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ESTIMATING THE SPATIAL DISTRIBUTION OF POSSIBLE LIVESTOCK PRODUCTION LEVEL USING A MATHEMATICAL MODEL AND THE SMAP SOIL MOISTURE DATA: *THE CASE OF BOTSWANA*

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Abstract. In a traditional livestock farming, the livelihood of animals depends highly on existing plant biomass, which is affected by the level and intensity of temperature, rainfall, humidity and other meteorological variables. Understanding the interaction of such meteorological factors and agricultural production in general is an important aspect in planning at the macro and micro levels. Particularly livestock agriculture is heavily affected by the changing climate, and hence the variation in major meteorological variables. However, there is still limited research regarding the impacts of meteorological variables on livestock production in each particular region. Soil moisture is one of the main factors in agricultural production and hydrological cycles with better memory of previous weather conditions. It also involves complex structural characteristics and meteorological factors. In this study, a soil moisture dependent mathematical model for the interaction of plants and herbivores is developed and analysed. The Soil Moisture Active Passive level 4 satellite soil moisture data is used in the model to simulate the possible spatial distribution of plants and the corresponding potential livestock production level for Botswana. A global dynamic sensitivity analysis is employed to study the sensitivity of the solution of the model with a variation in

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the involved parameter values. The results of the simulations of the model show that estimated livestock harvest in wet regions is more than triple as compared to what is estimated for dry regions. If some important parameters are properly estimated and the soil moisture data is available for each region, it is possible to estimate the livestock production level for each spatial region with better accuracy using the proposed model.

Keywords: ecological model; plant–herbivore interaction dynamics; non-constant harvest; soil moisture; livestock production; spatial distribution.

2010 AMS Subject Classification: 37N25, 70K20, 92B05, 92D40, 92D25.

1. INTRODUCTION

Livestock agriculture is the most important industry across sub-Saharan Africa. The industry represents overall 25% of the gross domestic product (GDP) of the region and, in certain countries, provides enough stock for export [37]. For instance, the livestock industry is Botswana's original export activity at its independence and it is by far the most significant sub-sector of the Botswana agricultural economy, accounting for about 80% of its output by value [10]. However, either due to declining per capita production or due to unbalanced increase in livestock population as compared to the increase in human population, growth in livestock production has barely kept pace with the growth in demand for human food of animal origin in the region. Climate change is one of the factors to be blamed. Most of the livestock production activities in the region are carried out through traditional farming mechanisms where grazing is the interaction and they are highly affected by climate variability.

In a traditional livestock farming, the livelihood of animals depends highly on the availability of direct food sources, that is the plant biomass and the dynamics of growth of plants depends on the soil type and moisture of the soil, which serves as an important component for them to grow. Plants cannot have a normal growth if there is excess or insufficient moisture in the soil [21]. If there is a lack of oxygen supply from excess moisture, the growth of plants is aggravated because the root cannot absorb nutrients and the required moisture [21]. Water stress, and nutrients, could also cause abscission of leaves and reduction in leaf area and seed production [25]. Too dry or too wet soil prohibits nutrient-uptake by roots and water stress reduced fruit size and yield [25, 31].

Generally, plant growth is affected by different factors where meteorological variables are the main constraints. Soil moisture is directly related to plant growth and has a better memory of previous weather conditions. As a result in drought monitoring and early warning mechanisms, it serves as a metric to forecast and classify the intensity and severity of droughts [11, 12, 27]. Especially for dry regions, like Botswana, where soil moisture is between wilting point and critical point, the growth of plants is highly controlled by soil moisture [38].

Although some studies have addressed the effect of climate variability on the livestock population [1, 16, 26], no studies have described the use of mathematical models to examine the impact of soil moisture for the spatial distribution and the potential level of livestock production in a certain region.

In [4, 5] the effect of changes in the environmental factors on the plant herbivore interaction was considered using temperature and rainfall dependent deterministic dynamical model and a stochastic model, at a point level. However, the model in [5] assumes that the values of the climatic variables used in the model are the same across each of the three zones (Cold highlands, Hot lowlands, Sub-tropic zone) described in the article and it does not account the spatial variation of the amount of rainfall and temperature. It is to be noted that considering spatial variability of such determining meteorological factors is essential to understand spatial variability of plant growth in each region and livestock population which can be supported by the plant biomass. Moreover, amount of vegetation coverage and type of plants in the area also depend on the soil structure at each particular point of the region.

For a given amount of rainfall and temperature, depending on the type of the soil, the moisture which will be available for plants varies and it affects the plant growth differently. For instance, for sandy soil, water drains down very quickly and the soil will have less moisture compared to a clay soil which holds water. In addition, soil moisture amount has indirect information about organic matters which are essential for plant growth [29, 31]. As a result incorporating soil moisture information in plant growth modelling is more informative as soil moisture itself is a result of interaction of more meteorological variables and soil type, in addition to temperature and rainfall [23].

The authors believe that the effect of climatic factors as well as soil type and texture have not been used in the mathematical model analyses that appear in the existing literature to study the complex interaction between animal population and the plant density. Our aim in this article is to exploit the rich information in the soil moisture data in modelling the time profile of the complex dynamics of the plant-herbivore interaction and thereby study its applications in agricultural planning. To this end, we propose a prey-predator type mathematical model as an extension of the work by [5]. The proposed mathematical model includes the soil moisture data in the dynamics of the model.

In land surface models like Joint UK Land Environment Surface (JULES), soil moisture is used in modelling the link between water balance, carbon cycle and vegetation [8]. In this article however, we are using soil moisture variable to model plant growth separately. The plant growth here refers to increase in plant biomass which is edible for the livestock.

Moreover, by considering spatial variability of soil moisture, it is possible to pinpoint the needs and potential productivity for each grid-point (or grid-cell) on the surface of the Earth. Knowing the amount of soil moisture helps us to project the potential plant productivity of that grid-cell and as a result this determines the spatial variation of the potential livestock that can be supported. This in turn helps farmers and agricultural planners to adjust on what is needed at different regions. For example, regions with scarce plant growth projections are likely in need of more supplemental feed for the livestock production to have productive livestock and will help farmers to decide exactly where to invest.

In addition, the proposed model can also be used to show the dependence and impact of soil moisture over the plant biomass and livestock population. It also helps to identify regions favourable for livestock production, and indicate the possible level of production at each spatial point by suggesting the amount of livestock harvest (or off-take) at any time or at any place.

This manuscript has been organized within four sections without counting the references. Section two briefly describes materials and methods: the study area and the formulation and analysis of the mathematical model for the problem. The third section presents the results numerical simulations and discussions part. The paper is concluded with remarks and recommendations in section four.

2. MATERIAL AND METHODS

In ecology, mathematical modelling of plant dynamics often considers climatic conditions like rainfall and temperature as determining variables to study plant-herbivore interactions [5]. However, the soil type also play important role to determine the kind of plants grow in a certain region and how well they grow. For a given amount of rainfall, depending on the type of the soil, the moisture as well as nutrients which will be available for plants vary. In addition to soil type, there are other meteorological variables like humidity and pressure which would affect the moisture content of the soil and in turn the available moisture for plants. On the other hand, the soil moisture data has a combined information about meteorological variables as well as soil type of the region of interest. In this study, we modify the work by [5] in which we replace the role of temperature and rainfall by soil moisture. The details of model formulation is given in Subsection 2.2. Soil moisture is also a vital meteorological variable in flood forecasts, weather forecast, drought forecast and in hydrology, to mention a few. As a result, efforts to obtain soil moisture data has shown a significant rise. The Soil Moisture Active Passive (SMAP) scheme is one of the satellite missions to provide soil moisture observations globally. Subsection 2.1 describes the SMAP soil moisture data we used in this study.

2.1. Study area and soil moisture data. Botswana (l8° – 27°S; 20° – 29°E) is a large semi-arid country with a small population and it covers an area of approximately 582, 000 square kilometres. The country is land-locked and centrally located in the heart of southern Africa, bordered by South Africa in the east and south-east, Namibia in the north-west, Zimbabwe in the north-east and Zambia in the north. According to the Center for Applied Research of Botswana [13], the country is a relatively high (1000m above sea level), flat, undulating plain covered in deep sandy soils with occasional rocky outcrops, low hills and a network of dry riverine valleys and scattered and extensive salt pans, with sand dunes to the extreme south west. Rainfall in the country is low ranging from 250 mm per annum in the southwest to 650 mm in the north.

Agriculture in Botswana is important, and is dominated by livestock. Indeed, livestock, especially extensive cattle keeping on natural range, dominates land use in Botswana. Land in the country is roughly shared between traditional livestock keeping on communal lands (60 per cent), commercial livestock production on private or leasehold ranches (10 per cent), and wildlife-based activities on state and communal land (30 per cent) [6].

Soil moisture is a key variable to understand the link between fundamental earth system processes like water, energy and carbon cycles [24]. Most importantly for the purpose of this study, soil moisture determines the available water necessary for plant growth. While soil moisture is a key variable in understanding the interaction between the land surface and the atmosphere, the method of acquiring it is versatile as a result of different processes affecting the moisture content in the soil. Advancements in technology makes it possible for different satellite missions to be dedicated for soil moisture observations. One of them is the NASA Soil Moisture Active Passive (SMAP) [22].

SMAP is a satellite mission launched by NASA in 2015 and continue to provide soil moisture data globally [17]. The spatial resolution is 36 km and the observation frequency takes two to three days to observe the whole globe. That means, for a particular grid point, data is obtained every two to three days. However, to make the data more useful by increasing the spatial and temporal resolution, the technique called data assimilation is used. In data assimilation, numerical model and data are combined to obtain a variable of interest with specified spatial and temporal resolution and more realistic value, provided that forcing variables and land surface parameters are available [36].

In this study, the SMAP Level 4 soil moisture data with spatial resolution of 9km is used by combining the course resolution data with a land surface model [7, 33, 35]. The advantages of using the SMAP level 4 over level 3 are: bias corrected and finer resolution in space and time [35]. The data is publicly available with online registration on the web at https://nsidc.org/data /smap/smap-data.html. Figure 7a is the daily average SMAP L4 soil moisture data, in the years 2016 - 2020, for Botswana. Large proportion of Botswana is less than or equal to 0.1 m^3/m^3 mean soil moisture, which will be referred to as dry regions, few regions between $0.1-0.2$ m^3/m^3 mean soil moisture, referred to as medium level soil moisture and few regions with more than 0.2 m^3/m^3 mean soil moisture, referred to as wet areas. The climate is affected by the Kalahari desert to the West and as a result, rain-fed agricultural setting is challenged by lack of moisture and most of the agricultural production is from livestock mainly from cattle [43].

Note that: the white area around 25°S and 26°E in Figure 7a is the Makgadikgadi Pans where soil moisture observations are not available. In the following subsection (2.2), mathematical modelling of the plant-herbivore dynamics is presented where plant growth is characterised as a function of the soil moisture.

2.2. Mathematical model for plant-herbivore interaction.

2.2.1. *Model formulation and description.* To make a modification on the plant-herbivore mathematical model considered in [3] and [5] we additionally assumed that the growth rate of plants depends highly on the soil moisture function. This function contains an aggregate information about rainfall, temperature, pressure, soil texture and other factors and we will keep the animal feeding rate as constant.

The basic mathematical system we consider in this paper is the classical Lotka Volterra type model in the version presented in [3], where the effects of logistic growth of plants, Allee effect of herbivores and non constant death rate of animals are taken into account. The two populations, namely the plant biomass and the herbivores feeding on the plants, are considered. Therefore, the state variables are given by: the plant biomass, represented by P, and the herbivore density, represented by H. The dynamics is ruled by the following system of nonlinear ordinary differential equations:

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

$$\dot{H} = H\left[cF(P)\left(\frac{H}{h+H}\right) - D(F(P)) - \mu,\right] \tag{2}$$

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

where the upper dot denotes the time derivative, K, c, h, μ, m are positive constants, $r(\theta)$ is a soil moisture dependent plant growth rate, $F(P)$ is a function representing the value of consumption of plants by herbivores, to be described later. Here below we give the description of some of the important parameters and the basic assumptions used in defining them.

(i) **Carrying Capacity** K **:** The plant biomass dynamics in model equation (1) increases logistically in the absence of herbivore. That is, it grows only up to its carrying capacity K. This is biologically observable since the plant population growth depends on sunlight, available land, water source and nutrients in the soil and without animal interference they can grow only as much as the land can hold. This maximum plant biomass that can be found on this land is called the carrying capacity of the plant population. In this model it is assumed that the plant growth rate is a logistic function of the value of the soil moisture function.

(ii) **Plant growth rate function $r(\theta)$:** In plant growth modelling, process-based models are used to represent each of the sub-processes in the plant life cycle, and are based on a theoretical understanding of relevant ecological processes [15]. In process based models, intake of nutrients is also considered as a limiting factor in addition to meteorological factors. In this study we considered potential plant growth, with the only growth limiting factors to be meteorological factors [19]. In such a case, variables like radiation, temperature, evapotranspiration etc. are supposed to be considered for plant growth modelling. However, soil moisture function has a signature of the interactions of many of the meteorological variables with the land. For example, only by looking at a time series of soil moisture data, one can distinguish whether the data is from tropical regions (defined seasonal cycle) or temperate regions, and seasons of the year. As a result, using soil moisture for plant growth is much more simpler to implement without losing important phenomena. The plant growth in this study refers to the increase in plant biomass that are edible for the livestock. That means, the plant biomass grows as a function of soil moisture, $r(\theta)$, and is given by,

$$r(\theta) = m + (1-m)U_r(\theta)\beta_r(\theta), \tag{3}$$

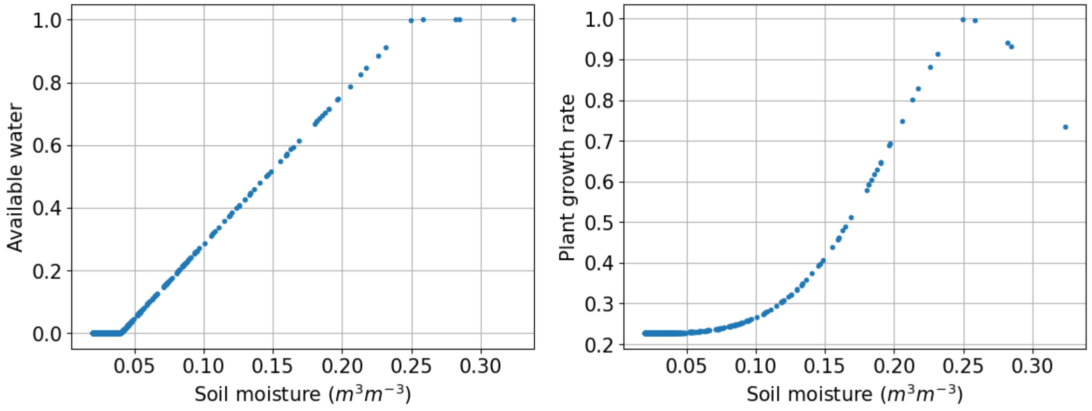
with the soil-moisture dependent component of the growth rate is given by

$$U_r(\theta) = \exp(-(\theta - \theta_c)^2/2\pi\sigma(\theta)^2),$$

and the function describing availability of enough water for plant growth is given by

$$\beta_r(\theta) = \begin{cases} 1, & \theta \geq \theta_c \\ \frac{\theta-\theta_w}{\theta_c-\theta_w}, & \theta_w < \theta < \theta_c \\ 0, & \theta \leq \theta_w, \end{cases} \tag{4}$$

where m is a constant between 0 and 1, representing the minimum growth rate before plants die (dry) due to lack of water, $\theta(m^3/m^3)$ is soil moisture, θ_c is critical soil moisture below which plant growth is affected due to lack of water, σ is standard deviation of θ from θ_c, and θ_w is wilting point soil moisture where plants no longer grow. The values for θ_c and θ_w (and other physical properties) can be approximated based on soil texture using pedo-transfer functions [30].



(a) Available water, $\beta_r(\theta)$

(b) plant growth rate($r(\theta)$)

Figure 1. Available water for plants, and plant growth rate, $r(\theta)$, with $m = 0.227$ $\theta_c = 0.25$ and $\theta_w = 0.04$. The soil moisture data considered is a level 4 SMAP observation soil moisture at a grid point in Botswana

In Figure 1(a) the availability of enough water for plants to grow is depicted as a function of soil moisture. As described in Eqn. (4), water can't be extracted by plants if soil moisture is below the wilting point and plants no longer survive. As soil moisture increases from wilting point upto critical soil moisture, available water for plants increases linearly and reaches to the maximum and stays constant after that. Figure 1(b) shows the rate of plant growth as a function of soil moisture. As water is a means of transporting nutrients to plant roots, increase in soil moisture increases the growth rate. After soil moisture reaches the critical point, the growth rate starts to decrease as a result of too much water and restricts air content in the soil (anaerobic environment) and not favourable for plant growth.

(iii) **Consumption function $F(P)$ and Allee-effect :** In the presence of herbivore that feed on the plant biomass, these herbivores graze feed only upto their saturation level. The grazing rate depends on different factors such as moisture of the graze, the temperature of the environment availability of water source and so on. In this work we considered the Holling type II function, $F(P) = \dfrac{aP}{b+P}$, where a is the feeding rate and b is the half saturation constant.

The average rate of reproduction for the herbivore population in Equation (2) is equal to $cF(P)\left(\frac{H}{h+H}\right)$. This reflects that individual herbivore reproduces more with the availability of food. Moreover, in the absence of food source we have, $cF(0)\left(\frac{H}{h+H}\right) = 0$ which describes that individuals are unable to reproduce if they could not find plants to consume. In addition, to reproduce or to give birth to a new herbivore, existence of enough mate in herbivore population is crucial and is taken care of by the term $\dfrac{H}{h+H}$ due to the fact that $cF(P)\left(\dfrac{H}{h+H}\right)$ 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 regard, see [3, 40]). Since we considered only a traditional livestock farming, the use of artificial insemination is not taken into account.

(iv) **Consumption-dependent animal death rate $D(F(P))$:** Decrease in number of herbivores or plants may be caused by various natural or manmade events such as diseases, scarcity of food and water, the occurrence of drought, floods grass/forest fires. In real life problems, it is not right to consider the death rate of animals as constants. Therefore, in this model the death rate of animals is taken to be a non constant function of the food density as given in the paper by [3]. Taking in to account the idea that animal survival mainly depends on availability of food, it is assumed that the consumption dependent animal death rate $D(F(P)) = D(F)$ 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

$$0 < d_1 \leq D(F) \leq d_2, \tag{5}$$

where the bounds d_1 and d_2 represent respectively the minimum and maximum possible death rates.

In [3], the explicit formula for $D(F(P))$ is given by

$$D(F(P)) = \frac{d_2K(1+d_1-d_2)(b+P)+P(b+K)(d_2-d_1)(d_2-1)}{K(1+d_1-d_2)(b+P)+(d_2-d_1)(b+K)P}. \tag{6}$$

(v) **Variable harvest rate $\mu(H)$:** The harvest rate μ in Equation (2) 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 animal is a wild animal) or culling or selling (if the animal is a domestic animal).

However, due to limited facilities of harvesting or resource protection the rate of harvesting for livestock can not always increase proportionally with the increase in the size of H. That means, the value of μ may vary depending on the population size of H. To this end, we assume that there is no harvest until the number of livestock reaches a value of $H_{\min}$, where $H_{\min}$ represents the minimum number of herbivore to guarantee existence of the herbivore population in the model system. This quantity can be obtained by setting the emergence rate of herbivores to be greater than the death rate. That is,

$$\begin{aligned} cF(P)H\left(\frac{H}{h+H}\right) &> D(F(P))H, \\ \frac{H}{h+H} &> \frac{D(F(P))}{cF(P)} > \frac{d_1}{cF(P)}, \\ cHF(P) &> d_1h+d_1H, \\ (cF(P)-d_1)H &> d_1h. \end{aligned}$$

Which implies that $H_{\min}$ must satisfy

$$H_{\min} > \frac{d_1h}{cF(P)-d_1}.$$

If the herbivore population exceeds the value $H_{\min}$, then the model allows a harvest of fixed constant rate μ_0 to be administered until the number reaches the threshold H_o. Once the population goes beyond the threshold value H_o, the harvesting rate will then be kept at a rate proportional to the count of the livestock, μH. Generally, the harvesting (off-take) function can be described as

$$\mu(H) = \begin{cases} 0, & 0 \le H \le H_{\min}; \\ \mu_o, & H_{\min} \le H \le H_o; \\ \mu H, & H > H_o. \end{cases} \tag{7}$$

If the values of μ_o and μ are given, then the harvesting threshold can be formulated as $H_o = \dfrac{\mu_o}{\mu}$.

The description of the remaining parameters of model system (1) – (2) is given in Table 1.

With the above modifications, the model system that we will study, therefore, takes the following form.

$$\begin{aligned} \frac{dP}{dt} &= r(\theta)P\left[1-\frac{P}{K}\right] - \frac{a}{b+P}PH \\ \frac{dH}{dt} &= H\left[c\left(\frac{a}{b+P}\right)P\left(\frac{H}{h+H}\right) - D(F(P))\right] - \mu(H), \end{aligned} \tag{8}$$

where $r(\theta)$ is given by Equation (3), $D(F(P))$ is as in Equation (6) for some given constants d_1 and d_2, and $\mu(H)$ is determined by Equation (7).

Hence when $0 \le H \le H_{\min}$ the model system (8) becomes

$$\begin{aligned} \frac{dP}{dt} &= r(\theta)P\left[1-\frac{P}{K}\right] - \frac{a}{b+P}PH \\ \frac{dH}{dt} &= H\left[c\left(\frac{a}{b+P}\right)P\left(\frac{H}{h+H}\right) - D(F(P))\right], \end{aligned} \tag{9}$$

when $H_{\min} \le H \le H_o$ the model system (8) becomes

$$\begin{aligned} \frac{dP}{dt} &= r(\theta)P\left[1-\frac{P}{K}\right] - \frac{a}{b+P}PH \\ \frac{dH}{dt} &= H\left[c\left(\frac{a}{b+P}\right)P\left(\frac{H}{h+H}\right) - D(F(P))\right] - \mu_0, \end{aligned} \tag{10}$$

and when $H > H_o$ the system (8) becomes

$$\begin{aligned} \frac{dP}{dt} &= r(\theta)P\left[1-\frac{P}{K}\right] - \frac{a}{b+P}PH \\ \frac{dH}{dt} &= H\left[c\left(\frac{a}{b+P}\right)P\left(\frac{H}{h+H}\right) - D(F(P))\right] - \mu H. \end{aligned} \tag{11}$$

2.2.2. *Model analysis.* Since our model, Eqn.(8), is a nonlinear system of differential equations, we rely on the numerical methods to obtain a solution. Therefore, we need to check if the solution depends on the initial values used in the method as well as on the time interval in which the numerics is set to run. This can be done by qualitatively analysing the model and studying the behaviour of the solution of the model in general. The qualitative analyses of the model are presented in the following subsections.

Region of Positivity. For the model described above 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 that starts with the values $P(0) \geq 0, H(0) \geq 0$. 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 of the real plane.

Lemma 2.1 (Positivity)**.** *All solutions of system* (8) *starting in* $int(\mathbb{R}_2^+)$*, remain positive.*

Proof. See Appendix A for the proof. □

Lemma 2.2 (Boundedness)**.** *For model system* (8)*, let* $\widehat{P} := \max\{P(0), K\}$*. Moreover, for constant values* $\eta = \dfrac{Kc(r(\theta)+d_1)^2}{4r(\theta)}$, $\eta^* = \dfrac{Kc(r(\theta)+d_1)^2}{4r(\theta)} - \mu_0$, *and* $\eta^{**} = \dfrac{Kc(r(\theta)+d_1+\mu)^2}{4r(\theta)}$, *where* d_1 *is defined as in* (5)*, let*

$$\widehat{H} := \max\left\{cP(0)+H(0), \frac{\eta}{d_1}, \frac{\eta^*}{d_1}, \frac{\eta^{**}}{d_1+\mu_o}\right\}. \tag{12}$$

Then, for any positive time $(t > 0)$ *we have* $P(t) \leq \widehat{P}$ *and* $H(t) \leq \widehat{H}$.

Proof. See Appendix A for the proof. □

The above results indicate that the model described by the system (8) is mathematically and biologically well posed.

Existence and local stability of equilibrium points. To find equilibrium points of the model system (8) we put the right hand side of the system equal to zero. That is,

$$\frac{dP}{dt} = P\left[r(\theta)\left(1-\frac{P}{K}\right)-\frac{aH}{b+P}\right]=0 \tag{13}$$

$$\frac{dH}{dt} = H\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)-D(F(P))\right]-\mu(H)=0. \tag{14}$$

From equation (13) we have

$$P\left[r(\theta)\left[1-\frac{P}{K}\right]-\frac{a}{b+P}H\right]=0.$$

Then, either $P=0$ or

$$r(\theta)-\frac{r(\theta)P}{K}-\frac{aH}{b+P}=0. \tag{15}$$

If $r(\theta)=0$ the expression in Eqn (15) implies that $H=0$. Assuming $r(\theta)\neq 0$ for all θ Eqn. (15) yields

$$P^* = \left(K+\frac{a}{r(\theta)}H-b\right)+\sqrt{\left(K+\frac{a}{r(\theta)}H-b\right)^2+4bK}$$

for a given H.

For the case $0<H<H_{\min}$ we have $\mu(H)=0$ and from equation (14) we get

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

A further simplification of which provides a quadratic equation in H:

$$[cF(P)-D(F(P))]H^2-[D(F(P))h]H=0.$$

Solving this quadratic equation in $int(\mathbb{R}_2^+)$ we get one positive solution, which is given by

$$(P^*,H^*)=\left(P^*,\frac{D(F(P))h}{(cF(P))-D(F(P))}\right). \tag{16}$$

For the case when $H_{\min}<H<H_o$, we have $\mu(H)=\mu_o$ and from equation (14) we get

$$H\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)-D(F(P))\right]-\mu_o=0,$$

which is again a quadratic equation in H and can be solved to give

$$(P^*,H^*)=\left(P^*,\frac{D(F(P))h+\mu_o+\sqrt{(D(F(P))h+\mu_o)^2+4(cF(P)-D(F(P)))\mu_o h}}{2(cF(P)-D(F(P)))}\right).$$

For the case when $H \geq H_o$ we have $\mu(H) = \mu H$ and from equation (14) we get

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

Then, either

$$H^* = 0 \quad \text{or} \quad H^* = \frac{h[D(F(P)) + \mu]}{cF(P) - [D(F(P)) + \mu]}. \tag{17}$$

The expressions in Eqns. (16) and (17) hold if the birth rate of herbivores is greater than the removal rate. Otherwise, the population will go to extinction.

When the herbivore population is always positive, *i.e.*, $H > 0$, from equation (14) 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

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

Among these possible equilibria points, the one that demonstrates the coexistence of the plant and animal population is of interest to this study. Therefore, finding a threshold value that guarantees the stability of this equilibrium is more important. To this effect, we shall define $\mathscr{R}_o = \frac{caK}{(d_1+\mu)(b+K)}$ to be a threshold parameter value for the system. This threshold value helps us to specify the non-extinction condition for the herbivore population, and hence can be considered as the effective reproduction of the livestock population. That means, to guarantee coexistence of both populations we need this ratio to be always $\mathscr{R}_o > 1$. As indicated in detail in [3] for the livestock population greater than the minimum H_{min} and with the availability of enough food (in this case, a critical value of $P(t)$), $\mathscr{R}_o > 1$ assures non extinction of the livestock population.

This threshold condition relates the parameter of the model system to the minimum and maximum values of the variables that can be attained. In other words, depending on the resources available it can determine the minimum and the maximum number of herbivores the system can support so that both the plant population and the herbivore population can coexist or do not go to extinction. To maintain this equilibrium we can either add herbivores or remove (through harvesting or hunting) them from the system.

3. NUMERICAL SIMULATIONS AND DISCUSSIONS

In this section, we presented parameter values used for simulations, time series model dynamics simulations for plant and herbivore populations, sensitivity analysis and simulations for spatial distribution of possible plant, herbivore and livestock production.

3.1. Parameter values. The parameters for the model are chosen corresponding to the units: kg to measure weight, km^2 for areal measure and each time rate is measured per day. The soil moisture data was retrieved from the web at `https://nsidc.org/data/smap/smap-data.html`. The growth rate of plants is defined in-terms of factors such as m a background plant growth rate, which is assumed to be a reservoir irrespective of the weather condition, θ_c critical soil moisture, and θ_w wilting point soil moisture. Once the water content reaches the wilting point, most of the plants die unless additional water is supplied to the soil [34]. Correspondingly since the soil moisture is a daily data, we have a growth rate which is a function of the daily data.

The values of the critical soil moisture θ_c and wilting point soil moisture θ_w were estimated based on the pedo-transfer functions [30], soil texture data from Harmonised World Soil Database (HWSD) [18] and [29]. Note that the estimation is made for a single point which is assumed to represent the entire grid cell throughout Botswana.

The value $m = 0.227$ is assumed to represent a value for which the rate of growth of plants that are supported by the driest possible time. Plants that grow with this rate are also assumed to be fully used as a forage for the livestock.

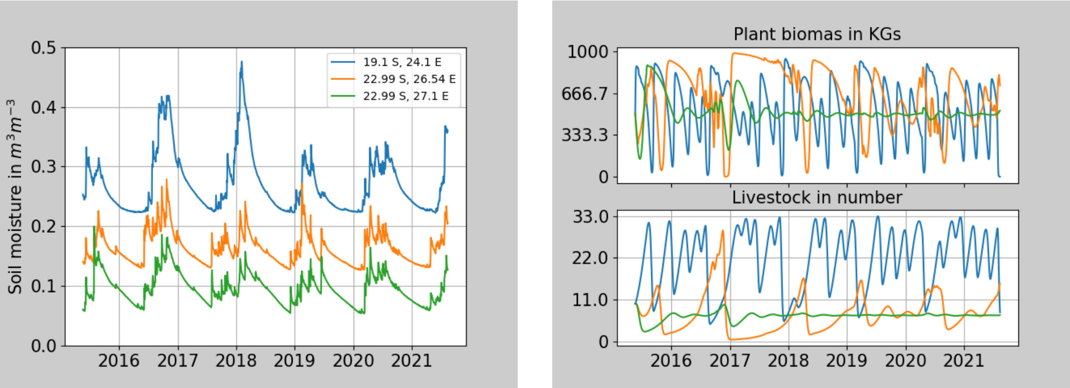
The initial herbivore population were calculated using a mechanism employed in [42]. Using the formula proposed in the reference we can have approximately $P_0 = 500kg$ of plant biomass on a 1km spatial resolution and it can be grazed by 10 herbivores that weigh an average of $544kg$

each, which is assumed to be an average weight of a cattle. i.e. $H_o = 10 \times 544$. For the feeding rate a, a cattle is assumed to consume at most 2.5% of its body weight per day [14], and for value of the half saturation constant b in the Hollying type II functional response, a number 160 is chosen so that it is significantly smaller than the carrying capacity of the environment. The remaining parameter values are indicated in Table 1. In the following subsection, we presented the numerical simulation by using the parameter values and initial conditions discussed above.

3.2. Simulations of the model dynamics. Even though Botswana is a semi-arid country [13] and large part of the country is dry with mean annual soil moisture less than 0.1 m^3/m^3, the soil in some region is relatively wet as can be observed from Figure 7a. By considering three points (grid-cells) in Botswana, numerical simulations of the model given by equation (8) are performed. The purpose of differentiating regions based on soil moisture content is because soil moisture is an important factor for plant growth and hence to livestock production. By doing so, we will be able to suggest specific solutions for each region for a better livestock production. From Figure 1, we can observe that if soil moisture is greater than 0.25, water is not a limiting factor for plant growth and plants are expected to grow without significant limitation from moisture deficit.

The three points are representative for wet, medium moisture content and dry regions. The classification of these three regions are: wet regions where daily average soil moisture is greater or equal to 0.2 m^3/m^3, medium level soil moisture where daily average moisture is between 0.1 m^3/m^3 and 0.2 m^3/m^3 and dry regions where daily average soil moisture is less than or equal to 0.1 m^3/m^3.

In wet regions, blue line, daily mean soil moisture is above the critical soil moisture which is 0.25, Table 1. As a result, plant biomass and corresponding herbivore number showed more dynamics than both medium and dry regions. The impact of soil moisture for herbivore number is clearly seen by the difference in number, in addition to the dynamics, i.e. wet regions have been found to be more favourable for livestock production than medium and dry regions. More discussion on impact of soil moisture for plant biomass and livestock production together with potential harvest for each region is discussed in details in Subsection 3.4.



(a) Soil moisture at different locations in Botswana.

(b) Example plot for plant biomass and herbivore number at corresponding locations.

Figure 2. Soil moisture at different locations in Botswana and corresponding model estimates of plant biomass and herbivore production. The left panel plots are soil moisture plots at latitude = 19.1 S, longitude = 24.1 E (daily average soil moisture = 0.27 m^3/m^3), at latitude =22.99 S, longitude = 26.54 E, (daily average soil moisture = 0.16 m^3/m^3) and at latitude = 22.99 S, longitude = 24.1 E (average soil moisture = 0.09 m^3/m^3). The right panel plots are model estimates for plant biomass and herbivore density for corresponding locations in Botswana. Here, the livestock number is calculated in average cattle equivalent weight value.

Parameter	units	Value	Description	Source
P_0	kg per km^2	500	Initial plant population	[42]
H_0	kg per km^2	10×544	Initial herbivore population	[42]
$r(\theta)$	per km^2 per day	variable	plant growth rate	calculated
a	kg per km^2 per day per head	2.5% of body weight	feeding rate	[14]
K	kg per km^2	1000	carrying capacity (for plant population)	[42]
b	kg per km^2 per day per head	160	half saturation constant of feeding of the herbivore	assumed
c		2.5	efficiency of converting	assumed
h	kg per km^2	3×544	Allee constant	assumed
d_1	per day	0.000136	minimum death rate	assumed
d_2	per day	1/7	maximum death rate	assumed
μ	kg per km^2 per day	1/365	min harvest rate	assumed
μ_0	kg per km^2 per day	4*544/365	max harvest rate	assumed
m	per km^2 per day	0.227	minimum plant growth rate	assumed
H_m	kg per km^2 per day	150	Maximum harvest	calculated
θ_c	m^3/m^3	0.25	Critical soil moisture	estimated [30]
θ_w	m^3/m^3	0.04	Wilting point soil moisture	estimated [30]

Table 1. Initial values of the variables and parameter values used for simulations

3.3. Sensitivity analysis. It is evident that mathematical models of ecological problems are symbolic representations of biological systems. In the process of formulating the model there are some possible loss of information which makes the prediction of model outcomes uncertain or imprecise. In addition, ecological models are composed by uncertain parameters, the model outcomes are non-linear functions of the parameters and the relationship among state variables is governed by non-linearity. More importantly, the nature and the existing relations between plants and herbivore is one of the main factors that influence changes in the values of the model parameters. Therefore, in this section we aim to explore sensitivity analysis of the model to changes in the assumptions made regarding the characteristics of the interactions.

In this study, some of the parameters used in simulating the model are not yet supported by field data. The values for some of them are assumed by considering similar studies conducted elsewhere, as indicated in Table 1. Therefore, we need to address first the question "what will happen to the result of the simulated values if any of these values change slightly?".

Sensitivity analysis can be used to quantify the effects of uncertainties on a mathematical model's input parameters and the subsequent effect on the model's output [2]. It can determine how variability of the inputs causes variability in the outputs. The purpose of sensitivity analysis is to quantify this relationship by analysing the variation of the output as a function of the input. This helps to identify which of the parameters are causing significant uncertainty and then reduce the robustness of the output.

Here the analysis is presented with the intention to capture time dependent nonlinear but monotonic relationships between model state variables and input parameters. This allows us to assess whether significance of one parameter occur over an entire time interval during model dynamics. We present results for state variables, plant biomass and herbivore population separately.

To this end, we consider a global dynamic sensitivity analysis of the mathematical model using the Latin hypercube sampling scheme following the sampling approach described in [20, 28]. The positive or negative influence of parameter values on the model variables P-plants and H- herbivores is observed for the time length for which the model is simulated that is for the years $2015-2020$. We note that some parameter values in the model may not have a direct influence on a specific variable but still lead to a significant change in that variable. In this method, we used $n = 1000$ simulations and performed the partial rank correlation coefficients (PRCCs) for each parameter value sampled and tracked for each run and for the duration over which the ODE system is simulated. The PRCCs coefficients are extracted for selected variables (P-plants or H-herbivores) at selected time points i.e. at $T = 180$ days (six months after the start date of observation), $T = 360$ days (around a year after the start date of observation), and $T = 1000$ days (around three years after the start date of observation) to represent time points when the system is anticipated to be early on the husbandry, midway through the husbandry, and near equilibrium respectively. To determine the significance of extracted PRCCs, a quantifiable measure, i.e. the p-value, is used to study the degree of influence. The parameters with p-values less than 0.05 are considered to be significant and those with higher p-values are considered to be not significant with respect to the corresponding state variable.

Again, note that the negative sign in the PRCC suggests that if we increase the parameter, the size of the response of the state variable decreases (and *vice versa*), while the positive sign indicates that if we increase the parameter the size of the response of the output variable also increases (and *vice versa*)

PRCCs of parameters based on the Plant biomass. Mathematical models for the plant herbivore interaction with different parameters whose PRCC is within the interval $(-0.2, 0.2)$ and at the same time have p-values less than 0.05 are considered to describe a vital processes [28]. The time varying PRCCs of the parameters on the change in the plant biomass are shown in Figure 3. According to [28], the parameters whose PRCCs are within the interval $(-0.2, 0.2)$ are rendered not to be significantly sensitive. In our analysis, we focus more on the sensitivity of parameters whose PRCCs satisfy the level of significance.

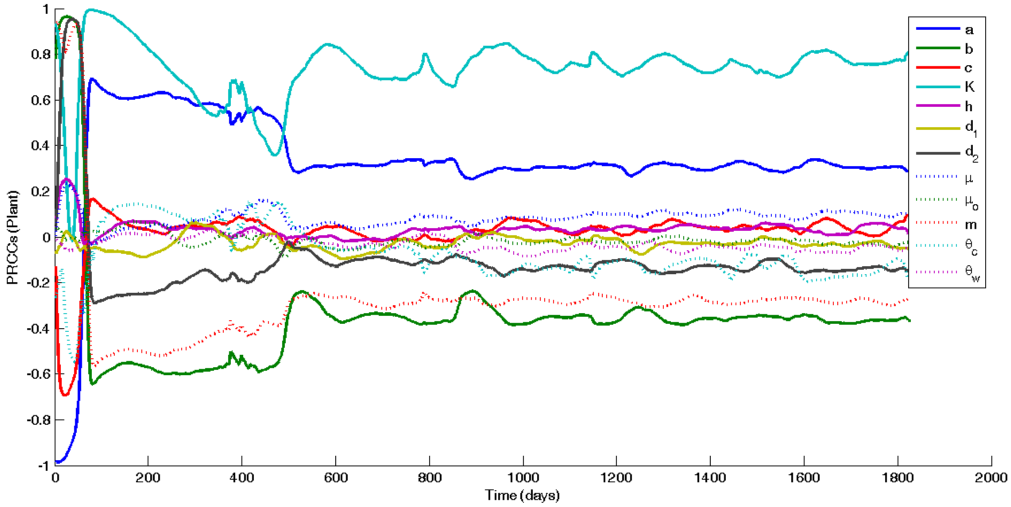


Figure 3. PRCC plots against time for the plant population and parameters

PRCC indexes can be calculated for multiple time points and are plotted versus time. This method gives a chance to asses whether significance of one parameter occur over an entire time interval during model dynamics.

As it can be observed in Figure 3, the effect of parameter a (feeding rate of herbivores) changes with respect to the plant population over time: it is negatively correlated (very strongly with PRCC -1) at the start of the dynamics and then it becomes positively correlated with PRCC $(0.4-0.6)$ as the interaction between plants and herbivore goes to its stability (towards coexistence equilibrium) and it remains above 0.2. The positive sign of its PRCC indicates that the slight increase in the feeding rate (in this case through grazing) can possibly increase the plant biomass slightly. This could be explained with an argument that as the animals feed over the leaves plants may quickly grow more other leaves to increase their metabolic processes. Moreover, the dung of the herbivores may also increase through time the soil fertility and as a result increase in the plant biomass can be observed.

The effect of the carrying capacity (K) is also strongly significant > 0.4 throughout the simulation time. The relation is positive meaning as we increase the carrying capacity of the land the plant biomass also increases.

The minimum growth rate m and the half saturation constant b of the animal feeding have strong negative relations with the dynamics of the plant biomass. This negative relation can be described as the half saturation constant of animals increase they will feed more to satisfy their needs and this results in a decrease of the plant population.

The remaining parameters are statistically less significant or have no significance as their PRCC is between $(-0.2, 0.2)$.

For the selected PRCC at $T = 180$ days (6 months), $T = 360$ days (a year) and $T = 1000$ days (after 2 years) p-values were computed and the results are given in Table 2.

From Table 2 we can observe that the feeding rate a has a p-value < 0.05, this indicates that it is a significant parameter throughout the simulation time. Moreover, it is positively correlated with the change in the plant biomass.

The parameter value K is observed to be significantly positively correlated with change in the plant biomass. The sensitivity of this parameters is observed to be significant for the entire duration of the simulation. we note that the parameter K is the carrying capacity of the land to hold the plant biomass. This parameter directly influences the increase in the plant biomass when increased.

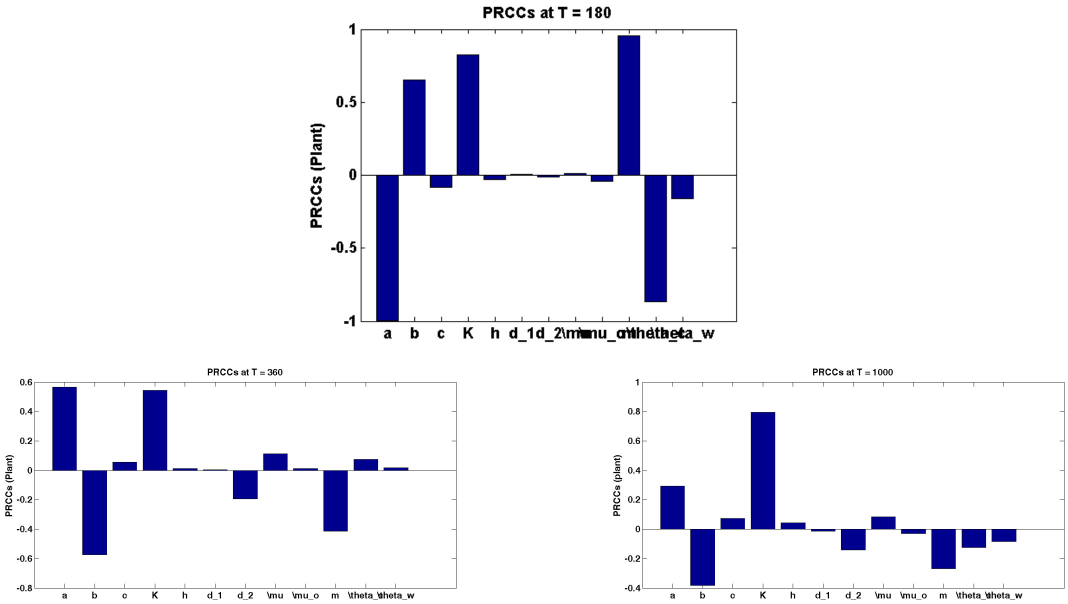


Figure 4. PRCC results for sample size of 1000 for the Plant population and the parameters at three different time points $T = 180$ days at the end of the first year $T = 360$ days at the end of the second year and $T = 1000$ at the end of the third year

		$T = 180$			$T = 360$			$T = 1000$	
var.	PRCC	p-value	Sign.	PRCC	p-value	Sign.	PRCC	p-value	Sign.
a	0.6072	0.00e+00	TRUE	0.5594	0.00e+00	TRUE	0.2840	0.00e+00	TRUE
b	-0.5786	0.00e+00	TRUE	-0.5384	0.000e+00	TRUE	-0.3630	0.00e+00	TRUE
c	0.1332	5.163e-05	TRUE	0.0956	3.905e-03	TRUE	0.1061	1.415e-03	TRUE
K	0.8788	0.00e+00	TRUE	0.5657	0.00e+00	TRUE	0.8001	0.00e+00	TRUE
h	0.0450	2.361e-01	FALSE	0.1071	1.261e-03	TRUE	0.0643	5.759e-02	FALSE
d_1	0.0199	5.804e-01	FALSE	-0.0118	7.756e-01	FALSE	-0.0283	4.489e-01	FALSE
d_2	-0.1222	1.972e-04	TRUE	-0.1212	2.905e-04	TRUE	-0.1410	1.661e-05	TRUE
μ	0.0331	3.582e-01	FALSE	0.0800	1.576e-02	TRUE	0.0708	3.893e-02	TRUE
μ_0	-0.0337	3.582e-01	FALSE	0.0622	6.061e-02	FALSE	-0.0217	5.406e-01	FALSE
m	-0.4982	0.00e+00	TRUE	-0.4323	0.000e+00	TRUE	-0.2270	1.200e-12	TRUE
θ_c	0.1686	2.168e-07	TRUE	0.1204	2.905e-04	TRUE	-0.1605	8.881e-07	TRUE
θ_w	0.0022	9.449e-01	FALSE	-0.0032	9.2e-01	FALSE	-0.0025	9.374e-01	FALSE

Table 2. Plant class parameter PRCC significance(FDR adjusted P-values)

The parameter b have significantly negatively correlation with changes in the plant biomass. We note that b represents the half saturation constant for the feeding of a single herbivore (cattle, in this case) on the plant biomass. Similarly, m represents the minimum growth rate, and is observed to be significantly correlated as its p-value is < 0.05 throughout the simulation period. Both these parameters are significant throughout and inversely influences the increase in the size of the plant biomass when increased. From Table 2 we can see that the remaining parameters do not have significance effect over the entire simulated time.

PRCCs of parameters based on the Herbivore population. As it can be observed from Figure 5, the change in the number of herbivores is highly influenced by the parameter values, the feeding rate a, the half saturation constant of feeding b, and the minimum growth rate for plants m. The PRCCs of the model parameters obtained for the duration of the entire simulation are given in Figure 5 and extracted values of PRCCs at selected time points are presented in Figure 6.

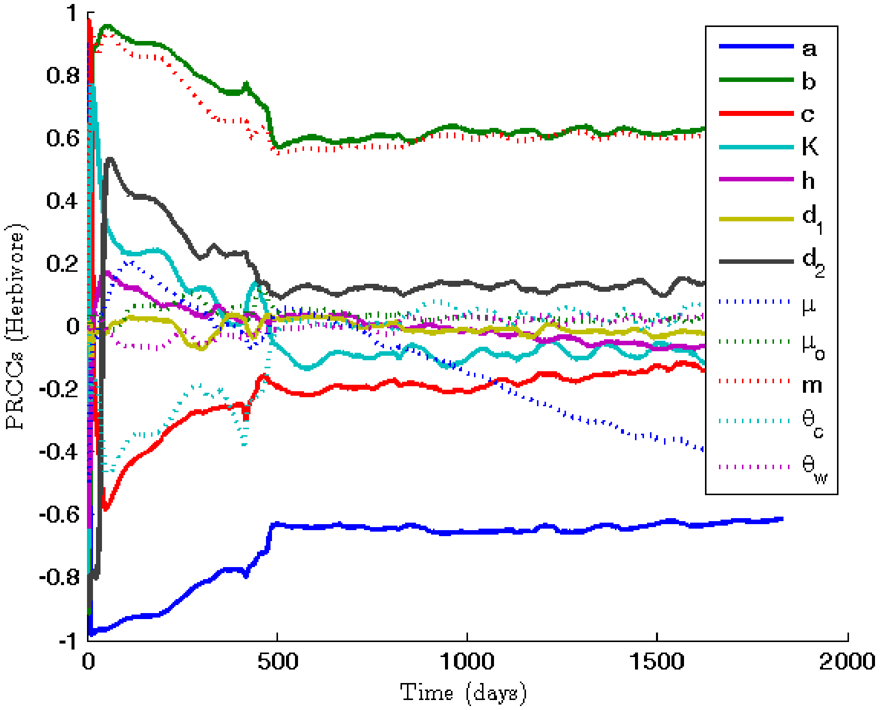


Figure 5. PRCC plots against time for the herbivore population and parameters

Moreover, for the selected PRCC at $T = 180$ days (6 months), $T = 360$ days (a year) and $T = 1000$ days (after 2 years) p-values were computed and the results are given in Table 3.

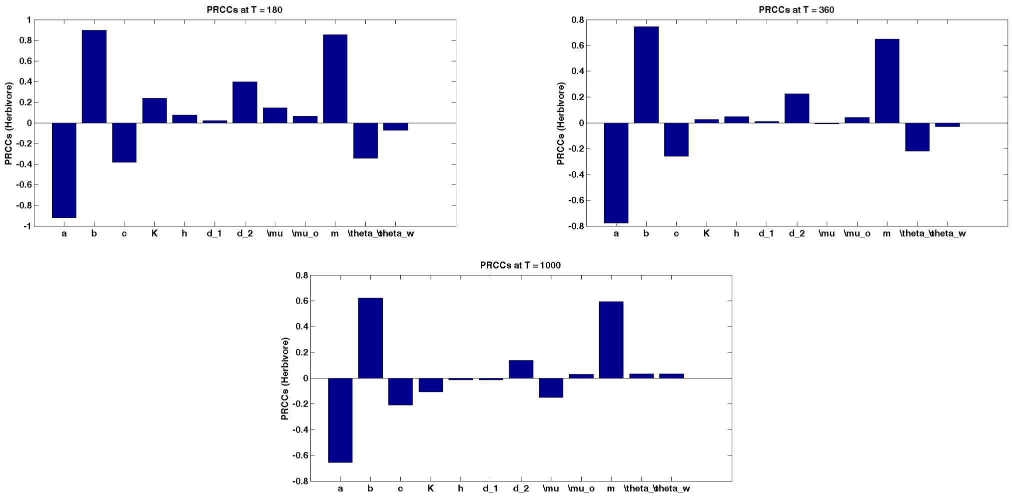


Figure 6. PRCC results for sample size of 1000 for the herbivore population and the parameters at three different time points $T = 180$days at the end of the first year $T = 360$ days at the end of the second year and $T = 1000$ at the end of the third year

		$T = 180$			$T = 360$			$T = 1000$	
var.	PRCC	p-value	Sign.	PRCC	p-value	Sign.	PRCC	p-value	Sign.
a	-0.9129	0.000e+00	TRUE	-0.7654	0.000e+00	TRUE	-0.6086	0.000e+00	TRUE
b	0.8775	0.000e+00	TRUE	0.7025	0.000e+00	TRUE	0.5673	0.000e+00	TRUE
c	-0.4167	0.000e+00	TRUE	-0.2512	1.998e-15	TRUE	-0.1824	2.083e-08	TRUE
K	0.2016	2.363e-10	TRUE	0.0423	2.206e-01	FALSE	-0.0187	6.309e-01	FALSE
h	0.0300	4.152e-01	FALSE	-0.0442	2.199e-01	FALSE	-0.0294	4.988e-01	FALSE
d_1	-0.0257	4.577e-01	FALSE	-0.0375	2.605e-01	FALSE	-0.0283	4.988e-01	FALSE
d_2	0.4008	0.000e+00	TRUE	0.2377	5.507e-14	TRUE	0.1727	1.034e-07	TRUE
μ	0.1726	6.579e-08	TRUE	0.0448	2.199e-01	FALSE	-0.1081	1.310e-03	TRUE
μ_0	-0.0479	1.763e-01	FALSE	-0.0648	7.129e-02	FALSE	-0.0177	6.309e-01	FALSE
m	0.8456	0.000e+00	TRUE	0.6397	0.000e+00	TRUE	0.5030	0.000e+00	TRUE
θ_c	-0.3570	0.000e+00	TRUE	-0.2437	1.386e-14	TRUE	0.0876	9.977e-03	TRUE
θ_w	-0.0187	5.570e-01	FALSE	-0.0241	4.491e-01	FALSE	-0.0091	7.751e-01	FALSE

Table 3. Herbivore class parameter PRCC significance(FDR adjusted P-values)

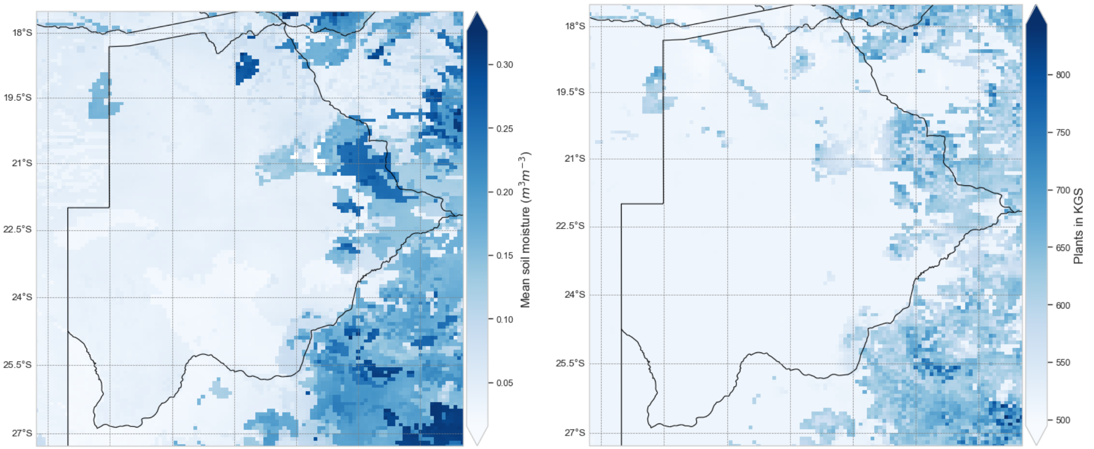
From the PRCC plots (Figure 6) and the *p*-value table (Table 3) we can observe that the parameter values *b* and *m* are observed to be significantly positively correlated with change in the number of herbivore populations (PRCC > 0.2). The sensitivity of these parameters (*b* and *m*) is observed to be significant for the entire duration of the simulation from Table 3. It is noted that the parameters *b* and *m* directly influence the increase in the number of the herbivore population when they are increased.

The parameter *a* has significantly negative correlation with changes in the number of herbivore population. We note that *a* is the feeding rate of herbivores on a plant biomass. Here we can argue that since herbivores are reproducing sexually we have the influence of the Allee-effect and we are working on a limited land with carrying capacity as the rate of feeding (through grazing) increases the plant biomass decreases and hence because of competition for survival the chance of reproducing may decrease and resulting in a decrease of herbivore population.

From Table 3 we can observe that the other parameters have no significant effect over the entire simulated period of time.

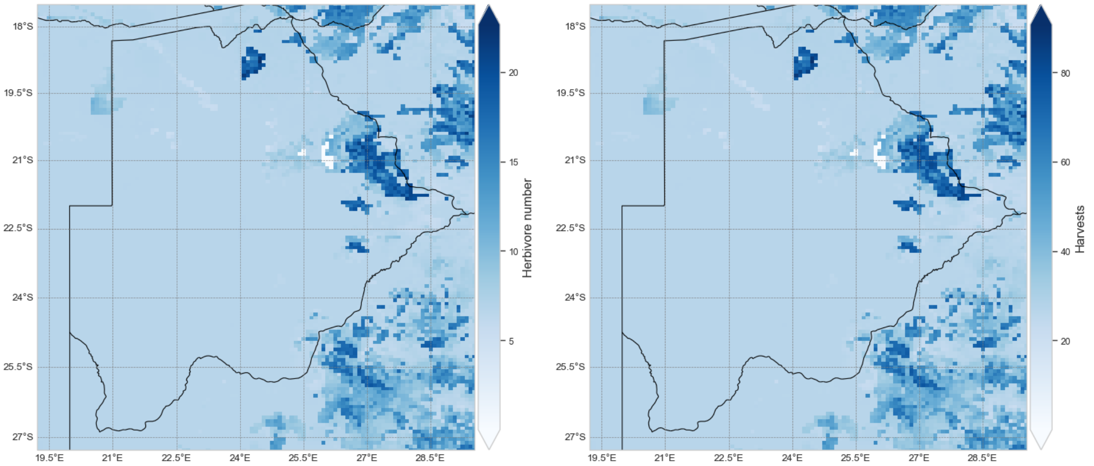
3.4. Livestock Capacities and harvest level in different regions.

In this section we showed the spatial distribution of plant biomass, livestock population and the potential livestock harvest to investigate their dependence on the soil moisture data extracted for each grid-cell on the surface. The impact of soil moisture on the interaction of plant biomass and livestock population is also explained. In addition, we identified regions favourable for livestock production, and indicate the possible level of production at each spatial point. Numerical results for the ODE system described in Equation (8) are solved by driving the model with soil moisture observations from SMAP, described in Subsection 2.1. The Runge Kutta 4th order (rk4) numerical scheme is implemented to integrate variables of the model at each grid-point. Parameter values given in Table 1 are used in the simulation process.



(a) Daily mean soil moisture in m^3m^{-3} (b) Daily mean plant biomass in KG

Figure 7. Distribution of daily mean soil moisture (SMAP observation) and plant biomass for Botswana and surroundings as predicted by the model, Eqn. (8) and parameter values as in Table 1. The daily mean is calculated for the years 2016 - 2020 inclusive.



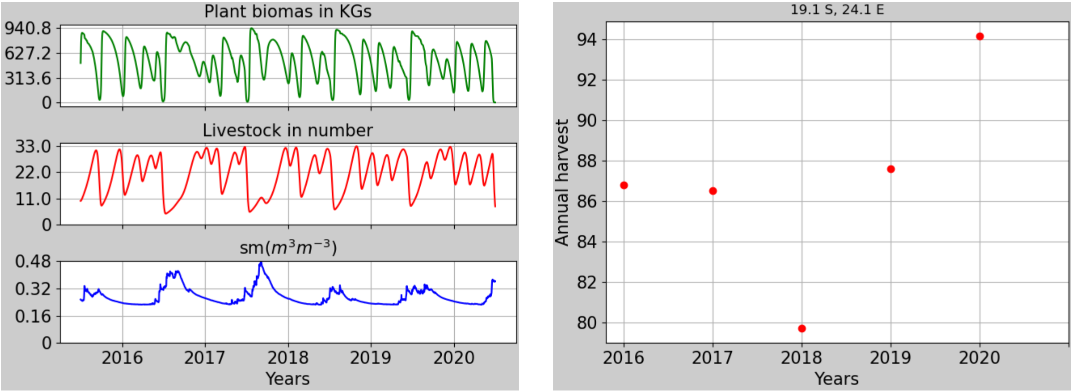
(a) Daily mean livestock in number (b) Annual mean livestock harvest in number.

Figure 8. As in Figure 7 but for livestock number and corresponding potential harvest. The livestock number is calculated in terms of the weight of average cattle equivalent.

Figure 7a shows soil moisture distribution as observed by the NASA SMAP satellite, as described in Subsection 2.1. Figure 7b is distribution of plant population as a result of soil moisture and herbivore interaction and Figures 8a and 8b are livestock and harvest distributions corresponding to soil moisture and plant distributions. From Figures 7 and 8, we can observe that variables show positive correlation almost everywhere. As soil moisture is a determining factor for plant growth, moisture rich areas are observed to have a better plant biomass cover as expected. This result reaffirms previous studies which pointed out that soil moisture is a major determining factor for plant growth [9, 32, 38]. Comparing plant biomass and herbivore number, we see negative correlation in some places. This is because herbivore number is affected not only by plant biomass, but also by the Alee effect, there should be enough number of herbivore for them to reproduce. When the herbivore population is below a critical number, their population remains low even though there is enough food, plant biomass. Note that the model assumes that only traditional ways of breading mechanisms are used and the use of artificial insemination is negligible.

To have a closer look at the numerical results presented in Figure 2 and investigate the effect of soil moisture on plant biomass and herbivore production, time series plots are presented for three grid-points corresponding to three relative climatic conditions. In each figure in the subsections below, the plots on the left panel represent livestock numbers (red line), plant biomass (green line), soil moisture (blue line), and the plots on the right panel indicate the corresponding potential annual average harvest of livestock (red dots) in that particular grid-cell of the surface.

3.4.1. *Relatively wet regions.* Figure 9(a) show soil moisture and corresponding plant biomass and livestock variability as a result of soil moisture differences. In Plant biomass shows a quick recovery after decreasing due to grazing. The herbivore population also managed to increase upto three time their number at the start of the dynamics. Their number starts to decrease due to lack of food when the plant biomass decreases, but stays lower for longer even when food is available. In fact, the minimum herbivore numbers are attained when plant biomass are higher numbers. This could be due to the fact that herbivore reproduction takes longer to reproduce and as their number reduces, it becomes harder to get a mate. However, it is only a few times when their minimum number is less than their initial number.



(a) Time series plot of model dynamics

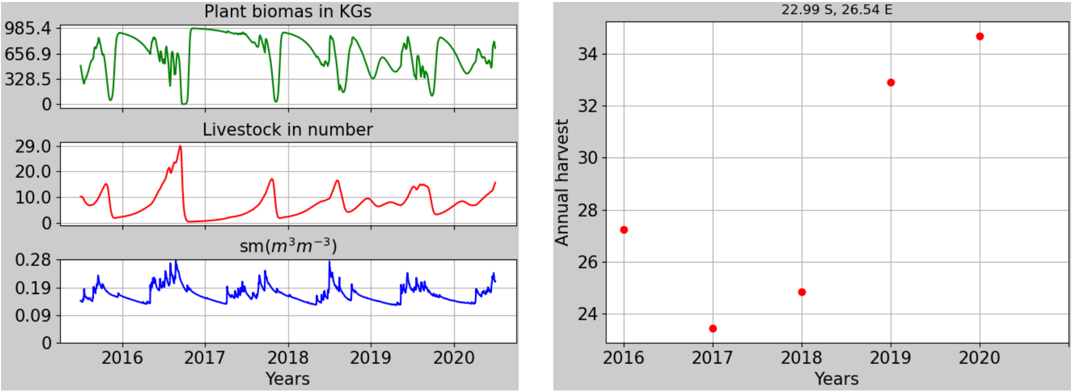
(b) Annual harvest

Figure 9. Model dynamics and potential livestock harvest model estimate for wet regions in Botswana.

Figure 9 is time series plots of model variables at 19.1°S and 24.1°E, representative of wet regions in Botswana. Figure 9b shows potential livestock harvest per year in wet regions in Botswana with the harvest function described as in Equation (7). In this region, the potential annual harvest ranges from 80 to 94 (in average cattle number equivalent). The lowest harvest in 2018 corresponds to delay in herbivore number recovery during the first half of the year, depicted by the red line in Figure 9a.

3.4.2. *Regions with medium-level soil moisture.* Here, we consider regions with soil moisture between 0.1 m^3/m^3 and 0.2 m^3/m^3. Unlike the wet regions we discussed above in Figure 9, in this region soil moisture content is between wilting point and critical point, plant growth is limited by soil moisture. Figure 10 represents time series plots of plants and herbivore interaction and possible harvest for a grid-point at 22.99°S and 26.54°E, which is taken as a representative of regions with medium soil moisture in Botswana.

In Figure 10a soil moisture is less than 0.25 m^3/m^3 except at a few points. Hence, the plant growth is expected to be constrained due to moisture deficit. At the start of the dynamics, both plant biomass and herbivore reduce due to lack of moisture and the dynamics follows the pattern of soil moisture. Particularly, when soil moisture content is greater than 0.25 m^3/m^3, the herbivore number increases quickly. In comparison to the dynamics in Figure 9, the plant biomass



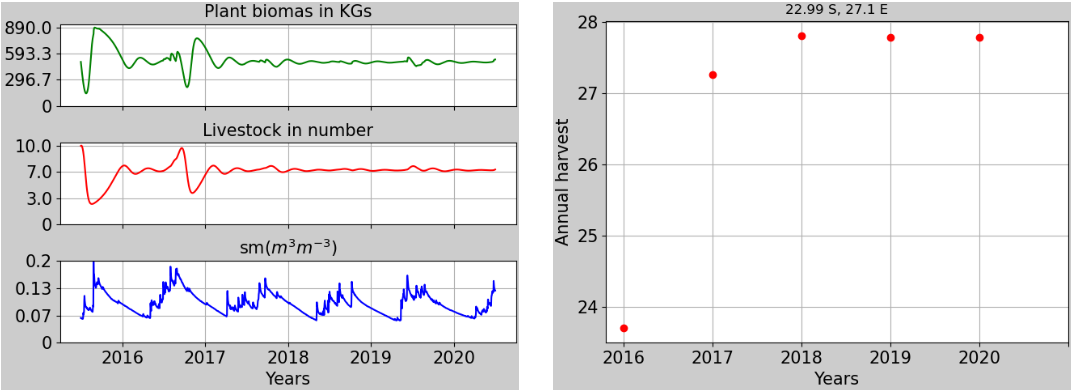
(a) Time series plot of model dynamics (b) Annual harvest

Figure 10. As in Figure 9 but for medium level soil moisture regions.

stays at higher numbers for longer period here but herbivore numbers are lower. Especially during the second half of the year 2017 in Figure 10a, the herbivore number stayed low while plant biomass is higher. As a result, the annual harvest for the year 2017 is the minimum in the five years presented in Figure 10b. In this region, the annual harvest ranges from around 23 to 34 (in average cattle number equivalent, where one cattle is assumed to have 544 kg). Comparing to the wet regions, the maximum annual harvest in wet regions is more than twice the maximum annual harvest of medium soil moisture regions.

3.4.3. *Relatively dry regions.* In this region, grid-points with average soil moisture of less than or equal to 0.1 m^3/m^3 are considered. Plant growth in this region are highly constrained by lack of soil moisture. From Figure 1b we can observe that the maximum growth rate of plant biomass is on average 0.4 per km^2 per day.

Figure 11 indicates the time series plots for the model dynamics variables (in Figures 9 and 10) for grid-point 22.99S, 24.1E. This point is considered as a representative for most regions in Botswana, which is dry with annual mean soil moisture of less than $0.1m^3/m^3$. As the plant biomass is not able to support the herbivore population due to lack of water, immediate decrease is observed for both plant and herbivore population. Then after a while the plant population stabilised and so does the herbivore population. Compared to the results presented in Figures 9 and 10, in Figure 11 we see that plant biomass, herbivore population as well as herbivore



(a) Time series plot of model dynamics

(b) Annual harvest

Figure 11. As in Figure 9 but for dry regions.

harvest are smallest as a result of soil moisture deficit. The maximum livestock harvest in dry regions is about one-third of the maximum harvest in wet regions.

4. CONCLUSIONS

In this study, we developed a mathematical framework to model the interaction of plant and herbivore dynamics by describing plant growth as a function of soil moisture, particularly for Botswana. The model thus formulated is mathematically analysed and stability of the equilibrium points is established. Results investigate the dependence of plant biomass on the soil moisture function and its impact on the livestock population. In addition, we identify regions that are favourable for livestock production, and indicate the possible level of production at each spatial point.

Some relevant model parameters are estimated from literature and others are calculated. However, to investigate the impact of any change on these parameter values on the output of the model we carried out a global sensitivity analysis. Sensitivity analysis of parameters shows that, in general the most important parameters are the average animal feeding rate (a), the carrying capacity (K) and half saturation constant (b). For the herbivore population, the half saturation constant is directly proportional while the average feeding rate is inversely proportional. Whereas for the plant population the feeding rate and the carrying capacity are positively correlated while the half saturation constant of feeding of herbivores (b) and the minimum plant growth rate(m) are inversely proportional. Therefore, for better prediction and reasonable recommendations it will be better to estimate the values of these parameters from a practical field data specific to the study region.

To make the model simulation more specific and to avoid dimensional variations, the weight of each animal is calculated to an average cattle equivalent weight. The spatial distributions of the livestock population and the corresponding harvests in Figure 8 show that, it is possible to have livestock production in most parts of Botswana but with different annual yield/harvest for different regions. The variation comes from the difference in water availability for plants. Regions with average soil moisture 0.2 and above show that there will be an annual harvest more than 90 (cattle head equivalent) livestock and above per year per spatial grid cell. The drier regions show a distribution of minimum annual harvest of 20 (cattle head equivalent) livestock. Regions with medium soil moisture show distribution of annual harvest between 20 and 60.

For relatively wet regions, plant biomass and herbivore population as well as the level of livestock harvest show a positive correlation. In this region, as water is not a limiting factor for plant growth, it is favourable for livestock production without needing extra expense for additional feeding. In comparison, medium soil moisture and dry regions livestock harvests are less than half and less than one-third of the harvest in the wet regions respectively, due to shortage of moisture for plant biomass. To increase livestock production and corresponding harvest, supplementing with additional food is necessary as the natural plant biomass may not be able to support the livestock and leads to the decrease in yield. However, the amount of additional feeding to support the production at each spatial grid cell is yet to be investigated.

In the model formulation, Eqn. (1b), parameter m represents a reservoir plant biomass which exists even though there is no rain or enough moisture in the soil which can be considered as shrubs. As a result of this assumption, we see constant (similar) livestock production for dry regions in Botswana even though with small amount. Considering a variable value for parameter m which changes according to the actual land cover of (shrubs) in a region could be more realistic. It is also assumed that soil properties like wilting point and critical soil moisture are constant throughout Botswana. In reality, soil texture changes in every few kilometres and so do related soil properties. One of the challenges is lack of observations of the state variables of the model to calibrate parameters. As a result, the values of most of the parameters in the model are assumed or estimated, or adopted from similar studies. Hence in the future, it is worth experimenting with varying initial plant cover and soil texture, and use observational data of the model sate variables, if any will be available, to calibrate parameters.

Forecasting the yield from farming activities at any place could be a challenging activity as there involve many variables in the process, and some of which are very difficult to predict. However, if it is possible to project the soil moisture variable, our model can be used to forecast the level of livestock production and possible vegetation coverage in a region where farming activities are being practiced.

APPENDIX A. PROOF FOR POSITIVITY AND BOUNDEDNESS OF SOLUTIONS

Proof of Lemma 2.1. For $0 < r(\theta(t)) < 1$,

$$\begin{aligned} P(t) &= P(0)exp\left\{\int_0^t r(\theta)\left[1-\frac{P}{K}\right] - F(P)Hds\right\} \text{ and} \\ H(t) &= H(0)exp\left\{\int_0^t cF(P)\left(\frac{H}{h+H}\right) - D(F(P)) - \frac{\mu(H)}{H}\right\}. \end{aligned}$$

If $P(0)=0$, then $P(t)=0$ and $H(t)=0$. Hence if there is no plant then the herbivore population will go to extinction. If $H(0)=0$, then $H(t)=0$ for all time $t>0$ and the plant population obeys the logistic growth law. Clearly, exponential functions are always positive. Therefore, if $P(0)>0$ and $H(0)>0$ we have the whole dynamics ranging within the first quadrant. i.e. $P(t)>0$ and $H(t)>0$. This is obvious from system (8); using the Cauchy-Lipschitz theorem (see Theorem 2.2 in [41] or Theorem 2.1 in [39]), as the $P-$axis, and the $H-$axis are orbits, the positive quadrant $int(\mathbb{R}_2^+)$ is positively invariant. □

Proof of Lemma 2.2. To find lower and upper bounds of the plant population let us consider the system in the absence of the animal population. That means, we have

$$\dot{P} = r(\theta)P\left(1-\frac{P}{K}\right) = P\left(r(\theta) - \frac{r(\theta)}{K}P\right).$$

Equating this rate to zero and solving for P we get $P=0$ or $P=K$ hence the plant population is bounded by $0 \le P \le K$.

Note that, $r(\theta)P\left(1-\frac{P}{K}\right)$ is continuous on the interval $[0,K]$ and is, therefore, bounded due to the standard Minimax Theorem in Analysis. Moreover, since $r(\theta)P\left(1-\frac{P}{K}\right)<0$ for $P>K$ the value of $P(t)$ decreases.

For the boundedness of the herbivore population, we use similar arguments as in [3] with the appropriate modifications corresponding the changes made in the model formulation. With this note, we now consider a bound for $H(t)$ from above. From the model formulation we have the emergence (birth) rate of the herbivores is always less than a linear multiple of the functional response. That is, $cF(P)\left(\frac{H}{h+H}\right)<cF(P)$ for some positive constant $c>0$ and also $D(F(P))\geq d_1$ for the positive constant d_1, defined in equation (5).

Combining these observations with the positivity result (from Lemma 2.1) and using equations of the model system (8), we have the following conditions for the three different cases of harvest and for $t>0$.

Case 1: When $0<H<H_{\min}$, there is no harvest and we have

$$\begin{aligned}
\frac{d}{dt}(cP+H) &= c\frac{dP}{dt}+\frac{dH}{dt}\\
&= cr(\theta)P\left(1-\frac{P}{K}\right)-cH\underbrace{\left(\frac{aP}{b+P}\right)}_{=F(P)}+H\underbrace{\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)\right]}_{<cF(P)}-\underbrace{D(F(P))}_{>d_1}H\\
&\leq cr(\theta)P\left(1-\frac{P}{K}\right)-cHF(P)+HcF(P)-d_1H\\
&= cr(\theta)P\left(1-\frac{P}{K}\right)-d_1H\\
&= cr(\theta)P\left(1-\frac{P}{K}\right)+d_1cP-d_1cP-d_1H\\
&= cr(\theta)P\left(1-\frac{P}{K}\right)+d_1cP-d_1(cP+H).
\end{aligned}$$

Here, we can observe that $cr(\theta)P\left(1-\frac{P}{K}\right)+d_1cP=-cr(\theta)\dfrac{P^2}{K}+c(r(\theta)+d_1)P$ is a quadratic expression in P and it can be easily seen to have a global maximum at

$$\frac{4(-cr(\theta)/K)-(c(r(\theta)+d_1+\mu))^2}{4\frac{-cr(\theta)}{K}}=\frac{Kc(r(\theta)+d_1)^2}{4r(\theta)}.$$

Hence, for this case $\eta = \dfrac{Kc(r(\theta)+d_1)^2}{4r(\theta)} \geq cr(\theta)P\left(1-\dfrac{P}{K}\right)+cd_1P$ and we have

$$\begin{aligned}\frac{d}{dt}(cP+H) &\leq \frac{Kc(r(\theta)+d_1)^2}{4r(\theta)} - d_1(cP+H)\\ &= \eta - d_1(cP+H).\end{aligned} \tag{18}$$

Then, it follows from the last step of (18) that $cP(t)+H(t) \leq W(t)$ for all $t \geq 0$, where $W(0) = cP(0)+H(0) \geq 0$ and $W(t)$ is a solution of $\dfrac{dW}{dt} = \eta - d_1 W$.

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

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

Hence, $cP(t)+H(t)$ 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 $\widehat{H}$ (whose value is given in (12)). Since the plant population has an upper bound K or $P(0)$ then the herbivore population will also have a corresponding upper limit as it depends on the relation $cP(t)+H(t) = W(t) \leq \widehat{H} \Longrightarrow H(t) \leq \widehat{H} - cP(t)$.

Case 2: In the case $H_{\min} < H < H_o$, $\mu(H) = \mu_o$, and hence we have

$$\begin{aligned}\frac{d}{dt}(cP+H) &= c\frac{dP}{dt} + \frac{dH}{dt}\\ &= cr(\theta)P\left(1-\frac{P}{K}\right) - cH\underbrace{\left(\frac{aP}{b+P}\right)}_{=F(P)} + H\underbrace{\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)\right]}_{<cF(P)} - \underbrace{D(F(P))}_{>d_1}H - \mu_o\\ &\leq cr(\theta)P\left(1-\frac{P}{K}\right) - cHF(P) + HcF(P) - d_1H - \mu_o\\ &= cr(\theta)P\left(1-\frac{P}{K}\right) - d_1H - \mu_o\\ &= cr(\theta)P\left(1-\frac{P}{K}\right) + d_1cP - d_1cP - d_1H - \mu_o\\ &= cr(\theta)P\left(1-\frac{P}{K}\right) + d_1cP - \mu_o - d_1(cP+H).\end{aligned}$$

Here, we can see that $cr(\theta)P\left(1-\frac{P}{K}\right)+d_1cP-\mu_o=-cr(\theta)\frac{P^2}{K}+c(r(\theta)+d_1)P-\mu_0$ is a quadratic expression in P and it can be easily seen to have a global maximum at

$$\frac{4(-cr(\theta)/K)(-\mu_o)-(c(r(\theta)+d_1))^2}{4\frac{-cr(\theta)}{K}}=-\mu_o+\frac{Kc(r(\theta)+d_1)^2}{4r(\theta)}.$$

Hence, $\eta^*=\dfrac{Kc(r(\theta)+d_1)^2}{4r(\theta)}-\mu_0\geq cr(\theta)P\left(1-\dfrac{P}{K}\right)+d_1cP-\mu_o$ and we have

$$\begin{aligned}\frac{d}{dt}(cP+H) &\leq \underbrace{\frac{Kc(r(\theta)+d_1)^2}{4r(\theta)}-\mu_0}_{\eta^*}-d_1(cP+H)\\ &\leq \eta^*-d_1(cP+H).\end{aligned}\tag{19}$$

Then, it follows from Equation (19) that $cP(t)+H(t)\leq W(t)$ for all $t\geq 0$ where $W(0)=cP(0)+H(0)\geq 0$ and $W(t)$ is a solution of $\dfrac{dW}{dt}=\eta^*-d_1W$.

Solving for W we have $W=\dfrac{\eta^*}{d_1}-\dfrac{A*}{d_1}e^{-d_1t}$ and then

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

Hence, using the same argument as in Case 1 above we can conclude that H is bounded from above by $\widehat{H}$.

The upper bound of the herbivore population is guaranteed through the plant population which has a an upper bound. The corresponding upper limit of the herbivore population as it depends on the relation $cP(t)+H(t)=W(t)\leq\widehat{H}\Longrightarrow H(t)\leq\widehat{H}-cP(t)$.

Case 3: When $H>H_o$, the harvest function becomes $\mu(H)=\mu H$, and hence we have

$$\begin{aligned}\frac{d}{dt}(cP+H)&=c\frac{dP}{dt}+\frac{dH}{dt}\\ &=cr(\theta)P\left(1-\frac{P}{K}\right)-cH\underbrace{\left(\frac{aP}{b+P}\right)}_{=F(P)}+H\underbrace{\left[c\left(\frac{aP}{b+P}\right)\left(\frac{H}{h+H}\right)\right]}_{<cF(P)}-\underbrace{D(F(P))}_{>d_1}H-\mu(H)\\ &\leq cr(\theta)P\left(1-\frac{P}{K}\right)-cHF(P)+HcF(P)-d_1H-\mu H\\ &=cr(\theta)P\left(1-\frac{P}{K}\right)-(d_1+\mu)H.\end{aligned}$$

Therefore, for $\mu(H) = \mu H$, we have

$$\begin{aligned}
&\frac{d}{dt}(cP+H) = c\frac{dP}{dt} + \frac{dH}{dt} \\
&\leq cr(\theta)P\left(1-\frac{P}{K}\right) + (d_1+\mu)cP - (d_1+\mu)cP - (d_1+\mu)H \\
&= cr(\theta)P\left(1-\frac{P}{K}\right) + (d_1+\mu)cP - (d_1+\mu)(cP+H).
\end{aligned}$$

Once again we can observe here that

$$cr(\theta)P\left(1-\frac{P}{K}\right) + (d_1+\mu)cP = -cr(\theta)\frac{P^2}{K} + c(r(\theta)+d_1+\mu)P$$

is a quadratic expression in P that has a global maximum at

$$\frac{-4(-cr(\theta)/K)(0) - (c(r(\theta)+d_1+\mu))^2}{4\frac{-cr(\theta)}{K}} = \frac{Kc(r(\theta)+d_1+\mu)^2}{4r(\theta)}.$$

Hence, $\eta^{**} = \dfrac{Kc(r(\theta)+d_1+\mu)^2}{4r(\theta)} \geq cr(\theta)P\left(1-\dfrac{P}{K}\right) + (d_1+\mu)cP$ and we have

$$\begin{aligned}
\frac{d}{dt}(cP+H) &\leq \frac{Kc(r(\theta)+d_1+\mu)^2}{4r(\theta)} - (d_1+\mu)(cP+H) \\
&\leq \eta^{**} - (d_1+\mu)(cP+H). \qquad (20)
\end{aligned}$$

Then, it follows from (20) that $cP(t)+H(t) \leq W(t)$ for all $t \geq 0$ where $W(0) = cP(0) + H(0) \geq 0$ and $W(t)$ is a solution of

$$\frac{dW}{dt} = \eta^{**} - (d_1+\mu)W.$$

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

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

Hence, employing the same argument as in Case 1 above we can conclude that H is bounded from above by $\widehat{H}$.

The plant population has an upper bound then using the relation $cP(t)+H(t) = W(t) \leq \widehat{H} \Longrightarrow H(t) \leq \widehat{H} - cP(t)$ the herbivore population will also have a corresponding upper limit.

Therefore, for all the three cases we can conclude that the solution of the model system is bounded at all times. □

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interests.

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