leq 0$. This is a contradiction.

It shows that for any solution $P(t)$ of equation (5.2) with $P(0) > 0$ only **case 2** appears Hence $P(t) \leq s\exp(M\omega)$ for all $t > t_1$.

On the other hand if $P(t) \leq u$ for all $t \geq 0$, then

$$\begin{aligned} P(t) &= P(0)\exp\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}P(t)\right)dt && (5.10)\\ &\geq P(0)\exp\int_0^{\omega}\left(r(t) - \frac{r(t)}{K}u\right)dt \text{ for all } t \geq 0 && (5.11) \end{aligned}$$

Since inequality (5.3) we have

$$\int_0^{\omega} \left(r(t) - \frac{r(t)}{K} u \right) dt > 0,$$

then

$$\begin{aligned} \int_0^{\infty} \left(r(t) - \frac{r(t)}{K} u \right) dt &= \int_0^{\omega} \left(r(t) - \frac{r(t)}{K} u \right) dt + \int_{\omega}^{2\omega} \left(r(t) - \frac{r(t)}{K} u \right) dt + \ldots + \int_{n\omega}^{\infty} \left(r(t) - \frac{r(t)}{K} u \right) dt \\ &= \lim_{n \to \infty} n \int_0^{\omega} \left(r(t) - \frac{r(t)}{K} u \right) dt = \infty, \end{aligned}$$

Using similar argument we get

$$\begin{aligned} P(0) \exp \int_0^{\omega} \left(r(t) - \frac{r(t)}{K} u \right) dt &\leq P(t) \leq u \\ u &\geq P(0) \exp \int_0^{\omega} \left(r(t) - \frac{r(t)}{K} u \right) dt \end{aligned}$$

Then letting $t \longrightarrow \infty$ we obtain $u \geq \infty$. This is again a contradiction.

Hence, there exist $t_1 > 0$ such that $P(t_1) > u$. Now we can prove $P(t) \geq u \exp(m\omega)$ for all $t \geq t_1$ where $m = \min \left\{ 0, \min_{0 \leq t \leq \omega} \{ r(t) - \frac{r(t)}{K} u \} \right\}$.

In fact, if there exists $t_2 > t_1$ such that $P(t_2) < u \exp(m\omega)$, then there exists $t_3 \in (t_1, t_2)$ such that $P(t_3) = u$ and $P(t) < u$ for all $t \in (t_3, t_2]$. Hence

$$u \exp(m\omega) > P(t_2) \geq P(t_3) \exp \int_{t_3}^{t_2} \left(r(t) - \frac{r(t)}{K} u \right) dt \geq u \exp(m\omega).$$

This is a contradiction. Hence the above argument shows that $P(t) \geq u \exp(m\omega)$ for $t \geq t_1$ and the solution $P(t)$ has a positive lower bound on $[0, \infty)$.

Let $P_1(t), P_2(t)$ are any two solutions of equation (5.2) with $P_1(0) > P_2(0) > 0$. By the theorem of uniqueness of solutions of initial value problems [Tes11], we obtain $P_1(t) \geq P_2(t)$ for all $t \geq 0$. Then there exist constants $N > n > 0$ such that $n \leq P_2(t) \leq P_1(t) \leq N$ for all $t \geq 0$.

Let function $V(t) = \ln P_1(t) - \ln P_2(t)$. Then

$$\frac{dV}{dt} = -\frac{r(t)}{K} (P_1(t) - P_2(t)) \leq -\frac{r(t)}{K} n V(t)$$

for all $t \geq 0$. By the differential inequality theorem [Tes11] we obtain,

$$V(t) \leq V(0) \exp \left(- \int_0^t n \frac{r(t)}{K} dt \right) \forall t \geq 0.$$

Since by positivity and periodicity of $r(t)$, $\int_0^\infty r(t)dt = \infty$, we have $V(t) \longrightarrow 0$ as $t \longrightarrow \infty$. Therefore, $P_1(t) - P_2(t) \longrightarrow 0$ as $t \longrightarrow \infty$.

By the existence theorem of periodic solutions in [Yos75; Zhi99] the system (5.2) has a positive ω-periodic solution. If the system (5.2) has two periodic solutions $P_1(t), P_2(t)$ with periods $\omega_1 > 0, \omega_2 > 0$ then $\omega_1 = n_1\omega, \omega_2 = n_2\omega$ and $P_1(0) \neq P_2(0)$, where n_1, n_2 are positive integers.

Let $P_1(0) > P_2(0)$ and $T = \max\{\omega_1, \omega_2\}$, then

$$P_1(t) > P_2(t), \qquad P_1(t+T) = P_1(t), \qquad P_2(t+T) = P_2(t)$$

for all $t \geq 0$. Since $\min_{t\geq 0}\{P_1(t) - P_2(t)\} = \min_{0\leq t\leq T}\{P_1(t) - P_2(t)\} > 0$, the difference $P_1(t) - P_2(t)$ does not tend to zero as $t \longrightarrow \infty$. This is a contradiction. Therefore, the system (5.2) has a unique globally asymptotically stable positive ω-periodic solution $P_0(t)$. □

For a continuous and bounded function $f(t)$ defined on $\mathbb{R}_+ = [0, \infty)$, we denote

$$f^M = \lim_{t\to\infty} \sup f(t) \text{ and } f^L = \lim_{t\to\infty} \inf f(t). \tag{5.12}$$

If f is $\omega-$periodic, then the average value of f on a time interval $[0, \omega]$ can be defined as

$$A_\omega(f(t)) = \frac{1}{\omega}\int_0^\omega f(t)dt. \tag{5.13}$$

For system (5.1), we introduce the following assumptions

$\mathbf{B}_1$ Functions $r(t)$ and $a(t)$ are all bounded functions.

$\mathbf{B}_2$ There exists a positive constant $\omega > 0$ such that

$$\lim_{t\to\infty} \inf \int_t^{t+\omega} r(\theta)d\theta > 0 \qquad \lim_{t\to\infty} \inf \int_t^{t+\omega} a(\theta)d\theta > 0. \tag{5.14}$$

In particular, when equation (5.12) degenerates into $\omega-$periodic system that is, $r(t)$ and $a(t)$ are continuous and periodic functions with period $\omega > 0$, assumption $\mathbf{B}_2$ is equivalent to the following forms.

$$\overline{\mathbf{B}}_2 \qquad A_\omega(r(t)) > 0, \qquad A_\omega(a(t)) > 0 \tag{5.15}$$

First, we consider the first equation of system (5.1), which is a non-autonomous logistic equation:

$$\frac{dP(t)}{dt} = P(t)\left[r(t) - \frac{r(t)}{K}P(t) - \frac{a(t)H(t)}{b+P(t)}\right], \tag{5.16}$$

where functions $r(t)$ and $a(t)$ are bounded, continuous, defined on $\mathbb{R}$ and $r(t) \geq 0, a(t) \geq 0$ for all $t \geq 0$.

Definition 5.1.1. *Suppose equation* (5.16) *satisfy assumption* $\boldsymbol{B}_2$. *Then,*

a) the solution of (5.16) *is said to be uniformly persistent if there exist positive constants* $\boldsymbol{m}$ *and* $\boldsymbol{M}$ *such that for any positive solution* $P(t)$ *of equation* (5.16)

$$\boldsymbol{m} < \lim_{t\to\infty} \inf P(t) \leq \lim_{t\to\infty} \sup P(t) \leq \boldsymbol{M}, \tag{5.17}$$

b) Each fixed positive solution $P^*(t)$ *of* (5.16) *is globally uniformly attractive if equation* (5.16) *satisfy assumption* $\boldsymbol{B}_2$.

c) Equation (5.16) *is said to have a uniformly attractive positive* $\omega-$*periodic solution, if equation* (5.16) *is* $\omega-$*periodic and condition* (5.14) *reduces to* $A_\omega(r(t)) > 0$ *and* $A_\omega(a(t)) > 0$.

Let us define

$$\mathcal{R}_{ot} = A_\omega\left(\frac{ca(t)P^*}{(b+P^*)(D(F(P^*))+\mu)}\right) = \frac{cP^*}{(b+P^*)(D(F(P^*))+\mu)}A_\omega(a(t)) \tag{5.18}$$

which is the definite integral over the period ω, and is a real number. where $A_\omega(a(t))$ is the average value of $a(t)$ over a time interval ω. This can be biologically interpreted as the average number of herbivore born by a single female herbivore where $\frac{1}{D(F(P^*))+\mu}$ is the life time of the herbivore and $\frac{cA_\omega(a(t))P^*}{(b+P^*)}$ is the birth rate of herbivores in the availability of sufficient food.

Theorem 5.1.1. *Suppose that* $P^*(t)$ *is the unique periodic solution of system* (5.1) *as given in Lemma 5.1.2. Then system* (5.1) *is permanent if* $\mathcal{R}_{ot} > 1$.

Remark 5.1.1. *If* $P^* = K$ *and* $d_1 \leq D(F(K))$ *then the condition* (5.18) *can be reduced to the value of* $\mathcal{R}_o$ *as in Chapter 3 which was found for the constant coefficient case.*

Note that, since equation (5.2) *is a Ricatti equation we can integrate it and obtain the analytic expression of the* ω*-periodic solution:*

$$P^*(t) = \frac{1 - e^{-\int_0^\omega r(s)ds}}{\int_0^\omega \frac{r(t-s)}{K} e^{-\int_0^s r(t-\tau)d\tau} ds} \tag{5.19}$$

which is positive and globally asymptotically stable under the conditions that $A_w(r(t)) > 0$ *and* $A_\omega(\frac{r(t)}{K}) > 0$. *Hence the periodic plant herbivore system* (5.1) *is permanent.*

To prove Theorem 5.1.1 we need the following propositions similar to the arguments as in [Cui05].

Proposition 5.1.2. *There exist constants* M_P *and* M_H *such that*

$$\limsup_{t\to\infty} P(t) \le M_P, \quad \limsup_{t\to\infty} H(t) \le M_H$$

for every solution $(P(t), H(t))$ *of system* (5.1) *with positive initial values.*

Proof:- $\Omega = \{(P, H) : P \ge 0, H \ge 0\}$ is the positively invariant set of system (5.1) as described by Lemma 5.1.1.

Given any positive solution $(P(t), H(t))$ of system (5.1), we have

$$\dot{P} \le P\left(r(t) - \frac{r(t)}{K}P\right) \text{ for all } t \ge 0.$$

Then the auxiliary equation $\dot{V} = V\left(r(t) - \frac{r(t)}{K}V\right)$ has a globally asymptotically stable positive ω-periodic solution $V^*(t)$ by Lemma 5.1.2. So, by comparison theorem [Tes11], there exists $T_1 > 0$ such that $P(t) < V^* + 1$, for $t > T_1$.

Let $M_P = \max_{0\le t\le\omega}\{V^*(t) + 1\}$, Then we have $\limsup_{t\to\infty} P(t) \le M_P$.

From the second equation of (5.1) we get

$$\dot{H} \le H\left(c\left(\frac{a(t)P}{b+P}\right) + |-\mu - D(F(P))|\right)$$

for $t > T_1$, since $\left(\frac{H}{h+H}\right) < 1$.

Using the argument similar to the above discussion we can find constant M_H, such that

$$\limsup_{t\to\infty} H(t) \le M_H.$$

Therefore, the solution set of the system (5.1) is bounded from above. □

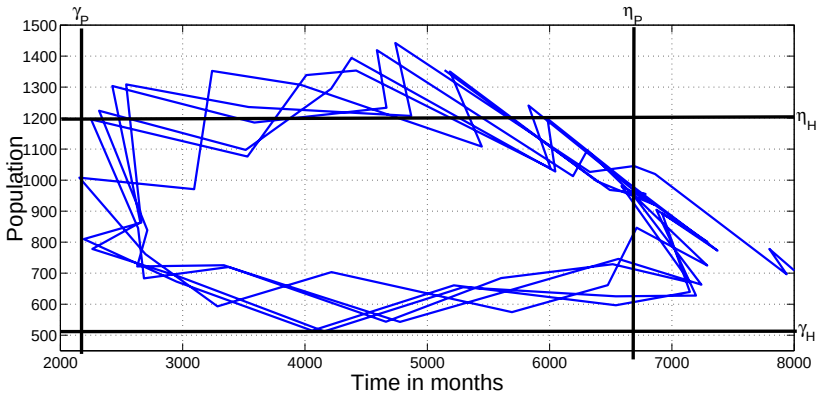

Figure 5.1: the phase portrait of plant herbivore system given in example 1 Figure 5.2 in section 5.2. This plot indicates the lower limits of the supermum values of P and H and the upper limits of the infmum values of P and H that are discussed in the propositions 5.1.3 and 5.1.4

Proposition 5.1.3. *Under the assumption* $\overline{\boldsymbol{B}}_2$, *there exist positive constants* η_P *and* γ_P *such that*

1. $$\lim_{t\to\infty} \sup P(t) \geq \eta_P \tag{5.20}$$

2. $$\lim_{t\to\infty} \inf P(t) \geq \gamma_P \tag{5.21}$$

for every solution $(P(t), H(t))$ *of system* (5.1) *with positive initial values.*

Proof:-

1. Denote by $(P(t, z_n), H(t, z_n))$ the solution of the system (5.1) with initial condition $(P(0, z_n), H(0, z_n)) = z_n \in \mathbb{R}^2_+ = \{(P, H) : P > 0, H > 0\}$.

   Suppose that (5.20) is not true, That is $\lim_{t\to\infty} \sup P(t) \ngeq \eta_P$. Then there is a sequence $z_n \subset \mathbb{R}^2_+$, such that

   $$\lim_{t\to\infty} \sup P(t, z_n) < \frac{1}{n}, \qquad n = 1, 2, \ldots \tag{5.22}$$

   where $(P(t, z_n), H(t, z_n))$ is the solution of system (5.1) with $(P(0, z_n), H(0, z_n)) = z_n$. Choosing sufficiently small positive numbers $\varepsilon_P < 1$ and $\varepsilon_H < 1$, such that

   $$A_\omega \left(-\mu + c \left(\frac{a(t)\varepsilon_P}{b + \varepsilon_P} \right) \left(\frac{\varepsilon_H}{h + \varepsilon_H} \right) - D(F(\varepsilon_p)) \right) < 0 \tag{5.23}$$

   and

   $$A_\omega \left(\phi_\varepsilon(t) \right) > 0 \tag{5.24}$$

   where

   $$\phi_\varepsilon(t) = r(t) - \frac{r(t)}{K}\varepsilon_P - \frac{a(t)\varepsilon_P}{b + \varepsilon_P}\varepsilon_H e^{\alpha\omega}, \qquad \alpha = \max_{0\leq t\leq\omega} \left(\frac{ca(t)}{b} + \mu \right), \tag{5.25}$$

Then by (5.22), for the given $\varepsilon_P > 0$, there exists a positive integer N_0, such that

$$\lim_{t\to\infty} \sup P(t, z_n) < \frac{1}{n} < \varepsilon_P. \qquad n > N_0. \tag{5.26}$$

For the rest of the proof we assume that $n > N_0$. Equation (5.26) implies that there exists $\tau_1^{(n)} > 0$, such that

$$P(t, z_n) < \varepsilon_P, \text{ for } t \geq \tau_1^{(n)},$$

and further

$$\dot{H}(t, z_n) \leq H(t, z_n) \left(-\mu - D(F(\varepsilon_P)) + \frac{ca(t)}{b} \varepsilon_P \frac{\varepsilon_H}{h} \right), \text{ for } t \geq \tau_1^{(n)}.$$

By (5.23), any solution $V(t)$ of the equation

$$\dot{V} = V \left(-\mu - D(F(\varepsilon_P)) + \frac{ca(t)}{b} \varepsilon_P \frac{\varepsilon_H}{h} \right),$$

with positive initial conditions satisfies $\lim_{t\to\infty} V(t) = 0$.

Hence $\lim_{t\to\infty} H(t, z_n) = 0$, from Comparison theorem [Tes11] of differential equations. So, there is a $\tau_2^{(n)} > \tau_1^{(n)}$, such that $H(t, z_n) < \varepsilon_H$, for $t \geq \tau_2^{(n)}$. It follows that

$$\dot{P}(t, z_n) \geq P(t, z_n) \left(r(t) - \frac{a(t)}{b} \varepsilon_H - \frac{r(t)}{K} P(t, z_n) \right), \text{ for } t \geq \tau_2^{(n)}. \tag{5.27}$$

Then because of (5.24), the equation,

$$\dot{P} = P \left(r(t) - \frac{a(t)}{b} \varepsilon_H - \frac{r(t)}{K} P \right), \tag{5.28}$$

has a positive and ω-periodic solution $P^*(t)$ which is globally asymptotic stable. Hence $P(t, z_n) > \dfrac{P^*(t)}{2}$ for sufficiently large $t > 0$ and $n > N_0$, which is a contradiction to (5.22). Hence $\lim_{t\to\infty} \sup P(t) \geq \eta_P$.

2 Suppose that (5.21) is not true, that is, $\lim_{t\to\infty} \inf P(t) \not\geq \gamma_P$. Then, there exist a sequence $\{z_n\} \subset \Omega$ such that

$$\lim_{t\to\infty} \inf P(t, z_n) < \frac{\eta_P}{2n^2} \qquad n = 1, 2, \ldots$$

On the other hand, by the first part of this proposition (5.20) we have,

$$\lim_{t\to\infty} \sup P(t, z_n) > \eta_P \qquad n = 1, 2, \ldots$$

Hence there are time sequences $\left\{s_q^{(n)}\right\}$ and $\left\{t_q^{(n)}\right\}$ satisfying $0 < s_1^{(n)} < t_1^{(n)} < s_2^{(n)} < t_2^{(n)} < \ldots < s_q^{(n)} < t_q^{(n)} < \ldots,\ s_q^{(n)} \to \infty,\ t_q^{(n)} \to \infty$ as $q \to \infty$ and

$$P(s_q^{(n)}, z_n) = \frac{\eta_P}{n},\ \ P(t_q^{(n)}, z_n) = \frac{\eta_P}{n^2},\ \frac{\eta_P}{n^2} < P(t, z_n) < \frac{\eta_P}{n},\ t \in \left(s_q^{(n)}, t_q^{(n)}\right) \tag{5.29}$$

By proposition , for a given positive integer n, there is $T_1^{(n)} > 0$, such that

$$P(t, z_n) \le M_P,\ \ H(t, z_n) \le M_H \text{ for } t > T_1^{(n)}$$

Because of $s_q^{(n)} \to \infty$ as $q \to \infty$, there is a positive integer $U^{(n)}$, such that $s_q^{(n)} > T_1^{(n)}$ as $q \ge U^{(n)}$, hence,

$$\dot{P}(t, z_n) \ge P(t, z_n)\left(r(t) - \frac{r(t)}{K}M_P - \frac{a(t)}{b}M_H\right) := \zeta(t)P(t, z_n), \tag{5.30}$$

for $q > U^{(n)}$, integrating (5.30) from $s_q^{(n)}$ to $t_q^{(n)}$ yields

$$P(t_q^{(n)}, z_n) \ge P(s_q^{(n)}, z_n) \exp\left(\int_{s_q^{(n)}}^{t_q^{(n)}} \zeta(t)dt\right),$$

or

$$-\int_{s_q^{(n)}}^{t_q^{(n)}} \zeta(t)dt \ge \ln n \text{ for } q \ge U^{(n)}. \tag{5.31}$$

If $A_\omega(\zeta(t)) \ge 0$, inequality 5.31 leads to a contradiction. Otherwise $A_\omega(\zeta(t)) < 0$ and we have $t_q^{(n)} - s_q^{(n)} \to \infty$ as $n \to \infty,\ q \ge U^{(n)}$, according to the boundedness of $\zeta(t)$.

Then by (5.23) and (5.24), there are constants $L > 0$ and $N_0 > 0$, such that

$$\frac{\eta_P}{n} < \varepsilon_P, \qquad t_q^{(n)} - s_q^{(n)} > 2L, \tag{5.32}$$

and

$$M_H \exp\left(\int_0^L \left(-\mu + ca(t)\frac{\varepsilon_P}{b}\frac{\varepsilon_H}{h} - D(F(\varepsilon_P))\right)\right) dt < \varepsilon_H, \qquad \int_0^{\dashv} \phi_\varepsilon(t)dt > 0, \tag{5.33}$$

for $n \ge N_0$, $q \ge U^{(n)}$, and $\dashv \ge L$ (5.32) implies

$$P(t, z_n) < \varepsilon_P, \qquad t \in [s_q^{(n)}, t_q^{(n)}] \tag{5.34}$$

for $n \ge N_0$, $q > U^{(n)}$. For the positive ε_H satisfying (5.24) and (5.22), we have the following two cases,

i) $H(t, z_n) \ge \varepsilon_H$ for all $t \in [s_q^{(n)}, s_q^{(n)} + L]$,

ii) these exists $\tau_{q2}^{(n)} \in [s_q^{(n)}, s_q^{(n)} + L]$, such that $H(\tau_{q1}^{(n)}, z_n) < \varepsilon_H$.

If i) holds, by (5.34) and (5.33), we have

$$\begin{aligned}
\varepsilon_H &\leq H(s_q^{(n)} + L, z_n) \\
&\leq H(s_q^{(n)}, z_n) \exp \int_{s_q^{(n)}}^{s_q^{(n)}+L} \left(-\mu + \frac{ca(t)\varepsilon_P}{b} \frac{\varepsilon_H}{h} - D(F(\varepsilon_P)) \right) dt \\
&\leq M_H \exp \int_0^L \left(-\mu + \frac{ca(t)\varepsilon_P}{b} \frac{\varepsilon_H}{h} - D(F(\varepsilon_P)) \right) dt \\
\varepsilon_H &< \varepsilon_H
\end{aligned}$$

which is a contradiction. Hence $H(t, z_n) \not\geq \varepsilon_H$ for all $t \in [s_q^{(n)}, s_q^{(n)} + L]$.

If ii) holds, we now claim that

$$H(t, z_n) \leq \varepsilon_H \exp(\alpha\omega) \text{ for } t \in (\tau_{q1}^{(n)}, t_q^{(n)}] \tag{5.35}$$

Otherwise, there exist $\tau_{q2}^{(n)} \in (\tau_{q1}^{(n)}, t_q^{(n)}]$ such that $H(t, z_n) > \varepsilon_H \exp(\alpha\omega)$. By continuity of $H(t, z_n)$, there must exist $\tau_{q3}^{(n)} \in \left(\tau_{q1}^{(n)}, \tau_{q2}^{(n)}\right)$, such that $H(\tau_{q3}^{(n)}, z_n) = \varepsilon_H$ and $H(t, z_n) > \varepsilon_H$ for $t \in \left(\tau_{q3}^{(n)}, \tau_{q3}^{(n)}\right)$.

Denote $Q^{(n)}$ to be the nonnegative integer, such that

$$\tau_{q2}^{(n)} \in \left(\tau_{q3}^{(n)} + Q^{(n)}\omega, \tau_{q3}^{(n)} + (Q^{(n)} + 1)\omega\right].$$

Then from equation (5.23), we have

$$\begin{aligned}
\varepsilon_H \exp(\alpha\omega) &< H(\tau_{q1}^{(n)}, z_n) \\
&< H(\tau_{q3}^{(n)}, z_n) \exp \int_{\tau_{q3}^{(n)}}^{\tau_{q2}^{(n)}} \left(-\mu + ca(t) \frac{\varepsilon_P}{b} \frac{\varepsilon_H}{h} - D(F(\varepsilon_P)) \right) dt \\
&= \varepsilon_H \exp \left(\int_{\tau_{q3}^{(n)}}^{\tau_{q3}^{(n)}+Q^{(n)}\omega} + \int_{\tau_{q3}^{(n)}+Q^{(n)}\omega}^{\tau_{q2}^{(n)}} \right) (-\mu + ca(t) \frac{\varepsilon_P}{b} \frac{\varepsilon_H}{h} - D(F(\varepsilon_P)))dt \\
&< \varepsilon_H \exp(\alpha\omega)
\end{aligned}$$

Which is again a contradiction. This contradiction establishes that (5.35) is true. Particularly (5.35) holds for $t \in [s_q^{(n)} + L, t_q^{(n)}]$. Therefore, using (5.29) and (5.33), we have

$$\begin{aligned}
\frac{\eta_P}{n^2} &= P(t_q^{(n)}, z_n) \\
&\geq P(s_q^{(n)} + L, z_n) \exp \int_{s_q^{(n)}+L}^{t_q^{(n)}} \left(r(t) - \frac{r(t)}{K}\varepsilon_P - \frac{a(t)}{b}\varepsilon_H \exp(\alpha\omega) \right)
\end{aligned}$$

$$= P(s_q^{(n)} + L, z_n) \exp \int_{s_q^{(n)}+L}^{t_q^{(n)}} \phi_\varepsilon(t)dt$$
$$> \frac{\eta_P}{n^2},$$

which is a contradiction too. Hence $\lim_{t\to\infty} \inf P(t) \geq \gamma_P$. □

Proposition 5.1.4. *Under the assumption of* $\overline{\boldsymbol{B}}_2$ *and* $\mathcal{R}_{0t} > 1$ *there exist positive constant* η_H *and* γ_H *such that*

$$1. \qquad \lim_{t\to\infty} \sup H(t) > \eta_H \tag{5.36}$$

$$2. \qquad \lim_{t\to\infty} \inf H(t) \geq \gamma_H \tag{5.37}$$

for every solution $(P(t), H(t))$ *of system* (5.1) *with positive initial values.*

Proof:-

1 By assumption inequality (5.15) for $\mathcal{R}_{0t} > 1$ we can choose a constant $\xi_0 > 0$ such that

$$A_\omega \left(\psi_{\xi_0}(t)\right) > 0, \tag{5.38}$$

where

$$\psi_{\xi_0}(t) = -\mu + \left(\frac{ca(t)(P^*(t) - \xi_0)}{b + (P^*(t) - \xi_0)}\right)\left(\frac{\xi_0}{h + \xi_0}\right) - D(F(P^*(t))). \tag{5.39}$$

Consider the following equation with positive parameter α,

$$\dot{P} = P\left(r(t) - \frac{2a(t)}{b}\alpha - \frac{r(t)}{K}P\right). \tag{5.40}$$

Because $r(t) > 0$, we know that $A_\omega\left(r(t) - \frac{2a(t)}{b}\alpha\right) := A_\omega(\varepsilon(t)) > 0$ for sufficiently small $\alpha > 0$. By Lemma 5.1.2 equation (5.40) has a unique positive ω-periodic solution $P_\alpha(t)$, which is globally asymptotically stable. Let $\overline{P}_\alpha(t)$ be the solution of (5.40) with initial condition $\overline{P}_\alpha(0) = P^*(0)$ in which $P^*(t)$ is the unique periodic solution of the herbivore free plant system (5.2) as given by Lemma 5.1.2.

Hence, for the value ξ_0, there exist sufficiently large $T_2 > T_1$, such that

$$|\overline{P}_\alpha(t) - P_\alpha(t)| < \frac{\xi_0}{4} \qquad \text{for } t \geq T_2.$$

By the continuity of the solution in the parameter, we have $\overline{P}_\alpha(t) \longrightarrow P^*(t)$ uniformly in $[T_2, T_2+\omega]$ as $\alpha \to 0$. Hence, for $\xi_0 > 0$, there exists $\alpha_0 = \alpha_0(\xi_0) > 0$ such that

$$|\overline{P}_\alpha(t) - P^*(t)| < \frac{\xi_0}{4} \qquad \text{for } t \in [T_2, T_2+\omega], \qquad 0 < \alpha < \alpha_0.$$

So, we have

$$|\overline{P}_\alpha(t) - P^*(t)| < \frac{\xi_0}{2}, \qquad t \in [T_2, T_2+\omega].$$

Note that $P_\alpha(t)$ and $P^*(t)$ are all ω-periodic, hence

$$|\overline{P}_\alpha(t) - P^*(t)| < \frac{\xi_0}{2}, \text{ for } t \geq 0, \ 0 < \alpha < \alpha_0.$$

Choosing a constant α_1 with $0 < \alpha_1 < \alpha_0$ and $2\alpha_1 < \xi_0$, we have,

$$P_\alpha(t) \geq P^*(t) - \frac{\xi_0}{2}, \qquad t \geq 0. \tag{5.41}$$

Now, suppose that (5.36) is not true, that is $\lim_{t\to\infty} \sup H(t) \not> \eta_H$. Then there exists $z \in \Omega$, such that

$$\lim_{t\to\infty} \sup H(t, z) < \alpha_1,$$

where $(P(t,z), H(t,z))$ is the solution of system (5.1) with $(P(0,z), H(0,z)) = z$. So, there exists $T_3 \geq T_2$, such that

$$H(t,z) < 2\alpha_1 < \xi_0 \text{ for } t \geq T_3,$$

and hence

$$\dot{P}(t,z) \geq P(t,z)\left(r(t) - \frac{2a(t)}{b}\alpha_1 - \frac{r(t)}{K}P(t,z)\right).$$

Let $u(t)$ be the solution of (5.40) with $\alpha = \alpha_1$ and $U(T_3) = P(T_3, z)$. Then $P(t,z) \geq u(t)$, for $t \geq T_3$.

Due to the global asymptotic stability of $P_{\alpha_1}(t)$, for the given $\xi = \frac{\xi_0}{2}$, there exists $T_4 \geq T_3$ such that

$$|u(t) - P_{\alpha_1}(t)| < \frac{\xi_0}{2} \qquad \text{for} \qquad t \geq T_4.$$

So, $P(t,z) \geq u(t) > P_{\alpha_1}(t) - \frac{\xi_0}{2}$ for $t \geq T_4$, and hence, $P(t,z) > P^*(t) - \xi_0$ for $t > T_4$. From (5.41), this implies that

$$\dot{H}(t,z) \geq H(t,z)\left(-\mu + \left(\frac{ca(t)(P^*(t)-\xi_0)}{b + (P^*(t)-\xi_0)}\right)\left(\frac{\xi_0}{h+\xi_0}\right) - D(F(P^*(t)))\right) := \psi_{\xi_0} H(t,z) \tag{5.42}$$

for $t \geq T_4$. Integrating the inequality (5.42) from T_4 to t yields

$$H(t,z) \geq H(T_4,z) \exp \int_{T_4}^{t} \psi_{\xi_0}(s) ds,$$

which implies $H(t,z) \longrightarrow \infty$ as $t \longrightarrow \infty$ from (5.38) is a contradiction to proposition 2.1.

Hence $\lim_{t\to\infty} \sup H(t) \geq \eta_H$.

2 Suppose that $\lim_{t\to\infty} \inf H(t) \ngeq \gamma_H$. Then there exists a sequence $\{z_n\} \subset \Omega$, such that

$$\lim_{t\to\infty} \inf H(t,z_n) < \frac{\eta_H}{(n+1)^2} \qquad n = 1,2,\ldots$$

But $\lim_{t\to\infty} \sup H(t,z_n) > \eta_H$ for all $n = 1,2,\ldots$, from the first part of this proposition (5.36)

Hence, there are two time sequences $\{s_q^n\}$ and $\{t_q^n\}$ satisfying the following conditions.

$$0 < s_1^n < t_1^n < s_2^n < t_2^n < \ldots < s_q^n < t_q^n < \ldots, s_q^n \to \infty, t_q^n \to \infty, \text{as } q \to \infty$$

and

$$\begin{aligned} H(s_q^n, z_n) = & \frac{\eta_H}{n+1}, \qquad H(t_q^n, z_n) = \frac{\eta_H}{(n+1)^2}, \\ & \frac{\eta_H}{(n+1)^2} < H(t,z_n) < \frac{\eta_H}{n+1}, \text{ for } t \in \left(s_q^n, t_q^n\right). \end{aligned} \tag{5.43}$$

By proposition 2.1, for any given integer $n > 0$, there is a $T_1^{(n)} > 0$ such that

$$H(t,z_n) \leq M_H \qquad \text{for } t \geq T_1^{(n)}$$

Because of $s_q^n \to \infty$ as $q \to \infty$, there is a positive integer $Q^{(n)}$, such that $s_q^n > T_1^n$ for some $q \geq Q^{(n)}$. Hence

$$\dot{H}(t,z_n) \geq H(t,z_n)\left(-\mu - D(F(M_P))\right))$$

for $q > Q^{(n)}$ and $t \in \left[s_q^n, t_q^n\right]$.

Integrating the above inequality from s_q^n to t_q^n, we have

$$H(t_q^n, z_n) \geq H(s_q^n, z_n) \exp \int_{s_q^n}^{t_q^n} \left(-\mu - D(F(M_P))\right)) \, dt.$$

Or

$$\int_{s_q^n}^{t_q^n} \left(\mu + D(F(M_P))\right)) \, dt \geq \ln(n+1) \text{ for } q > Q^{(n)}.$$

Due to the boundedness of the function $\mu + D(F(M_P)))$, we know that

$$t_q^n - s_q^n \longrightarrow \infty \text{ as } n \longrightarrow \infty, \text{ for } q \geq Q^{(n)}. \tag{5.44}$$

By equation (5.38) there is a real constant $X > 0$ and a positive integer N_0, such that

$$\frac{\eta_H}{n+1} < \alpha_1 < \xi_0, \qquad t_q^n - s_q^n > 2X \tag{5.45}$$

and

$$\int_0^e \psi_{\xi_0}(t)dt > 0, \tag{5.46}$$

for $n \geq N_0, q \geq Q^{(n)}$ and $e \geq X$. Further,

$$H(t, z_n) < \alpha_1 < \xi_0, \text{ for } t \in \left[s_q^n, t_q^n\right], n \geq N_0\, q \geq Q^{(n)}. \tag{5.47}$$

In addition, $\dot{P}(t, z_n) \geq P(t, z_n)\left(r(t) - \dfrac{2a(t)}{b}\alpha_1 - \dfrac{r(t)}{K}P(t, z_n)\right)$.

Let $u(t)$ be the solution of (5.40) with $\alpha = \alpha_1$ and $u(s_q^n) = P(s_q^n, z_n)$, then $P(t, z_n) \geq u(t), \text{ for } t \in [s_q^n, t_q^n]$, from comparison theorem.

Further, by Propositions 2.1 and 2.2 we can choose $Q_1^{(n)} > Q^{(n)}$, such that $\gamma_P \leq P(s_q^n, z_n) \leq M_P$ for $q \geq Q_1^{(n)}$.

For $\alpha = \alpha_1$ equation (5.40) has a unique positive ω- periodic solution $P_{\alpha_1}(t)$ which is globally asymptotically stable. In addition, by the periodicity of equation (5.40), the periodic solution $P_{\alpha_1}(t)$ is uniformly asymptotically stable with respect to the compact set $\Sigma = \{P : \gamma_P \leq P \leq M_P\}$. Hence, for the given ξ_0 in Proposition 2.2, there exist $T_0 > X$, which is independent of n and q such that,

$$u(t) \geq P_{\alpha_1}(t) - \frac{\xi_0}{2} \text{ for } t \geq T_0 + s_q^n.$$

Thus, $u(t) \geq P^*(t) - \xi_0\ t \geq T_0 + s_q^n$ from equation (5.41).

By equation (5.44), there exists a positive integer $N_1 \geq N_0$, such that

$t_q^{(n)} > s_q^{(n)} + 2T_0 > s_q^{(n)} + 2X$ for $n \geq N_1$ and $q > Q_1^{(n)}$. So, we have

$$P(t, z_n) \geq P^*(t) - \xi_0 \text{ for } t \in \left[s_q^{(n)} + T_0, t_q^{(n)}\right), \tag{5.48}$$

as $n \geq N_1$ and $q \geq Q_1^{(n)}$.

Hence,

$$\dot{H}(t, z_n) \geq \psi_{\xi_0}(t)H(t, z_n) \text{ for } t \in \left[s_q^{(n)} + T_0, t_q^{(n)}\right] \tag{5.49}$$

from (5.47) and (5.48).

Integrating the inequality (5.49) from $s_q^{(n)} + T_0$ to $t_q^{(n)}$ yields

$$H(t_q^{(n)}, z_n) \geq H(s_q^{(n)} + T_0, z_n) \exp \int_{s_q^{(n)}+T_0}^{t_q^{(n)}} \psi_{\xi_0}(t)dt,$$

and hence $\frac{\eta_H}{(n+1)^2} > \frac{\eta_H}{(n+1)^2} \exp \int_{s_q^{(n)}+T_0}^{t_q^{(n)}} \psi_{\xi_0}(t)dt > \frac{\eta_H}{(n+1)^2}$ from equation (5.45). This is a contradiction. Hence $\lim_{t\to\infty} \inf H(t) \geq \gamma_H$. □

The proof of Theorem 5.1.1 follows from the above propositions (Propositions 5.1.2 -5.1.4).

On the other hand if the number of offspring produced by a single female herbivore is on average less than one. It means the herbivore population cannot even replace it self in the long run hence it leads to the extinction of species. The following theorem explains this situation.

Theorem 5.1.5. *Suppose that assumption $\overline{\boldsymbol{B}}_2$ holds and $\mathcal{R}_o \leq 1$. Then $\lim_{t\to\infty} H(t) = 0$ for any solution $(P(t), H(t))$ of system* (5.1) *with positive initial conditions where P^* is the unique periodic solution of* (5.2) *as given by Lemma 5.1.2.*

Proof:- By assumption (5.15), for every $\epsilon < 1$ there exist ϵ_1 $(0 < \epsilon_1 < \epsilon)$ and $\epsilon_0 > 0$, such that

$$\begin{aligned} A_\omega \left(\frac{ca(t)(P^*(t)+\epsilon_1)}{(b+(P^*(t)+\epsilon_1))} \left(\frac{\epsilon}{h+\epsilon} \right) - D(F(P^*(t)+\epsilon_1)) - \mu \right) \\ \leq -\frac{\epsilon}{2} A_\omega \left(\mu + D(F((P^*(t)+\epsilon_1)))) < -\epsilon_0. \end{aligned} \tag{5.50}$$

Then, for the given ϵ_1 there exists $T^{(1)} > 0$, such that

$$P(t) \leq P^*(t) + \epsilon_1 \text{ for } t > T^{(1)}. \tag{5.51}$$

In addition, from (5.50) and (5.51), we have

$$A_\omega \left(\frac{ca(t)P(t)}{(b+P(t))} \left(\frac{\epsilon}{h+\epsilon} \right) - D(F(P(t))) - \mu \right) \leq -\epsilon_0 \text{ for } t > T^{(1)}. \tag{5.52}$$

First, we show that there exist $T^{(2)} > T^{(1)}$, such that $H(T^{(2)}) < \epsilon$. Otherwise, we have

$$\epsilon \leq H(t) \leq H(T^{(1)}) \exp \int_{T^{(1)}}^{t} \left(\frac{ca(s)P(s)}{(b+P(s))} \frac{\epsilon}{h+\epsilon} - D(F(P(s))) - \mu \right) ds \to \infty \tag{5.53}$$

as $t \to \infty$. This implies $\epsilon \leq 0$, which is a contradiction.

Second, we show that

$$H(t) \leq \epsilon \exp(M(\epsilon)\omega), \qquad \text{for } t \geq T^{(2)}, \tag{5.54}$$

where $M(\epsilon) = \max\limits_{0\leq t\leq \omega} \left\{ \dfrac{ca(t)(P^*(t)+\epsilon)}{(b+(P^*(t)+\epsilon))} \left(\dfrac{\epsilon}{h+\epsilon}\right) + D(F((P^*(t)+\epsilon))) + \mu \right\}$.

Otherwise, there exists $T^{(3)} > T^{(2)}$, such that $H(T^{(3)}) > \epsilon \exp(M(\epsilon)\omega)$. By the continuity of $H(t)$, there must exist $T^{(4)} \in (T^{(2)}, T^{(3)})$ such that $H(T^{(4)}) = \epsilon$ and $H(t) > \epsilon$, for $t \in (T^{(2)}, T^{(3)}]$. Let X_1 be the nonnegative integer, such that $T^{(3)} \in \left[(T^{(4)} + X_1\omega, T^{(4)} + (X_1+1)\omega\right]$ by (5.51) and (5.52).

Then, we have

$$\begin{aligned}
\epsilon \exp(M(\epsilon)\omega) &< H(T^{(3)}) \\
&< H(T^{(4)}) \exp \int_{T^{(4)}}^{T^{(3)}} \left(\frac{ca(t)P(t)}{(b+P(t))} \left(\frac{\epsilon}{h+\epsilon}\right) - D(F(P(t))) - \mu \right) dt \\
&= \epsilon \exp \left(\int_{T^{(4)}}^{T^{(4)}+X_1\omega} + \int_{T^{(4)}+X_1\omega}^{T^{(3)}} \right) \left(\frac{ca(t)P(t)}{(b+P(t))} \left(\frac{\epsilon}{h+\epsilon}\right) - D(F(P(t))) - \mu \right) dt \\
&< \epsilon \exp \left\{ \int_{T^{(4)}+X_1\omega}^{T^{(3)}} \left(\frac{ca(t)P(t)}{(b+P(t))} \left(\frac{\epsilon}{h+\epsilon}\right) - D(F(P(t))) - \mu \right) dt \right\} \\
&< \epsilon \exp(M(\epsilon)\omega),
\end{aligned}$$

which is a contradiction. This means (5.54) holds. Since ϵ is arbitrary we derive $H(t) \longrightarrow 0$ as $t \longrightarrow \infty$. □

5.2 Simple Sinusoidal Functions for $r(t)$ and $a(t)$

In this example we shall consider the parameters $K, b, m, c, d_1, d_2, \mu$ to be constants and $r(t), a(t)$ are periodic functions of period one year. For simplicity we shall consider sinusoidal perturbations, that is

$$r(t) = r_0(1 + \varepsilon \sin 2\pi t) \qquad a(t) = a_0(1 + \varepsilon \sin 2\pi t) \tag{5.55}$$

where r_0 and a_0 are the average values, εr_0 and εa_0 are the amplitudes of perturbations of $r(t)$ and $a(t)$ respectively. We assume that $0 \leq \varepsilon \leq 1$ because r and a cannot be negative $\varepsilon = 0$ corresponds to absence of seasonality while $\varepsilon = 1$ means the growth rate of plants and the consumption/feeding rate of herbivores are in their most unfavorable season.

Then the mathematical model is of the form

$$\begin{aligned} \dot{P} &= P f_1(t, P, H) \\ \dot{H} &= H f_2(t, P, H) \end{aligned} \tag{5.56}$$

with f_1 and f_2 are periodic functions with respect to t and $f_1(t, 0, H)$ and $f_2(t, P, 0)$ are bounded for all $t, P, H \geq 0$. It is therefore a positive dynamical system since $P(0), H(0) \geq 0$ implies $P(t), H(t) \geq 0$ for all $t \geq 0$. In the autonomous case the system (5.56) have a single attractor limit cycle in the first quadrant (see Chapter 3 for the details).

Table 5.1: Table of parameters and their meaning

Parameter	Description	Value	Source
r	plant growth rate	variable	Assumed
a	feeding rate	variable	Assumed
K	carrying capacity(for plant population)	10000	Table 3.3
b	half saturation constant of herbivore feeding on the plant biomass	1100	Table 3.3
c	efficiency of converting what is eaten in to a newborn	0.25	Table 3.3
h	Allee constant	40	Assumed
d_1	minimum death rate	0.1	Table 3.3
d_2	maximum death rate	0.3	Table 3.3
μ	harvest rate	0.025	Assumed

The effect of the periodic time dependent parameters $r(t)$ and $a(t)$ is seen as small periods with smaller amplitudes. Figure 5.2 shows what is explained in this paragraph.

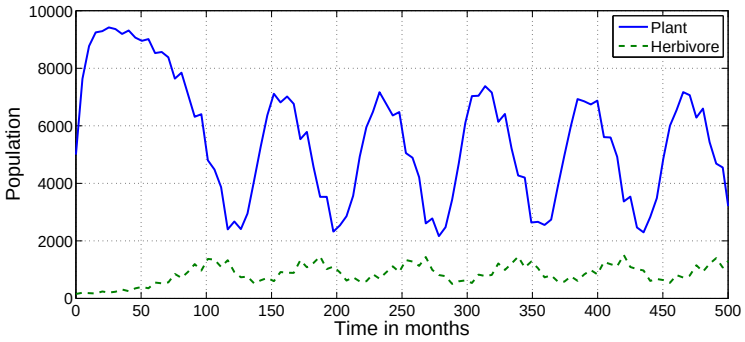

Figure 5.2: Plant herbivore interaction dynamics with $r(t)$ and $a(t)$ are periodic functions of time (where $r(t) = 0.25(1 + 0.3\sin(\frac{\pi t}{4}))), a(t) = 0.75(1 + 0.75\sin(\frac{\pi t}{4})))$

From the plot we can see that the existence of unique periodic positive solution and coexistence limit cycle still exists in the periodic case. Let us now consider the special case where $r(t)$ and $a(t)$ are dependent on temperature and rainfall.

For our study, we chose the Genale-Dawa river basin in the south-eastern part of Ethiopia, the river basin ranges from $4^o00'N - 7^o30'N$ and $38^o00'E - 44^o00'E$. It

represents the three major climatic zones of the country, the cool zone, temperate zone and hot lowlands.

The monthly rainfall distribution of the Genale-Dawa river basin in the years 1996-2016, was collected from Ethiopian National Meteorology Agency (NMA) and the intensity is plotted in Figure 5.3. The blue region indicates places where annual rainfall is greater than $1200mm$; this region is mainly the highland area where the Bale mountains are located. The red region indicates places where annual rainfall is less than $500mm$; this region is mainly the hot lowland area where desert type conditions are observed.

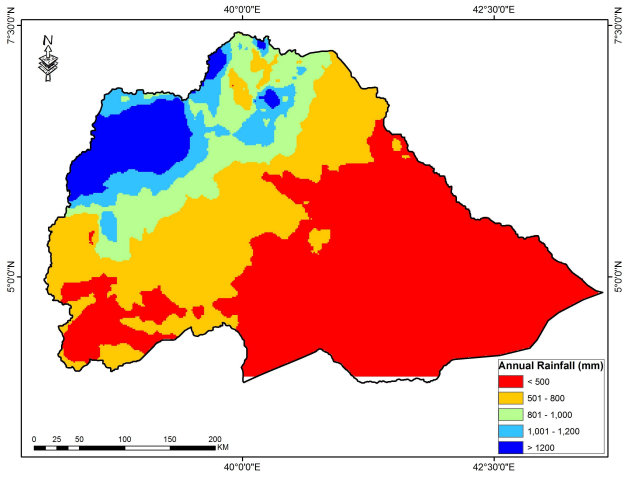

Figure 5.3: Mean annual rainfall of Genale-Dawa basin, Ethiopia

5.3 The Growth Rate r(T,R) and Feeding Rate a(R)

After the end of the rainy season in the study area, the fields are green and the herbivore is free to move around and graze/browse. Therefore it is considered that there is a relationship between seasonal variation (of temperature, rainfall) and plant growth and herbivore feeding rate. In this model, it is assumed that the intrinsic growth rate for plants and the feeding rate for herbivores are functions of temperature and rainfall. The parameter $r(t) = r(T, R)$, for the intrinsic growth rate of plants, is defined in this study as

$$r(T, R) = \alpha_r U_r(T) V_r(R)$$

where $U_r(T)$ and $V_r(R)$ account for the effect of temperature and rainfall on a monthly growth rate of new plants. The parameter α_r represents the correction factor that keeps the rate between 0 and 1. The increase in temperature and increase in rainfall meaning availability of favorable water and heat that facilitates the growth

of plant population until it reaches its maximum level, which is the carrying capacity of the environment.

In case of high temperature and low rainfall, plants tend to dry (or to be dormant until favorable condition) as the temperature rises. In addition, in case of high rainfall (fluids) the nutrients in the soil will be washed away by flood/overflow. Hence plant growth rate decreases in these both cases but avoiding the extreme cases the formula works well.

Herbivores move around to graze their feed, where a suitable time for them is when there is moderate temperature and low rainfall. If the temperature is high they usually prefer to stay in shades (during the day) and change their time of feeding to cooler hours (dusk or during the evening). So we assumed that the feeding rate is not significantly affected by temperature. However if the rainfall is high they prefer to stay in one place and not move around to graze. Moreover, the soil will be water-logged and lack of air prohibits plant growth, or plants may die as a result of floods. Hence, their feeding rate is significantly affected by the variation in the rainfall.

Similarly, the consumption rate parameter $a(R)$, is defined as

$$a(R) = \alpha_a Y_a(R),$$

where $Y_a(R)$ accounts for the effect of rainfall on the feeding rate of herbivores on plants. Furthermore, α_a represents the correction factor that keeps the rate between 0 and 1.

Large mammals have a smaller surface area to volume ratio as well as thicker skin boundary layers than that of smaller mammals. Because of this, large mammals are less capable of dealing with extreme temperatures outside their thermoneutral zone as the ability to dissipate heat becomes more difficult. It has been found in cattle that grazing and traveling creates three and five times more heat respectively compared to being idle and direct sun can produce two to four times higher thermal loads than shades [Val15]. Some studies such as [Val15] and references therein have looked at the temporal shift in activity levels with respect to temperature, that during hot periods, animals shift to being more active in feeding at cooler hours and less active during the day.

The temperature dependent component function $U_r(T)$ is defined as

$$U_r(T) = e^{\frac{(-(T-\overline{T}_r)^2}{\sigma^2}} \tag{5.57}$$

$$T(t) = T_{av} + A\sin(\omega t + \phi) \tag{5.58}$$

where $\overline{T}_r$ is the most favorable temperature for the growth rate of plants to reach its maximum, and σ is the standard deviation from the mean.

Even though the feeding pattern of herbivores is affected by the temperature changes they have their own mechanism to overcome the problem such as shifting the time of feeding to dusk or to night times when the temperature is cooler hence the overall effect of temperature in our case does not vary with temperature.

To capture the effect of rainfall as described above, we used component functions

$$V_r(R) = e^{-\frac{(R-\overline{R}_r)^2}{\nu^2}} \tag{5.59}$$

$$Y_a(R) = e^{-\frac{(R-\overline{R}_a)^2}{\upsilon^2}} \tag{5.60}$$

$$R(t) = R_{av} + A\sin(\omega t + \phi) \tag{5.61}$$

where $\overline{R}_r$ is the rainfall when the growth rate of plants reaches its maximum, ν is the standard deviation from $\overline{R}_r$. $\overline{R}_a$ is the rainfall when herbivore population feel comfortable to feed on the plants, and υ is the standard deviation from $\overline{R}_a$.

Depending on altitude, the type of vegetation (grass, leaves, shrub) and type of herbivore (cattle, sheep, goat, camel) differ in the three regions.

5.3.1 Cold Highlands with Annual Rainfall > 1200mm

From Figure 5.3 areas with annual rainfall > 1200mm, are the cool to cold humid highlands. This place has a mosaic of croplands vegetation [Gon96]. In this area vegetation growth starts increasing in June and reaches its maximum growth in September and October which is two months after the highest rainfall in July. Following the dry season (December, January and February) the lowest vegetation growth is observed from December to May.

The coordinates of the places for the rainfall range > 1200mm, indicated in blue in Figure 5.3, were selected and the monthly rainfall data from $1996 - 2016$ was collected. Average monthly rainfall for the 252 months in this geographic region is plotted against time using a continuous line in Figure 5.4, and the fitted periodic function curve (selected to be periodic on purpose) is plotted alongside on the same figure in broken lines.

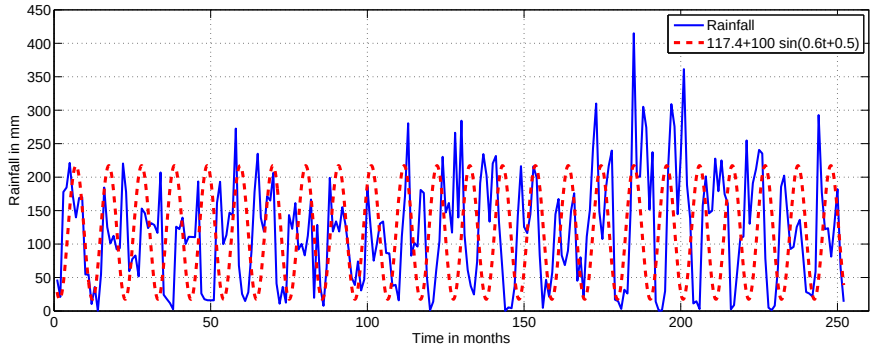

Figure 5.4: The average monthly rainfall of the cold zone in Genale dawa basin, Ethiopia, in the year $1996 - 2016$

In Figure 5.4 the fitted curve has the equation $R(t) = 117.4 + 126\sin(0.6t - 2)$ (with accuracy of 95% confidence interval) where t is the number of months and 117.4 is the average mean rainfall of the region.

From this same region and coordinates the monthly maximum and minimum temperature data for the year 1994 to 2014 is collected from the Ethiopian National Meteorology Agency. Average monthly temperature data for 252 months are plotted in Figure 5.5. The corresponding fitted periodic function curve, the broken line (selected to be periodic on purpose), is plotted alongside in the same Figure.

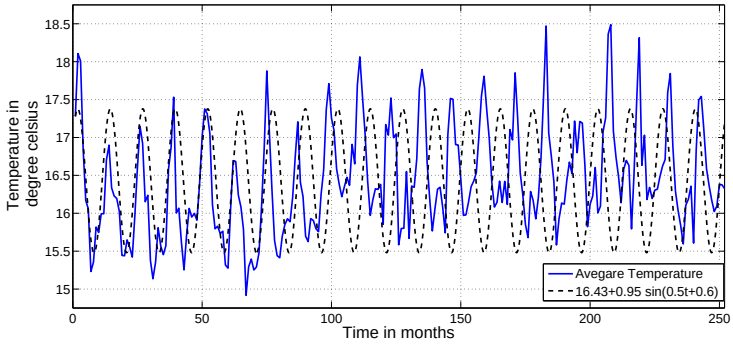

Figure 5.5: The monthly average temperature of the cold zone in Genale-dawa basin, Ethiopia, from year 1994 to 2014

In Figure 5.5, in order to have a mathematical equation that approximates the curve obtained from the data it was fitted by another curve, the fitting is done by a built in program in MATLAB which gives a confidence interval of 95%. The equation of the fitted curve is given as $T(t) = 16.43 + 0.95\sin(0.5t + 0.6)$. Where t is the number of months and 16.43 is the average temperature of the region.

The temperature ranges of cold highlands is from 6.75^oC to 27^oC; we chose the most suitable time for growth rate $\overline{T}_r = 16.43$ and using the equations of the fitted

curves, using the standard deviation $\alpha = 10$. We have the temperature dependent component of the growth rate as;

$$U_r(T) = 0.8 \exp - \frac{(T - 16.43)^2}{10^2} \tag{5.62}$$

$$T_{ave}(t) = 16.43 + 1.5 \sin(0.6t + 0.05) \tag{5.63}$$

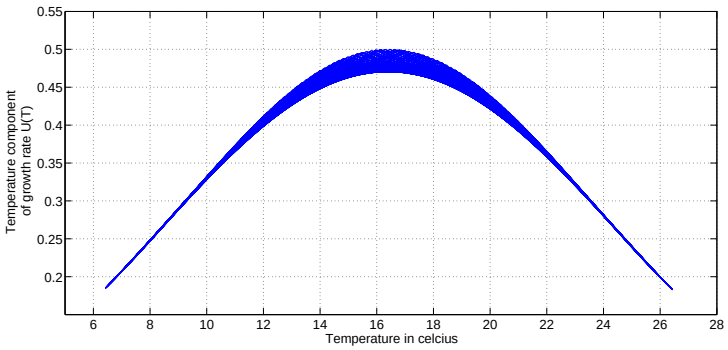

Figure 5.6: Growth rate of plants as a function of temperature U(T).

Figure 5.6 shows that at both extreme ends of the temperature plant growth rate decreases. That is, when it is cold (below 10^oC) they loose the warmth of the soil and cannot grow; and when it is hot (above 24^oC) due to evaporation they loose a lot of water and plants go to dormancy or die.

For rainfall, we chose the value $\overline{R}_r = 117.4$mm for which growth rate would reach its maximum with the standard deviation of $\nu = 120$. The feeding rate would reach its maximum at $\overline{R}_a = 200mm$ with the standard deviation of $\upsilon = 85$ for the simulation,

$$V_r(R) = 0.6 \exp \left\{ - \frac{(R - 117.4)^2}{120^2} \right\} \tag{5.64}$$

$$Y_a(R) = 0.5 \exp \left\{ - \frac{(R - 200)^2}{(85^2))} \right\} \tag{5.65}$$

$$R(t) = 117.4 + 100 \sin(0.6t + 0.1) \tag{5.66}$$

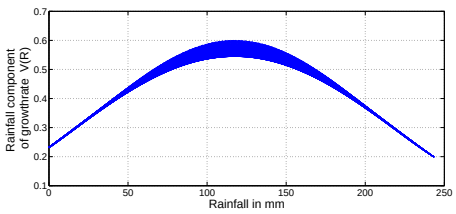

Figure 5.7: Growth rate of plants as a function of rainfall V(R).

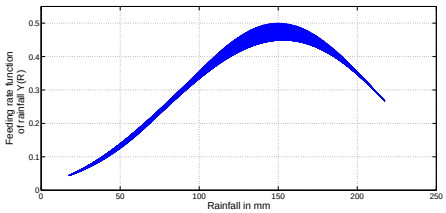

Figure 5.8: Feeding rate of herbivore on plants as a function of rainfall $Y(R)$.

Figure 5.7 shows that at both extreme ends of rainfall plant growth rate decreases. That is, when it is low (lack of enough water) plants cannot grow or die and when it is high (flood) soils will be water-logged and lack of air prohibits plant growth or plants may die.

Figure 5.8 shows that at both extreme ends of rainfall herbivore feeding rate decreases. That is, when it is low (lack of enough water) since herbivores need moisture in their feed and when it is high (flood) herbivores cannot move around and look for feed and/or the plants themselves will be washed away and there is no feed.

Therefore, the growth rate of plants, as a function of temperature and rainfall is defined as equation (5.67) and plotted in Figure 5.9.

$$r(T,R) = 0.4\left(\exp\left\{-\frac{(T-16.4)^2}{10^2}\right\}\right)\left(\exp\left\{-\frac{(R-117.4)^2}{120^2}\right\}\right) \quad (5.67)$$

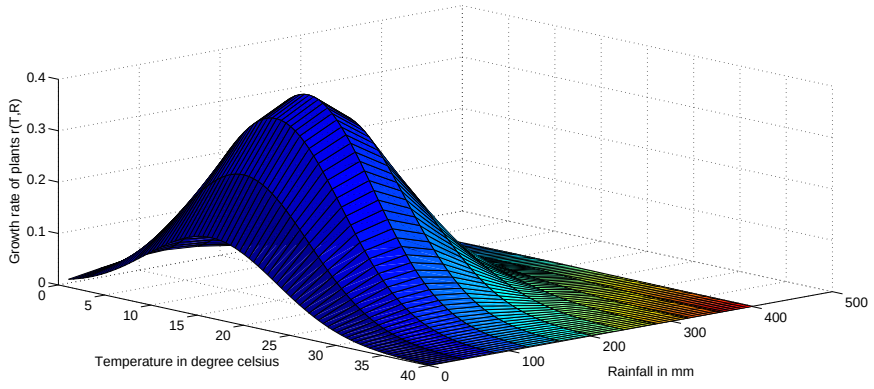

Figure 5.9: Growth rate of plants as a function of temperature and rainfall $r(T,R)$.

The feeding rate of herbivores on plants, as a function of rainfall is defined as

$$a(R) = 1.675\exp\left\{-\frac{(R-200)^2}{(85^2))}\right\}$$

Remark 5.3.1. *Here it is assumed that the feeding rate of herbivores is only a function of rainfall because in the case of extreme temperature, they only change their grazing time and it is assumed that the rate remains almost the same.*

Once again, the graphs of temperature and rainfall are assumed to be periodic functions of same period (1 year) hence the growth rate function $r(T,R)$ and the feeding rate function $a(R)$ are also periodic functions of same period as temperature and rainfall functions (1 year).

Plants in this part of the study area are mostly moist evergreen broad leaved. But most of them are non-palatable.

Next using this time dependent parameters $r(T, R)$ and $a(R)$ in the model (5.1) and parameter values from Table 5.1, we discuss the existence and stability of both populations in the cold highland region numerically.

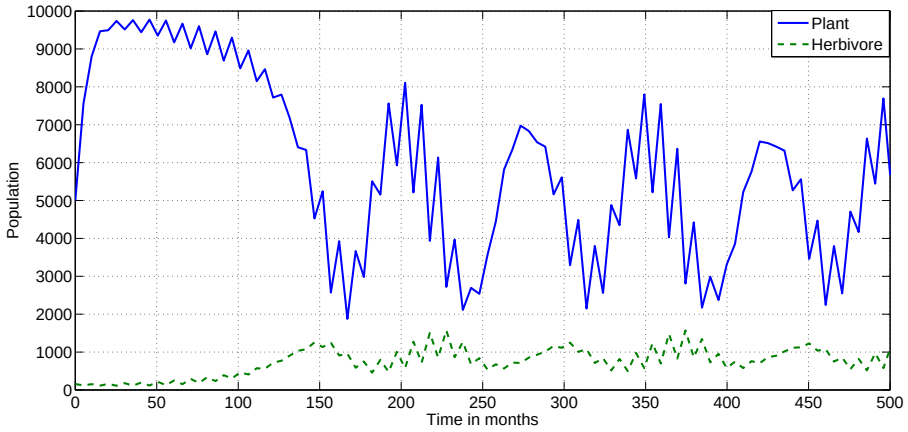

Figure 5.10: Plant herbivore population dynamics in the cold highlands of Genale-Dawa basin using $r(T.R)$ and $a(R)$ in mean rainfall and average temperature.

From Figure 5.10 one can observe that the plant population decreases as a result of herbivore population increase and a lot of plant biomass is consumed and or damaged. Then as the food source decreases the herbivore population also starts decreasing. This gives the chance for the plant population to grow again and this cycle continues. Hence coexistence of plant and herbivore populations in the cold highland region is attained. Furthermore, keeping the rainfall the same and varying the temperature from the minimum to maximum in that area varies the rate of growth and the feeding rate.

In the Cold highlands of the Genale-Dawa region, if the rainfall amount varies by 10% (increase or decrease by 10%) the effect on the whole population dynamics is shown in Figure 5.11 and Figure 5.12. This means, due to global climate change if we have upto 10% more rain in the area the herbivore population would disappear and go to extinction in this zone, perhaps shifting their locations (migration) (Figure 5.11).

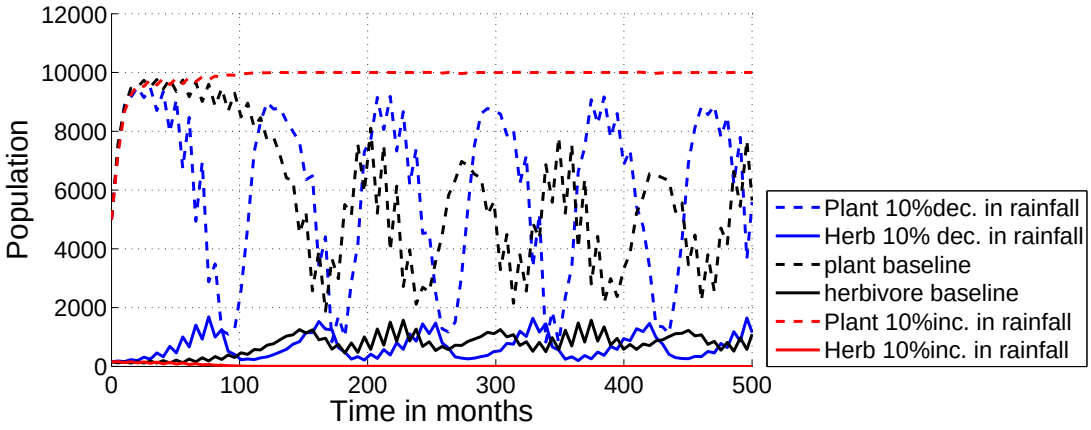

Figure 5.11: Plant herbivore population dynamics in the cold highlands of Genale-Dawa basin using $r(T.R)$ and $a(R)$in average temperature and 10% increase/decrease in mean rainfall.

In this climatic zone, if rainfall increases by 10% of the baseline rainfall amount it would lead to herbivore population extinction because they cannot move around and feed themselves. On the other hand if rainfall decreases by 10% of the baseline rainfall amount then they feed themselves, find a mate and reproduce. In this case, one can observe better herbivore population.

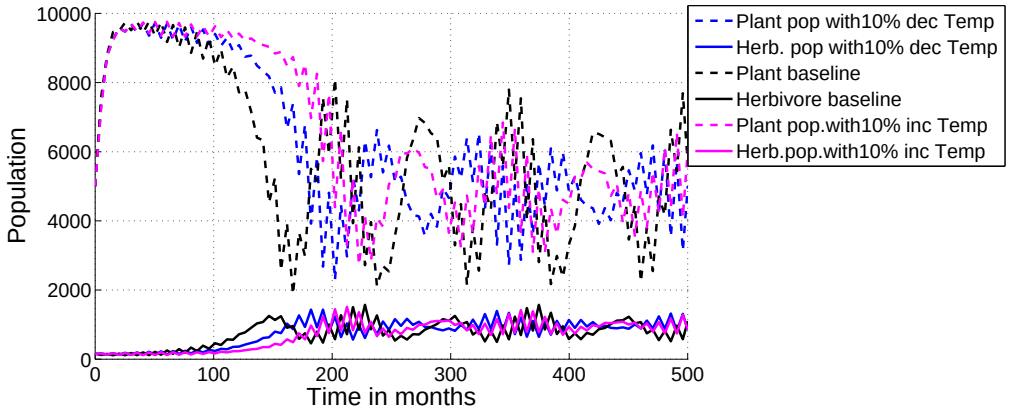

Figure 5.12: Plant herbivore population dynamics in the cold highlands of Genale-Dawa basin using $r(T.R)$ and $a(R)$ in average rainfall and 10% increase/decrease in mean temperature.

In the highlands of Genale-Dawa if temperature increases by 10% we can observe the herbivore population would take less time to increase its number while in case of 10% decrease it would take longer time to pass the Allee constant.

5.3.2 Hot Lowlands with Annual Rainfall $< 500mm$

Area with annual rainfall $< 500mm$ is hot semi-arid lowlands [Gon96]. This place has a sparse vegetation. The hot lowland region has two rainy seasons: the first is between March and May and the second is October to November. Lowest vegetation cover is observed in June and July following the dry months of May and June.

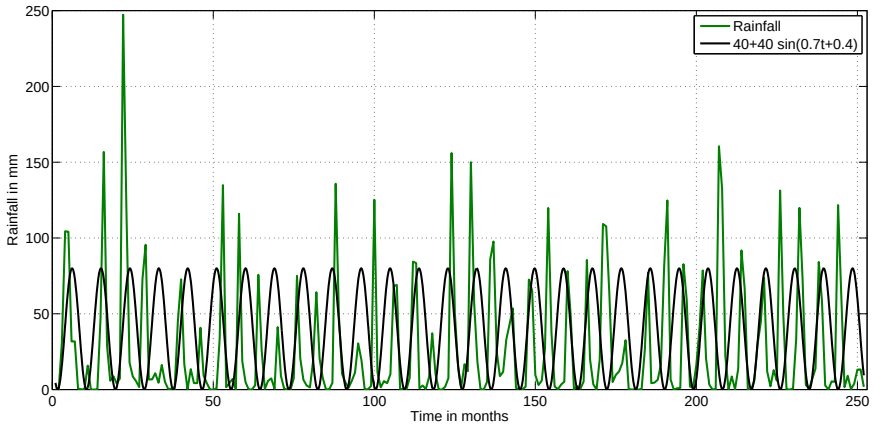

Figure 5.13: The monthly rainfall of the hot zone in Genale-dawa basin of Ethiopia in the years $1996 - 2016$

For average monthly rainfall of the hot lowlands, the original data (from the red region in Figure 5.3) is drawn in continuous line while the fitted curve is shown in the broken lines.

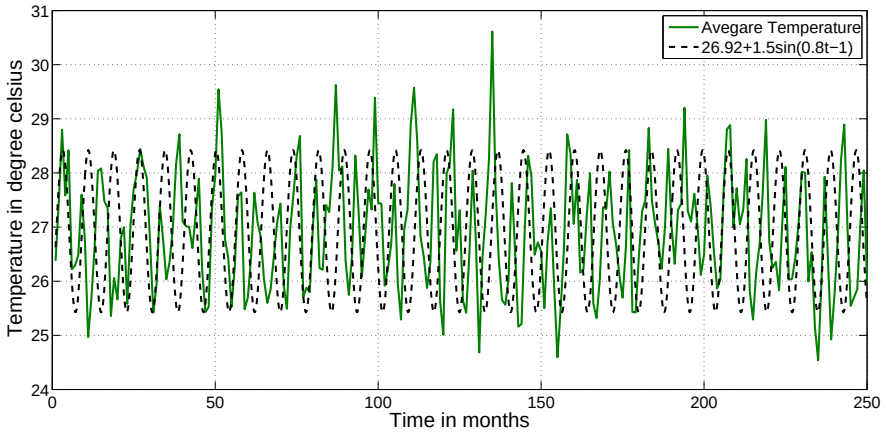

Figure 5.14: The monthly average temperature of the hot zone in Genale dawa basin, Ethiopia, from year 1994 to 2014

In the hot lowlands of Genale dawa river basin, the temperature ranges from 24.5^oC to 38^oC. We chose the temperature suitable for the growth of plants in this area $\overline{T}$ to be 30^oC and hence have the temperature dependent component of the growth rate

which takes the same form except that the plants in this region require a different suitable temperature $\overline{T}$ to grow;

$$U_r(T) = 0.7 \exp\left\{-\frac{(T-30)^2}{10^2}\right\} \tag{5.68}$$

$$T(t) = 26.92 + 1.5\sin(0.8t - 1) \tag{5.69}$$

As the temperature increases more than $\overline{T}$ the plant growth rate decreases. That is, when it is very hot (above 34^oC) due to evaporation they loose a lot of water and plants go to dormancy and loose their leaves to minimize loss of water or die.

We choose some values of rainfall for which growth rate would reach its maximum R_r and the feeding rate would reach its maximum R_a for the simulation,

$$V_r(R) = 0.7 \exp\left\{-\frac{(R-80)^2}{4000}\right\} \tag{5.70}$$

$$Y_a(R) = 1.85 \exp\left\{-\frac{(R-107)^2}{4000}\right\} \tag{5.71}$$

$$R(t) = 40 + 40\sin(0.7t + 0.4) \tag{5.72}$$

As rainfall increases plant growth rate also increases. Likewise, as rainfall increases herbivore feeding rate also increases since herbivore prefer to consume food when there is moisture in it. But as the rainfall reachs “too much" herbivore find it difficult to move around. Furthermore the soil will be water-logged and lack of air prohibits plant growth as a result of the excess soil moisture.

Therefore, the growth rate of plants, as a function of temperature and rainfall is given as $r(T,R) = \left(0.7 \exp\left\{-\frac{(T-30)^2}{10^2}\right\}\right)\left(0.7 \exp\left\{-\frac{(R-80)^2}{4000}\right\}\right)$ and is plotted in Figure 5.15

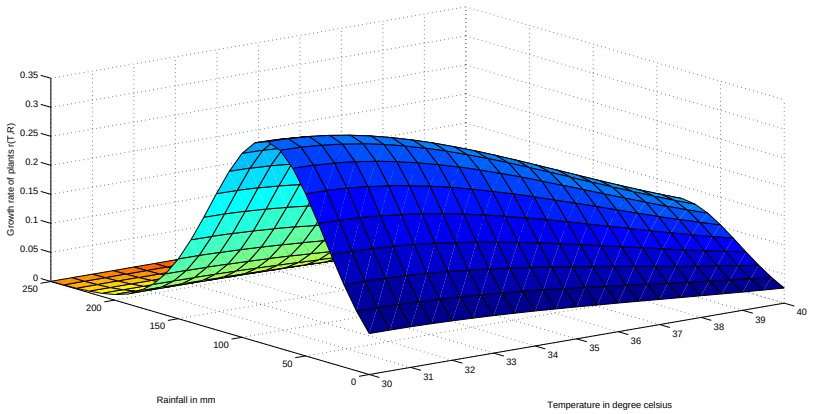

Figure 5.15: Growth rate of plants as a function of temperature and rainfall $r(T,R)$.

The feeding rate of herbivores on plants, as a function of rainfall is defined as

$$a(R) = 1.85 \exp\left\{-\frac{(R-107)^2}{4000}\right\}$$

and is plotted in Figure 5.16

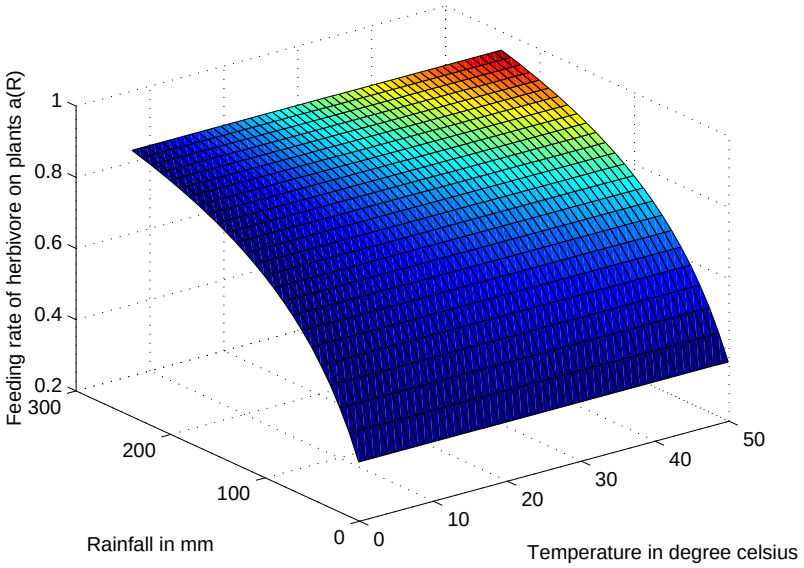

Figure 5.16: Feeding rate of herbivores on plants $a(R)$ as a function of rainfall.

To study the dynamics of the interaction of plants and herbivore in the hot lowlands, we use the temperature and rainfall dependent parameters. The thresholds for the coexistence of both plant and herbivore populations are discussed. Furthermore to study the significance of the parameters in the time dependent parameter expressions, we use the model (5.1) with the time dependent parameters $r(T, R)$ and $a(R)$.

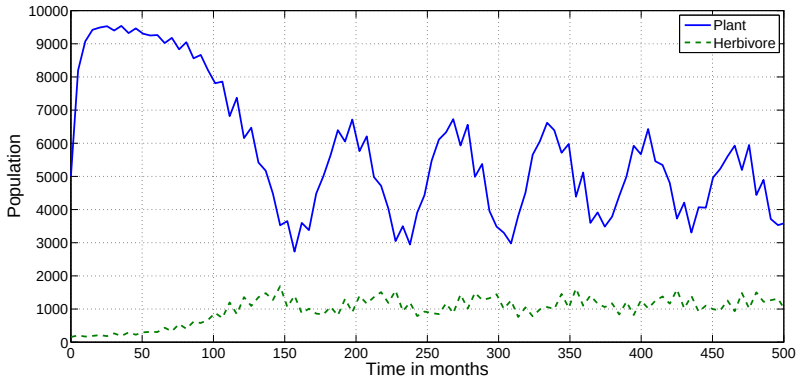

Figure 5.17: Plant herbivore population dynamics in the lowlands of Genale-Dawa basin using $r(T.R)$ and $a(R)$in mean rainfall and average temperature data.

In Figure5.17 one can observe that the plant population starts decreasing as the herbivore population increases; this is due to the increased consumption by herbivores. As the plant population decreases, the herbivore population also decreases as it depends on the availability of feed. Once again as the herbivore population decreases the plant population starts growing again. This cycle continues and it shows the coexistence of plant and herbivore populations in the hot lowlands in the Genale-Dawa.

Plants in hot lowland areas usually grow along the river courses. Vegetation type is savanna grassland and non-palatable bush. Even though it is green a good part of it is not palatable to herbivores. The type of herbivore in the hot lowlands includes goats and camels. Therefore they have a natural mechanism to stand the temperature and adjust themselves to the hotness of the place so that they can exist in the region.

It needs the attention of the environment conservation authorities or the government to intervene because the hot lowland area in the Genale-Dawa basin is now expanding to the areas of the temperate zone. This might result in the desertification of the region. If the rainfall in the hot lowlands increase by 10 percent and we keep the maximum temperature, we can see that there will be a better number of herbivore which drives the dynamics to be more oscillatory (see Figure 5.18).

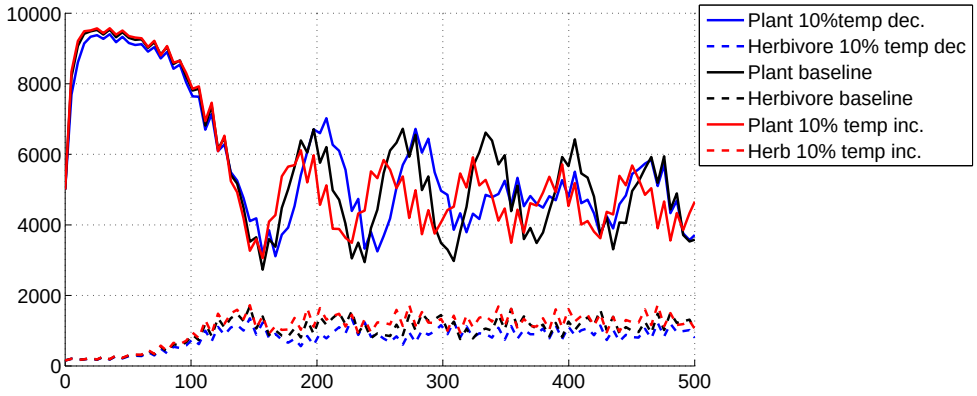

Figure 5.18: Plant herbivore population dynamics in the hot lowlands of Genale-Dawa basin using mean rainfall and 10% increase/decrease in average temperature.

On the other hand if the rainfall decreases by as small as 1.5% then the herbivore population will disappear in this zone and go to extinction or migrate to other regions (see Figure 5.19). This should be given much attention since this climatic zone is expanding, the herbivore in the area might be at real risk.

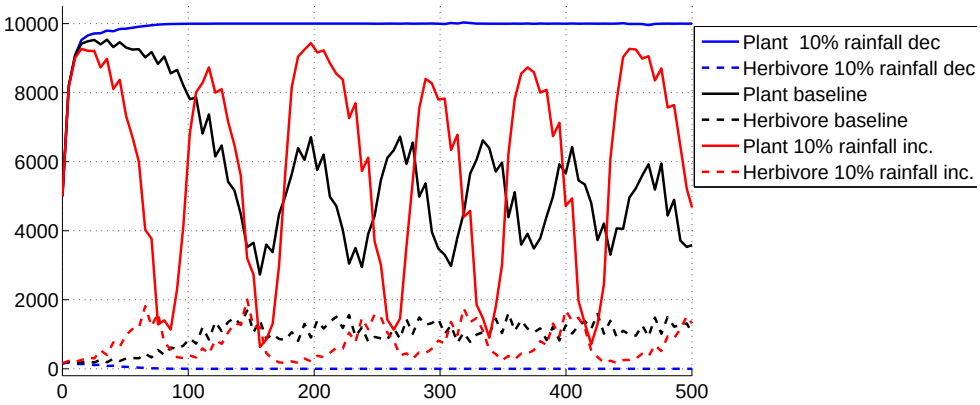

Figure 5.19: Plant herbivore population dynamics in the hot lowlands of Genale-Dawa basin using average temperature and 10% decrease/increase in mean rainfall.

5.3.3 Sub-Tropic Zone with Annual Rainfall $501mm - 800mm$

The region with annual rainfall between $501mm$ and $800mm$ is the temperate cool sub humid highlands [Gon96]. This region has a mosaic of forest-shrubs-grassland vegetation. This area has its peak rainy season in July and August and its dry months are December through March. Vegetation cover starts increasing in May and reach its maximum in November. The lowest vegetation cover of the region is in March immediately after the lowest rainfall in February.

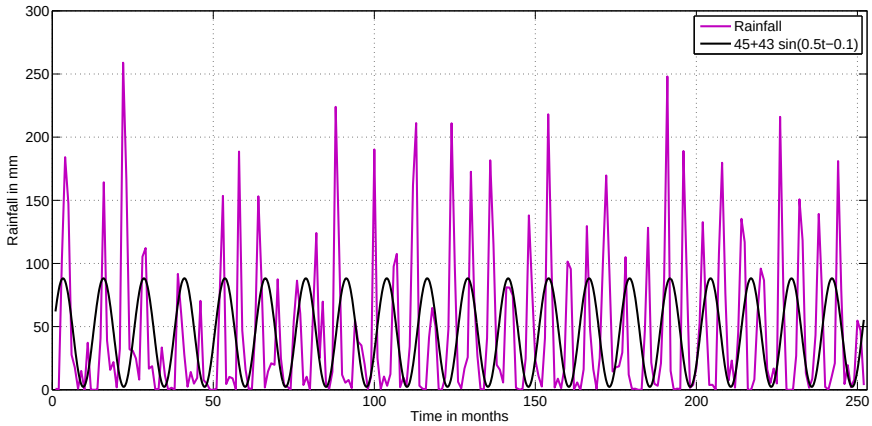

Figure 5.20: The monthly rainfall of the sub tropic zone in Genale dawa basin, Ethiopia, in the years $1996 - 2016$

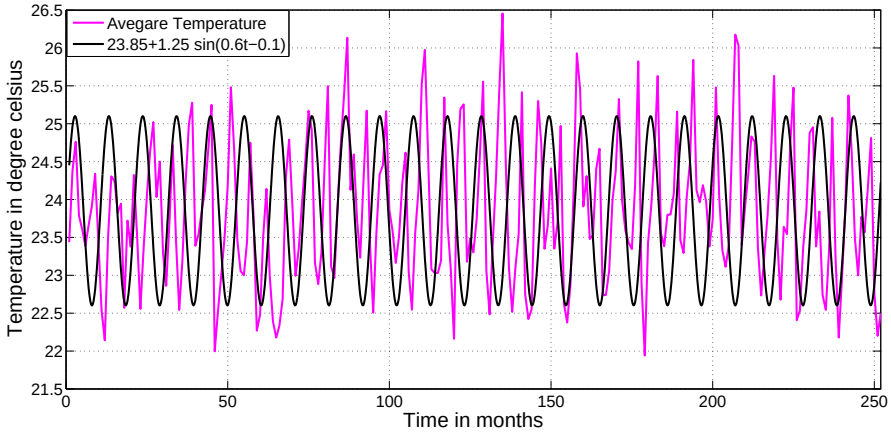

Figure 5.21: The monthly average temperature of the sub tropic zone in Genale dawa basin, Ethiopia, from year 1994 to 2014

In the temperate zone, the temperature ranges from 16^oC to 31^oC; we chose the favorable temperature $\overline{T}$ to be 26 and we employed the same formula for the temperature dependent component of the growth rate as in (5.62) but with different suitable temperature due to the presence of different plant and herbivore species;

$$U_r(T) = 0.8\exp\left\{-\frac{(T-26)^2}{30^2}\right\}, \tag{5.73}$$

$$T(t) = 23.85 + 1.25\sin(0.6t - 0.1) \tag{5.74}$$

A decrease in the plant growth rate as the temperature is above 29 can be justified due to evaporation. They loose a lot of water and plants go to dormancy or die.

We chose suitable rainfall values and temperature values for which growth rate would reach its maximum and the feeding rate would reach its maximum for the simulation as

$$V_r(R) = 0.9\exp\left\{-\frac{(R-206)^2}{400^2}\right\}, \tag{5.75}$$

$$Y_a(R) = 1.42\exp\left\{-\frac{(R-207)^2}{40000}\right\}, \tag{5.76}$$

$$R(t) = 45 + 43\sin(0.5t - 0.1). \tag{5.77}$$

At the initial stage, as the rainfall increases plant growth rate also increases, and herbivore feeding rate increases. That is, when rainfall is low (lack of enough water) and when rainfall is high (water-logged condition) herbivores cannot move around and look for food and or the plants themselves will be washed away and there is no food.

Therefore, the growth rate of plants, as a function of temperature and rainfall can be expressed as $r(T,R) = \left(0.8\exp\left\{-\frac{(T-26)^2}{30^2}\right\}\right)\left(0.9\exp\left\{-\frac{(R-206)^2}{400^2}\right\}\right)$, and is plotted in Figure 5.22

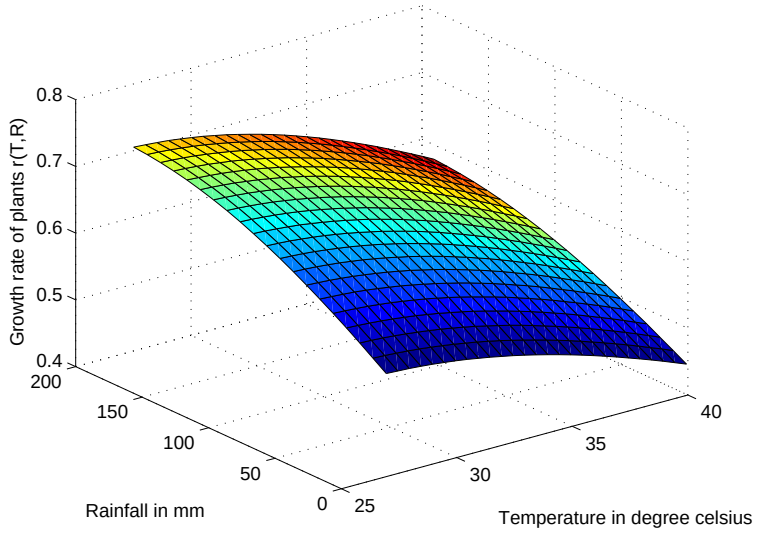

Figure 5.22: Growth rate of plants as a function of temperature and rainfall $r(T,R)$.

The feeding rate of herbivores on plants, as a function of rainfall is defined as

$$a(R) = 1.85\exp\left\{-\frac{(R-107)^2}{4000}\right\},$$

and is plotted in Figure 5.23

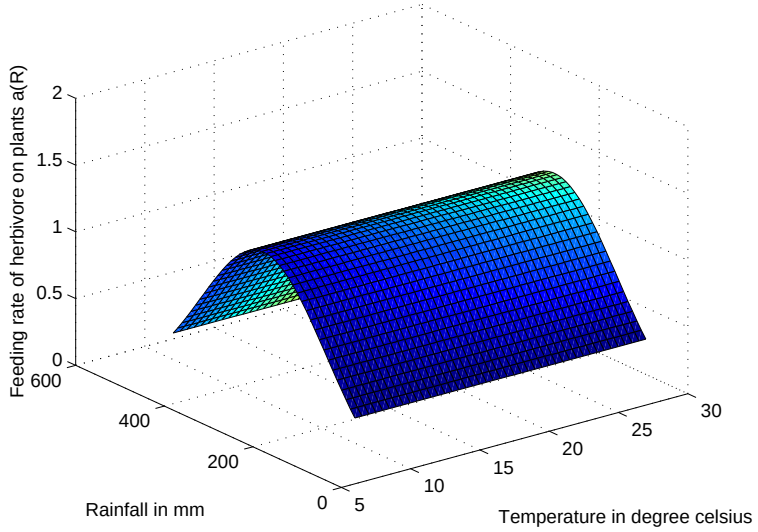

Figure 5.23: Feeding rate of herbivores on plants as a function of rainfall $a(R)$.

To study the dynamics of the plant herbivore interaction in the temperate subtropic zone we use the model (5.1) with time dependent parameters $r(T, R)$ and $a(R)$ in the model (5.1) we discuss the existence and stability of coexistence limit cycle.

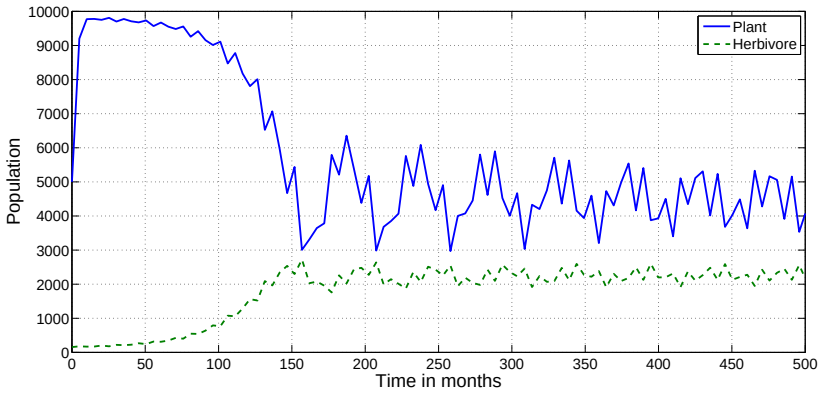

Figure 5.24: Plant herbivore population dynamics in the sub-tropic zone of Genale-Dawa basin using $r(T.R)$ and $a(R)$ in mean rainfall and temperature.

Figure 5.24 shows that it takes longer time for the herbivore population to grow and once it passes the Allee effect reaches a certain amount it oscillates slightly around an average number.

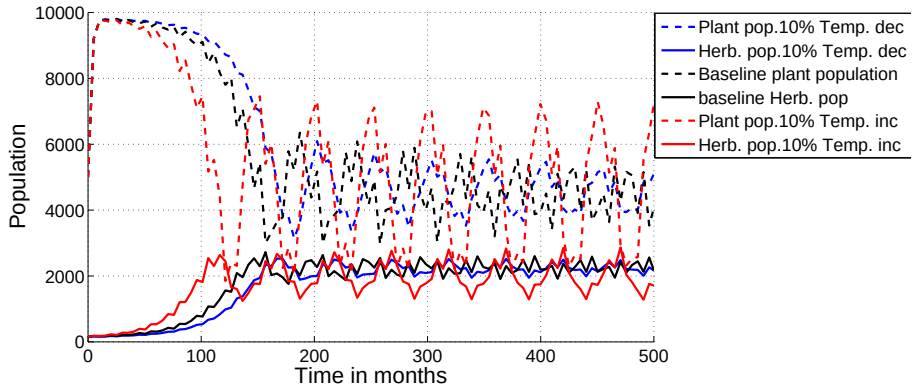

Figure 5.25: Plant herbivore population dynamics in the sub-tropic zone of Genale-Dawa basin using the mean rainfall and letting the temperature to increase/ decrease by 10%.

Plants in the subtropic temperate zone are usually scrub grass lands. In the subtropic temperate zone of Genale Dawa basin, there is a considerable human population that influence the dynamics. There is crop production and hence in addition to grazing, herbivore also use crop residue as a source of food.

To see the effect of temperature and rainfall keeping one constant and varying the other we do the following analysis. If rainfall is fixed to the mean as it is and if

temperature increases and decreases by 10% there is no significant change in the dynamics (see Figure 5.25).

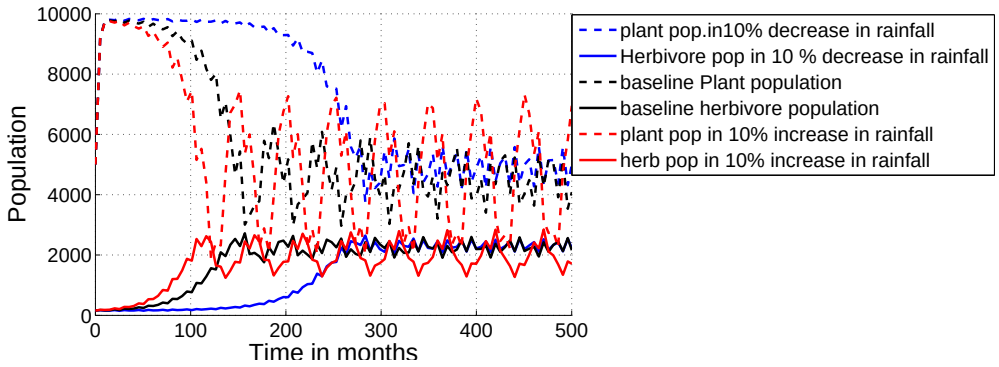

Figure 5.26: Plant herbivore population dynamics in the sub-tropic zone of Genale-Dawa basin using the mean temperature and letting the rainfall to increase/ decrease by 10%.

However, If the temperature is kept to the average and if the rainfall increases/decreases by as much as 10% there is a significant change in this region. In the temperate zone the 10% increase in rainfall allows the plant to grow faster and this in turn encourage the fast emergence of herbivore. But in this case life is short and fast. on the other hand, a 10% decrease in rainfall leads the herbivore to take a long time to exceed the Allee constant and guarantee its existence in the region (see Figure 5.26).

5.4 Discussion and Summary

A mathematical model that takes the periodic variation of some of the essential climatic parameters is considered in this study. The Plant-Herbivore interaction system is then analyzed for wel-posedness, existence and uniqueness of periodic solutions. The average threshold value $\mathcal{R}_o$ was found for the coexistence of both populations. The lower limits of the supermum values of both species (P and H) and the upper limits of the infmum values of both species are obtained. That is, the interval of coexistence of both species . The result shows the effect of a changing environment in the dynamics remains in this region. For $\mathcal{R}_o > 1$ and provided the positivity and periodicity of the time dependent parameters $r(t)$ and $a(t)$ the unique periodic coexistence solution remain bounded in the infimum and suprimin as shown in Theorem 5.1.1. To validate the time dependent mathematical model, two examples were used. One simple periodic functions of $r(t)$ and $a(t)$ is taken as sinusoidal. Furthermore, using field data for temperature and rainfall, the varying parameters are estimated as function of time. In all the three climatic zones chosen we are able to use our proposed model (5.1) to show coexistence of plant and

herbivore populations. Although the amplitudes, the periods and phase angels are not similar it has shown coexistence in all the regions.

Keeping the rainfall constant as the temperature varies by 10% upwards and downwards the growth rate parameter increases. As a result we can observe variations in the whole dynamics of the plant-herbivore interaction. As the temperature varies periodically the population dynamics path is perturbed from its smooth path it was taking while considering a constant case (see Chapter 3).

Furthermore, varying the amplitudes of the growth rate $r(t)$ and the feeding rate $a(t)$ results in the herbivore population extinction and plant population reaching the carrying capacity.

As altitude varies in the Genale-Dawa river basin, there are three climatic zones. For the three climatic zones we can observe that there are different plant and animal species which can adapt themselves to the existing environment and sustain the coexistence. In the cold highlands the number of herbivores is few because of the temperature constraint. Furthermore the plants in this region are mostly non-palatable species. In the hot lowlands the number of herbivore is again few because the rainfall or water shortage is the constraint. Moreover, the number of herbivore is much smaller than the plant population since the plant needs just two rainy seasons to survive. In the hot lowlands, the herbivore population cannot grow (appear in the picture quickly) only because of availability of rainfall, as there are cases to consider such as the Allee effect. A problem in the Genale-dawa river basin is that the hot lowland climatic region is likely to expand due to global climate change. In the sub-tropic temperate region we have better herbivore population because this part of the basin has high human population and therefore the herbivore feed on crop residues as a supplement.

6 Conclusion

The expansion of deserts, extinction of endemic species, overgrazing of vegetation and climate change are some of the problems in the developing world. To address these problems we need to understand the interaction between plants and herbivores. In this study, we started with a plant-herbivore mathematical model and took assumptions on the interactions. The effect of taking a plant density-dependent herbivore death rate, Allee effect and harvest rate in a plant-herbivore model where the plant population grows logistically and the functional response of herbivores as Holling type II function was of interest to us. In addition, since plant herbivore interaction is highly affected by the environmental perturbation, the use of a stochastic differential equation model is discussed to get a better insight on the environmental noises. Such noises could be either factors that affect plant population only, factors that affect herbivore population only or factors affecting both populations.

We are also interested in the study of the effect of temperature and rainfall variation on the plant herbivore system, that is, the effect of some climatic factors on the herbivore feeding, growth, reproduction, on the plant growth and the dynamics as a whole. We have also studied the effect of temperature variation on the environment and on the dynamics of this interaction.

6.1 Concluding Remarks

In this work a plant-herbivore interaction model has been studied under different assumption such as assuming a constant environment, stochastic environment and a periodic environment. The question when is coexistence possible and how to avoid extinction of species or overgrazing of vegetation is addressed.

In the first part of the main results, which started in the third chapter, a plant-herbivore model with logistic growth rate for the plant population and Holling type II functional response was assumed for the feeding interaction. For herbivore emergence rate, a linear multiple of the functional response and the Allee effect were considered since herbivore population is more prone to the Allee effect than plants. Under the assumption that the mortality of herbivores depends on the availability of food source, we used density dependent variable mortality rate which is a decreasing function of the functional response instead of constant death rate (which is usually

considered in literature). The mortality rate is positive and bounded below since no animal can leave forever, and we also considered the effect of human interference in terms of the harvest rate μ.

As a result, a multiple equilibrium is obtained similar to the results by Terry [Ter15] and Verdy [Ver10], in which constant death rate was considered. That means, two herbivore free equilibrium $(0, 0)$, which is unstable and $(K, 0)$, which is locally asymptotically stable, were found. We have also defined the reproduction number $\mathcal{R}_o$, which can be interpreted as the average rate in which the herbivore population is replacing themselves. Using this threshold value, conditions for existence/coexistence of the herbivore population are formulated and analyzed.

Moreover, depending on the initial plant and herbivore population being less or greater than the respective minimum values (that is availability of sufficient food and mate) and due to the newly defined density dependent death rate, we have presented specific conditions that determine the extinction of the herbivore population. Even though $\mathcal{R}_o > 1$, the plant population can grow to the carrying capacity of the environment while herbivore extinction occurs either if the initial herbivore population is less than the least number of herbivore population needed to keep the population existing in the system and the initial plant population is positive, or if the initial herbivore population is greater than the least number of herbivore population needed to keep the population existing in the system but there is no enough plant population to feed on and reproduce. That means, if the initial herbivore population is less than the least number of herbivore population needed to keep the population existing in the system with the initial plant population is positive then the herbivore population goes to extinction irrespective of the value of other parameters. This minimum number of herbivore population is due to the Allee effect. In the absence of Allee effect, Equation (**??**),$H_m = 0$ and there will be no threshold for the least number of herbivores.

In addition, it is found that if the initial herbivore population is greater than the least number of herbivore population needed to keep the population existing in the system, then the herbivore population can still go to extinction if there is no enough plant population to feed on and reproduce. Furthermore, to guarantee the non-extinction of the herbivore population we need the initial density of herbivore population to be greater than the least number of herbivore population needed to keep the population existing in the system; and the initial plant population must be above the minimum required level so that there is sufficient plant population for the herbivore to feed on. This is a new addition as compared to the previous findings, for example see [Ter15].

We have also found a stable limit cycle for coexistence state inside the trapping region Σ. Numerical simulations for the main results are also discussed using parameter values in Table 3.3 and sample initial values. In this work the sensitivity of the parameters with respect to the threshold $\mathcal{R}_o$ and with respect to each other is also discussed using the Latin hyper-cube sampling method/ partial rank correlation coefficient (LHS/PRCC) method with P-value < 0.01. It is found that the feeding rate a has a direct influence independent of any other parameters on the reproduction number while the harvest rate μ has an inverse influence. Furthermore, even if they appear as a product in the reproduction number, a and c are independently sensitive parameters to $\mathcal{R}_o$.

In Chapter4 the model in Chapter 3 was extended to include the randomness of the environment by including noise terms. We analyzed the effect of noise in system model (4.2) for two different scenarios when environmental noises β_1 and β_2 influence the rate of change of plant and herbivore populations, respectively. First, we analyzed the simplified model (4.2) for positivity, existence and uniqueness of solution in a bounded set and then extended the idea to the proposed model (4.1). We obtained an insight into the complicated effect and consequence of the stochastic noise on the behavior of both populations. When noises of different intensities are added, it is observed that the stability of the deterministic state becomes quasi stable around the deterministic steady state. By increasing the noise intensity of the food source β_1, the effect on both species is slow and is only significant in the long run. The effect is manifested more visibly in the plant population than the herbivore population.

On the other hand, increasing the noise term in the herbivore population, β_2, results in an immediate and more significant change in both species. The effect of both noises β_1 and β_2 can significantly affect the co-existence of both species including the possibility of extinction of the herbivore population. Therefore, ignoring environmental noises would affect the quality of the environment, this in turn could lead to extinction of both population or to a smaller number of the herbivore population such that they cannot overcome the Allee effect.

These results have implications for the management of game parks where the park area is confined but the herbivore population is allowed to increase and culling takes place at irregular intervals. The herbivore population could affect the quality of the park. We can give two examples in support of our model revelations. First, the elephant population has increased rapidly in the Chobe National Park, North Botswana, due to introduction of water supplementation and better than average rainfall in certain years resulting in good vegetation which have provided a conducive environment for the elephant population. However, the increase in the population has fluctuated depending on food availability[Loa+09]. On the other hand, the

antelope number has been reduced due to frequent droughts, increased predation by lions and loss of habitat due to human invasion [Hav+16]. The provision of artificial water-points within the antelope's range also resulted in extensive habitat degradation and competition with other herbivores.

Then instead of considering the environmental change as a random noise, we identified among the coefficients that are highly influenced by the environmental factors such as a change in temperature and rainfall. It is clear that not all coefficients of the model system are dependent on these factors. Therefore, in Chapter 5, a mathematical model with only the parameters plant growth rate $r(t)$ and herbivore feeding rate $a(t)$ were considered to be positive and periodic functions of time. The Plant-Herbivore interaction system is then mathematically analyzed for welposedness, existence and uniqueness of periodic solutions. The average threshold value $\mathcal{R}_o$ was found for the coexistence of both populations. The trapping region for the dynamics is formulated and analyzed. That is, the interval of coexistence of both species is obtained. The result shows that the effect of a changing environment in the dynamics remains in this region.

For $\mathcal{R}_o > 1$ and provided the positivity and periodicity of the time dependent parameters $r(t)$ and $a(t)$ the unique periodic coexistence solution remain bounded in the trapping region as shown in Theorem 5.1.1. To validate the time dependent mathematical model, two examples were used. The first one is simple periodic functions formulation for $r(t)$ and $a(t)$ are taken as sinusoidal function; and the other one is with the fitted function formulated from real data about temperature and rainfall that was collected from a place in Ethiopia. Using field data for temperature and rainfall, the varying parameters are estimated as function of time. Although the amplitudes, the periods and phase angels are not similar it has been shown that coexistence in all the regions is maintained.

Keeping the rainfall constant, when the temperature is varied by 10% upwards and downwards the growth rate parameter increases. As a result we have observed variations in the whole dynamics of the plant-herbivore interaction. As the temperature varies periodically the population dynamics path is perturbed from its smooth path it was taking while considering a constant case in Chapter 3.

Furthermore, varying the amplitudes of the growth rate $r(t)$ and the feeding rate $a(t)$ by varying the temperature and the rainfall by 10% it results in the possibility of extinction of herbivore population while plant population reaching the carrying capacity.

As the altitude varies in the Genale-Dawa river basin, we have three broad climatic zones. For the three climatic zones we can observe that there are different plant and

animal species which can adapt themselves to the existing environment and sustain the coexistence. In the cold highlands the number of herbivores is few because of the temperature constraint. Furthermore the plants in this region are mostly non palatable due to different reasons. In the hot lowlands the number of herbivore is again few because the rainfall or water shortage is the constraint. Moreover, the number of herbivore is much smaller than the plant population since the plant needs just two rainy seasons to survive. In the hot lowlands, the herbivore population cannot grow (come to existence) only because of availability of rainfall, there are cases to consider such as the Allee effect. The problem in the Genale-Dawa river basin is this that the hot lowland region is expanding. In the sub-tropic temperate region we have better herbivore population because this part of the Genale Dawa river basin has high human population and therefore the herbivore feed on crop residues as a supplement.

6.2 Recommendation

In ecology, it is important to consider all affecting factors as much as possible before making decision. In our model we have shown that considering the Allee effect on the herbivore population, plant-density dependent herbivore death rate, harvest rate and taking the environmental noise into account. The study indicated that, there is a possibility of extinction of the animal population from the region with the occurrence of small environmental perturbations. Therefore it is recommended that the animal husbandry or the game reserve authorities should take into account the environmental noises when they decide on any intervention mechanisms.

Due to global climate change it is likely that the temperature and rainfall distribution and intensity change accordingly. From the time dependent model we have seen that a change as small as 10% of the surrounding temperature and rainfall in the three different altitudes affects the dynamics of the plant herbivore population. The effect might even go upto leading to extinction or disappearance of the herbivore population from that specific region. These therefore, suggests that if environmental conservation works that correspond to the climate variation and altitude are made properly, a comfortable ecosystem for both plants and herbivore can be achieved and hence the animal population will be kept in the region.

Among the climatic factors, too much rainfall is a major problem in the cold highlands. On the contrary too little rainfall is the major restriction in the hot lowlands. The concerned authorities need to plan appropriate intervention to be made immediately after excessive rainfall in the case of highlands and immediately after shortage of rainfall on the low land so that the animal population remain in the region or do not decrease in size.

Environmental fluctuations due to global climate change are likely to cause the problem of expansion of desert in the Genale-Dawa river basin. To address this problem it is recommended to do pre-planned environmental protection works (such as planting indigenous trees, introducing artificial water sources and soon) that should benefit both density of plants and herbivore population.

Herbivores are reproducing sexually; that means, a female herbivore needs to stay alive and be able to find a mate to give birth to the new generation. The Allee effect indicates the smallest amount of herbivore required to overcome these challenges and to ensure the continuation of herbivore existence. On the other hand, too many herbivores in a certain region is also a danger to the vegetation as we have seen on the simulation of the model. These may lead to land degradation and also competition among herbivores. In the wild life, having too many herbivores might endanger them to their natural enemies, i.e it will make them easy targets. Therefore it is recommended to pay attention to the minimum number required based on the area coverage, in deciding when to harvest and also be cautious to the amount of harvesting. The authorities in the game reserves should also be cautious on when to allow or ban hunting depending on these threshold values.

6.3 Challenges and Future Work

Mathematical models are appropriate tools for the efficient assessment of environmental quality, for studying the ecosystem functioning properties and for monitoring biodiversity. Ecological models are used to reinforce policy design and environmental planning and management. However, when the models are formulated, the simpler the models the easier the mathematical analysis. But the simple models may not usually explain the ecology fully. Nature is usually interrelated and complex.

The challenges encountered in this work was mainly due to the limitation of theories in mathematics to qualitatively analyze non-autonomous models and non-linear stochastic representations. Moreover for the non-autonomous system and the stochastic system the theories have limitations in describing the sensitivity and bifurcation analysis.

The possible extensions of this work are:

- to make our model reliable and to make possible future predictions we need to perform parameter optimization. This will be done by collecting real data from the environment that are related to our model structure and estimating optimal values for the parameters involved;

- to make possible intervention plans, we need to know to which parameter is the model sensitive. Therefore, it is our plan to work on the sensitivity and bifurcation analysis for the non-autonomous and stochastic models;

- to get a better insight and practical results, we need to combine the stochastic model with the non-autonomous system.

- to consider the entire food chain that contains producers and consumers (plants, herbivores, carnivores and omnivores) in the analysis of a similar model. To have an insight on the whole dynamics along the food chain it is possible to add the population of carnivores to the system. This would further limit on the number of herbivore as they will be consumed by carnivores.

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