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ANALYSIS OF PLANT-SOIL MODELS WITH VARIOUS FUNCTIONAL NITROGEN UPTAKE KINETICS

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Abstract: This paper analyzes the Plant-Soil Models with functional nitrogen uptake kinetics. In this work we focus on the effects of using different forms of nitrogen uptake kinetic function for the dynamics of Plant-Soil model including Holling type II and III. We present the derivations of these two different type of functional kinetics for the general enzyme-substrate reaction process. For the Plant-Soil Model the local existence and positive invariance of the solution are investigated. Also some conditions to guarantee that the model possesses a unique positive equilibrium point are suggested.

AMS Subject Classification: 34A12, 34C11
Key Words: Plant-Soil Model, functional kinetics, enzyme-substrate reaction, positive invariance, positive equilibrium point

1. Introduction

The Plant-Soil Model is set up to simulate the effect of temperature increase on ecosystem carbon (C) storage and the cycling of carbon (C) and nitrogen

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(N) between plants and soil pool that is shallow and active. In this model the aboveground biomass is represent by P as the product of biogeometric reaction, soil carbon by C_s, soil nitrogen by N, plant carbon by C_p. The changes of these quantities in time for $t \in (0, \infty)$ are described as follows:

$$\begin{cases} \dfrac{dP}{dt} = -mP + \mu\, f(N)\, P, \\ \dfrac{dC_s}{dt} = mP - \nu\, C_s, \\ \dfrac{dN}{dt} = \eta - l_n\, N - \mu\, f(N)\, P + (1-q)\nu\, C_s, \\ \dfrac{dC_p}{dt} = \gamma\nu\, C_s - l_c\, C_p, \end{cases} \tag{1}$$

where the initial values $P(0)$, $C_s(0)$, $N(0)$, $C_p(0)$ are all positive, $f(N)$ is a function of N which represents density dependent nitrogen uptake kinetics, and m, μ, ν, η, l_n, l_c, q, γ represent positive constants. The details on the physical meanings of the coefficients and the agricultural, biochemical, biogemetrical backgrounds of this type of models may be found in [8], [10], [11] and references therein. Especially in [10] the Plant-Soil Model (1) is used to simulate the effects of climate warming on the quantities of carbon and nitrogen and their rate of changes in terrestrial ecosystem in arctic Alaska. In [10] the nitrogen uptake kinetic function $f(N)$ is set up as

$$f(N) = \frac{aN}{b+N}, \tag{2}$$

where a, b are positive constant. The function in (2) is called as Holling type II kinetics (see [5], [6]). It is also called as Michaelis-Menten kinetics (see [8], [9]).

In this work we focus on the effects of different forms of nitrogen uptake kinetic function $f(N)$ for the dynamics of the Plant-Soil model (1) including Holling type II (2) and Holling type III (see [5], [6]) which is

$$f(N) = \frac{cN^2}{d+N^2}, \tag{3}$$

where c, d are positive constant.

Nitrogen uptake process in plants is enzyme-substrate reaction where soil nitrogen N is the substrate and with an enzyme the biomass P is produced by

plants (see [2]). In Section 2, we present the derivations of these two different type of functional kinetics for the general enzyme-substrate reaction process. In Section 3, we analyze the Plant-Soil Model (1) with the two different forms of kinetic functions as in (2), (3).

2. Derivations of different types of Functional Kinetics

The process in plants that involves nitrogen uptake and biomass product is an enzyme-substrate biochemical reaction. Let us observe general enzyme-substrate reaction system with enzyme E, substrate S, enzyme-substrate complex H, and product P:

$$E + S \underset{k_1^-}{\overset{k_1^+}{\rightleftharpoons}} H \overset{k_2^+}{\to} E + P, \tag{4}$$

where k_1^+, k_1^-, k_2^+ are positive constants.

According to the law of mass action, we write out the governing equations for reaction (4) as follows. Here the variables E, S, H and P represent concentration of the enzyme, the substrate, the enzyme-substrate complex, and the product, respectively:

$$\frac{dE}{dt} = -k_1^+ ES + (k_1^- + k_2^+)H, \tag{5}$$

$$\frac{dS}{dt} = -k_1^+ ES + k_1^- H, \tag{6}$$

$$\frac{dH}{dt} = k_1^+ ES - (k_1^- + k_2^+)H, \tag{7}$$

$$\frac{dP}{dt} = k_2^+ H. \tag{8}$$

Many enzyme-substrate reaction models usually assume the quasi-steady-state approximation that the enzyme-substrate complexes turns into equilibrium state instantaneously with enzyme and substrate concentration (see [10]). Under this assumption, in equation (7)

$$\frac{dH}{dt} \approx 0$$

instantaneously, thus we have

$$ES = k\,H, \qquad \text{where} \quad k = \frac{k_1^- + k_2^+}{k_1^+}. \tag{9}$$

Substituting the relations in equation (9) to equation (6)

$$\frac{dS}{dt} = -k_1^+ kH + k_1^- H = -k_2^+ H. \tag{10}$$

During short time period in the beginning of the reaction, the amount of generated product P is very small, so for the total enzyme concentration $\tilde{E}$ the total substrate concentration $\tilde{S}$ we set

$$E + H = \tilde{E}, \qquad S + H = \tilde{S}. \tag{11}$$

Now equations (9) and (11) are solved:

$$(\tilde{E} - H)(\tilde{S} - H) = kH,$$

to the quadratic equation

$$H^2 - (k + \tilde{E} + \tilde{S})H + \tilde{E}\tilde{S} = 0 \tag{12}$$

that has two positive solutions

$$H = \frac{1}{2}\left((k + \tilde{E} + \tilde{S}) \pm \sqrt{(k + \tilde{E} + \tilde{S})^2 - 4\tilde{E}\tilde{S}}\right). \tag{13}$$

Here, considering that from (11)

$$H < \frac{1}{2}\left(\tilde{E} + \tilde{S}\right),$$

we have

$$\begin{aligned} H &= \frac{1}{2}\left((k + \tilde{E} + \tilde{S}) - \sqrt{(k + \tilde{E} + \tilde{S})^2 - 4\tilde{E}\tilde{S}}\right) \\ &= \frac{1}{2}(k + \tilde{E} + \tilde{S})\left(1 - \sqrt{1 - \frac{4\tilde{E}\tilde{S}}{(k + \tilde{E} + \tilde{S})^2}}\right). \end{aligned} \tag{14}$$

Now we observe two kinds of approximation of H in (14) as a function of two variables $\tilde{E}$ and $\tilde{S}$. First if we use the linear approximation for the function $\sqrt{1-x}$ regarding the quantity $\frac{4\tilde{E}\tilde{S}}{(k+\tilde{E}+\tilde{S})^2}$ is small enough, we have

$$\begin{aligned} H &\approx \frac{1}{2}(k + \tilde{E} + \tilde{S})\left(1 - \left\{1 - \frac{1}{2} \cdot \frac{4\tilde{E}\tilde{S}}{(k + \tilde{E} + \tilde{S})^2}\right\}\right) \\ &= \frac{\tilde{E}\tilde{S}}{k + \tilde{E} + \tilde{S}}. \end{aligned} \tag{15}$$

Secondly by comparing the three dimensional plots we see that the function H in (14) would be approximated as

$$H \approx \frac{\tilde{E}(\tilde{S})^2}{k + \tilde{E} + (\tilde{S})^2}. \tag{16}$$

An example set of graphs of the function H of two variables $\tilde{E}$ and $\tilde{S}$ in (14), the approximation in (15), and the approximation in (16) are shown in Figure 1. Figure 2 shows in certain range of the variables, the approximation (16) is more accurate than the approximation (15).

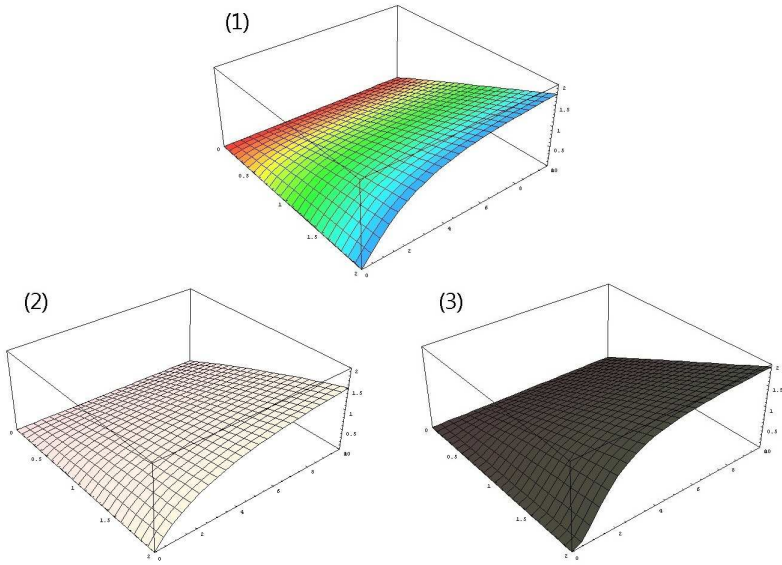

Figure 1: Example set of graphs of (1) the function H in (14), (2) the approximation in (15), and (3) the approximation in (16)

Using the approximation (15) and furthermore assuming that $k + \tilde{S}$ is dominant compare to $\tilde{E}$, we would use the form of the function H as

$$H = \frac{\tilde{E}\tilde{S}}{k + \tilde{S}}. \tag{17}$$

Substituting the function H in (17) to equation (10), we obtain the Holling type II form of the kinetic relation:

$$\frac{dS}{dt} = -\frac{aS}{k + S}, \tag{18}$$

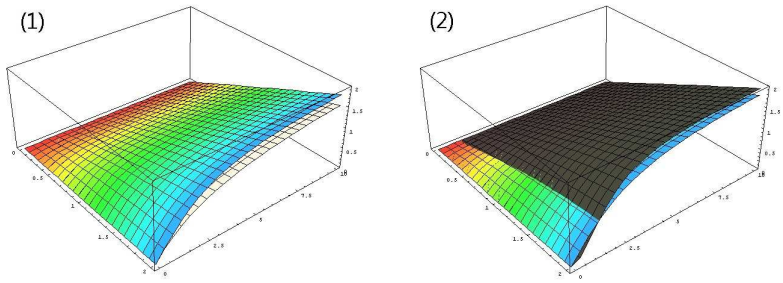

Figure 2: Example set of graph comparison of (1) the function H in (14) and the approximation in (15), (2) the function H in (14) and the approximation in (16)

where $a = k_2^+ \tilde{E}$ regarding $\tilde{E}$ as a constant approximately and S is used in the place of $\tilde{S}$ as usual in the modeling of enzyme-substrate reactions.

Using the approximation (16) and furthermore assuming that $k + (\tilde{S})^2$ is dominant compare to $\tilde{E}$, we would use the form of the function H as

$$H = \frac{\tilde{E}(\tilde{S})^2}{k + (\tilde{S})^2}. \tag{19}$$

Substituting the function H in (19) to equation (10), we obtain the Holling type III form of the kinetic relation :

$$\frac{dS}{dt} = -\frac{aS^2}{k + S^2}, \tag{20}$$

where $a = k_2^+ \tilde{E}$ regarding $\tilde{E}$ as a constant approximately and S is used in the place of $\tilde{S}$.

3. Analysis of Plant-Soil Model with two different kinetic functions

For the Plant-Soil Model (1) we consider the Holling type II and III kinetic functions as in (2) and (3). In (1) the right-hand side of each equations are continuous functions of the variables P, C_s, N, C_p, so the local existence of the solution to the system of differential equations (1) is guaranteed. And to examine the positivity of the solution to the system (1) we would apply Gronwall's Inequality as in the following theorem (refer p.169 in [4] for example).

Theorem 1 (Gronwall's Inequaity-differential form)**.** *Suppose* $g,\ h : [0,T] \to \mathbb{R}$ *are continuous functions, and* $u : [0.T] \to \mathbb{R}$ *is a* C^1 *function and satisfies*

$$u'(t) \le g(t)u(t) + h(t) \quad \text{for } t \in [0,T].$$

Then

$$u(t) \le u(0)\, e^{\int_0^t g(t)\,dt} + \int_0^t \left(e^{\int_0^t g(t)\,dt}\right) h(s)\,ds.$$

Lemma 2. *The region* $\Omega = \{(P, C_s, N, C_p) \mid P > 0,\ C_s > 0,\ N > 0,\ C_p > 0\}$ *in* $\mathbb{R}^4$ *is invariant for the system* (1).

Proof. In $\mathbb{R}^4$ on the hyperplane $N = 0$ the system (1) is reduced to

$$\frac{dP}{dt} = -mP, \tag{21}$$

$$\frac{dC_s}{dt} = mP - \nu\, C_s, \tag{22}$$

$$\frac{dC_p}{dt} = \gamma\nu\, C_s - l_c\, C_p. \tag{23}$$

Solving the differential equation (21) directly we obtain a nonnegative bounded solution $P(t)$. Now substituting this function $P(t)$ to the right-hand side of (22) and applying Gronwall's Theorem 1 it is shown that the solution $C_s(t)$ is a nonnegative bounded function. Similarly the solution $C_p(t)$ of equation (23) is shown to be a nonnegative bounded function. Thus on the hyperplane $N = 0$, solution orbits of the system (1) stay in the positive part $\{(P, C_s, C_p) \mid P > 0,\ C_s > 0,\ C_p > 0\}$.

For the hyperplanes $P = 0$, $C_s = 0$, $C_p = 0$ the same results are derived as well. From the fact that different orbits do not intersect each other, we conclude that the region Ω in $\mathbb{R}^4$ is invariant for the system (1). □

Lemma 3. *For the system* (1) *with the Holling type II kinetic functions*

$$f(N) = \frac{aN}{k+N}$$

where a *and* k *are positive constants, assume the condition*

$$a\mu > m, \quad \text{and} \quad \eta > l_n \cdot \frac{mk}{a\mu - m}. \tag{24}$$

And let us denote

$$\alpha = \frac{1}{q}\left(\eta - l_n \cdot \frac{mk}{a\mu - m}\right).$$

Then the Plant-Soil Model (1) *has a unique positive constant equilibrium point* $(\overline{P}, \overline{C}_s, \overline{N}, \overline{C}_p)$ *in* $\mathbb{R}^4$*, where*

$$\overline{P} = \frac{1}{m}\,\alpha, \qquad \overline{C}_s = \frac{1}{\nu}\,\alpha, \qquad \overline{N} = \frac{mk}{a\mu - m}, \qquad \overline{C}_p = \frac{\gamma}{l_c}\,\alpha. \tag{25}$$

Proof. For each equation in the system (1), let the derivatives of the functions to be zero to find equilibrium points. Then we have a system of four algebraic equations.

$$0 = -m\,\overline{P} + \mu\, f(\overline{N})\,\overline{P}, \tag{26}$$

$$0 = m\,\overline{P} - \nu\,\overline{C}_s, \tag{27}$$

$$0 = \eta - l_n\,\overline{N} - \mu\, f(\overline{N})\,\overline{P} + (1-q)\nu\,\overline{C}_s, \tag{28}$$

$$0 = \gamma\nu\,\overline{C}_s - l_c\,\overline{C}_p. \tag{29}$$

Since we look for positive equilibrium points, from equation (26) we have

$$\frac{m}{\mu} = f(\overline{N}) = \frac{a\overline{N}}{k + \overline{N}},$$

and find a unique solution

$$\overline{N} = \frac{mk}{a\mu - m}. \tag{30}$$

Solving equations (26), (27) and (27) we have

$$0 = \eta - l_n\,\overline{N} - qm\,\overline{P}.$$

Thus we obtain

$$\overline{P} = \frac{1}{qm}\left(\eta - l_n\,\overline{N}\right) = \frac{1}{m}\,\alpha,$$

and

$$\overline{C}_s = \frac{m}{\nu}\,\overline{P} = \frac{1}{\nu}\,\alpha.$$

And finally from equation (29) we have

$$\overline{C}_p = \frac{\gamma\nu}{l_c}\,\overline{C}_s = \frac{\gamma}{l_c}\,\alpha.$$

□

Lemma 4. *For the system* (1) *with the Holling type III kinetic functions*

$$f(N) = \frac{aN^2}{k + N^2}$$

where a *and* k *are positive constants, assume the condition*

$$a\mu > m, \quad \text{and} \quad \eta^2 > l_n^2 \cdot \frac{mk}{a\mu - m}. \tag{31}$$

And let us denote

$$\beta = \frac{1}{q}\left(\eta - l_n\sqrt{\frac{mk}{a\mu - m}}\right).$$

Then the Plant-Soil Model (1) *has a unique positive constant equilibrium point* $(\overline{P}, \overline{C}_s, \overline{N}, \overline{C}_p)$ *in* $\mathbb{R}^4$, *where*

$$\overline{P} = \frac{1}{m}\beta, \qquad \overline{C}_s = \frac{1}{\nu}\beta, \qquad \overline{N} = \sqrt{\frac{mk}{a\mu - m}}, \qquad \overline{C}_p = \frac{\gamma}{l_c}\beta. \tag{32}$$

Proof. Similar to the proof of Lemma 3. □

For an example to see the results obtained in Lemma 3 and Lemma 4, one may use the parameter values that suggested in [10] as $m = 0.01$, $\mu = 0.33$, $\nu = 0.0002$, $\eta = 0.1$, $l_n = 0.015$, $l_c = 1$, $q = 0.5$, $\gamma = 26$, $a = 1$, $k = 10$. With this set of parameter values, in Lemma 3 where the nitrogen uptake kinetic function is Holling type II form

$$f(N) = \frac{aN}{k + N},$$

we have

$$a\mu - m = 0.32, \qquad \eta - l_n \cdot \frac{mk}{a\mu - m} = 0.00953125,$$

so the condition (24)

$$a\mu > m, \quad \text{and} \quad \eta > l_n \cdot \frac{mk}{a\mu - m}$$

is satisfied, and thus the existence of the positive equilibrium points is guaranteed. Also in Lemma 4 with this set of parameter values, where the nitrogen uptake kinetic function is Holling type III form

$$f(N) = \frac{aN^2}{k + N^2},$$

we have

$$a\mu - m = 0.32, \qquad \eta^2 - l_n^2 \cdot \frac{mk}{a\mu - m} = 0.009296875,$$

so the condition (31)

$$a\mu > m, \quad \text{and} \quad \eta^2 > l_n^2 \cdot \frac{mk}{a\mu - m}$$

is satisfied, and thus the existence of the positive equilibrium points is guaranteed in this case.

4. Conclusions

In this work we focus on the effects of different forms of nitrogen uptake kinetic function $f(N)$ for the dynamics of the Plant-Soil model (1) including Holling type II and Holling type III. These two different types of functional kinetics are derived from the enzyme-substrate biochemical reaction process in plants that involves nitrogen uptake and biomass product under the assumption of the quasi-steady-state approximation. The Plant-Soil Model (1) with Holling type II and III kinetic functions is analyzed in terms of the local existence and the positivity of the solutions. A set of conditions for the parameters in the Plant-Soil Model (1) are suggested to guarantee the existence of the positive equilibrium points in the case of Holling type II and III kinetic functions, respectively. And we check with an example in [10] for these sets of conditions for the parameters.

The results could be directly applied to the Plant-Soil model in the field of biogeochemical studies for temperature warming effects. Also related to many ecological studies (for example, [1], [3], [7]) dealing with Michaelis-Menten kinetics, that is Holling type II, it would be worth considering extending investigations with Holling type III kinetics for subtle difference of response behaviors.

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