Seasonal Switching Affects Bacterial-Fungal Dominance in an Ecological System

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Abstract

We consider a model inspired by producer-herbivore-decomposer soil food webs and determine the effect of ecological parameters on the decomposer pool. In particular, we observe how seasonal changes in the stoichiometric quality of the producer coupled with the efficiency of herbivory over the calendar year can induce a shift in the composition of the decomposer pool. Decomposers have a significant effect on the movement of essential nutrients throughout an ecosystem; we further determine how this shift between a bacterially dominated decomposer pool and a fungally dominated pool affects primary production and relative distribution of biomass of the other compartments.
MONTCLAIR STATE UNIVERSITY

Seasonal Switching Affects Bacterial-Fungal Dominance in an Ecological System

by

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Introduction

Microbial biomass plays a pivotal role in nutrient cycling through food webs. Plant growth, and therefore herbivore growth, is determined by availability of nutrients and the interaction of stoichiometric inequalities between consumer and consumed. In particular, decomposers are the driving force behind primary production and nutrient cycling [1]. The inequality between microbial decomposers and soil organic matter (detritus) drives soil nutrient availability; the seasonal variability in the quality of producers and detrital matter drives bacterial versus fungal dominance [2].

In this thesis, we consider a plant-herbivore-decomposer soil network where primary production is determined entirely by availability of inorganic nitrogen. Inorganic nitrogen moves through the network via assimilation by microbial decomposers, herbivore excretion, and producer uptake. Decomposer growth is determined by the uptake of carbon (C) and nitrogen (X) of organic soil matter as well as the availability of inorganic nitrogen to supplement the nutrient intake. We use X to represent the essential nutrient nitrogen because depending on the model setting and ecosystem parameter values, our work can be applied to analyze any secondary nutrient, such as phosphorus or sulfur, though in this thesis we consider only carbon and nitrogen.

In soil food webs, decomposers take in biomass from the detritus, and either mineralize excess nitrogen to the inorganic pool, or immobilize nitrogen from the inorganic pool in order to supplement nutrient requirements. The tipping point between assimilation and mineralization from the microbial decomposer pool is determined by a ratio known as the decomposer Threshold Elemental Ratio (TER). In order to assimilate nutrients into biomass, decomposers need carbon and nitrogen in a ratio equal to their own; however, they also need excess carbon to stimulate this growth through respiration [3]. When we consider the decomposer C:X ratio along with the amount of excess carbon needed for assimilation, the result is the decomposer TER, also known as the demand ratio. Decomposers in any ecosystem have a growth efficiency which is the percentage of carbon that is ingested by the decomposer, not respired. We find the demand ratio by taking the quotient of the decomposer C:X ratio and the growth efficiency.

Decomposers get their nutrients from two pools: detritus and the inorganic nitrogen pool. If the decomposer TER is greater than the detritus C:X ratio, the decomposers will
take in excess nitrogen from the detrital pool, and will mineralize the excess nitrogen to the inorganic X pool; this is considered a C-limited decomposer environment, as the growth of the decomposer is entirely determined by the carbon uptake from the decomposer pool. However, if the detritus C:X ratio is greater than the decomposer TER, decomposers will need to supplement their nitrogen intake by taking from the inorganic X pool through a process called immobilization. This results in two possibilities. If the inorganic pool has enough biomass to adequately supplement the decomposers’ need for more nitrogen, decomposers are still considered C-limited, as they are still limited by the amount of carbon uptake from the detritus. If the inorganic pool does not have sufficient biomass to supplement the nutrients from the detritus, decomposers are known as being X-limited, or limited by the amount of inorganic X available. It is important to note that while we discuss ‘C-limited environments’ this does not mean that the entire system is carbon limited, rather, that the decomposer pool is carbon limited. The system taken as a whole, in particular primary production, is limited by inorganic nitrogen as stated above.

In this thesis, we observe how seasonal changes can induce a shift in the decomposer pool by modeling a change in the quality of the producer throughout the year, and consequently, a change in herbivore efficiency. This shift between a bacterially dominated decomposer pool and a fungally dominated pool provides insight into how biomass moves through an ecosystem, as well as how decomposers can affect primary production.

Model Description

We have developed a plant-herbivore-decomposer network model where primary production is determined entirely by inorganic nitrogen availability. Figure 1 shows our compartment model that consists of nine interacting pools from five compartments, tracking the movement of carbon (C) and a secondary essential nutrient (X) through a forest and shrubland setting. While X can represent any secondary nutrient, for our purposes and parameter values, we take X to be nitrogen. The nine interacting pools are producer C and X ($C_P$ and $X_P$), herbivore C and X ($C_H$ and $X_H$), detrital C and X ($C_M$ and $X_M$), decomposer C and X ($C_D$ and $X_D$), and inorganic nitrogen ($X_I$). Carbon and nitrogen are in ratio, so there is only one independently varying pool from
Figure 1: Compartment model showing the flow of carbon (C) and nitrogen (X) through a producer-herbivore-decomposer soil food web.

Each compartment. For consistency, we consider only the X mass balance equations.

The producers include plant roots and shoots. Though producers have a specified C:X ratio, as living organisms, they require an additional percentage of carbon to produce energy for growth. Recall that the growth efficiency of the producer is the percentage of carbon that is ingested, not respired, by the plant. Therefore, the quotient of the producer C:X ratio and growth efficiency determines the producer’s Threshold Elemental Ratio (TER). In our model, producer growth is determined entirely by inorganic X, as we assume an unlimited amount of carbon is available for plant uptake. It is for this reason that we do not address the producer TER. There is no general loss of producer mass from the system; any mass lost from the compartment is due to herbivory or death to the detrital pool.

Our herbivore pool is made up of root herbivore nematodes. Herbivore growth is determined entirely by herbivory. The herbivores respire excess carbon, which leaves the system completely, and excrete nitrogen to the inorganic compartment. The herbivore C:X ratio is held constant. In this thesis, we take a particular interest in herbivore efficiency, the percentage of plant biomass lost from herbivory that is ingested by the
herbivore. When herbivores eat, they generally do not consume the entire plant due to inedible shoots and roots, or sloppy grazing, and this leftover material enters the detritus compartment as unchanged producer mass. Similar to the producers, there is no general loss of herbivore mass, and we also assume no outside predation, though biomass is lost to the detrital pool due to death. Because the range for producer C:X is much larger than the herbivore C:X, especially in terrestrial systems such as ours, we do not address the herbivore TER, as herbivores are never limited by carbon intake [4]. Note that this model does not account for herbivore feeding strategies or optimal foraging, and we use a reasonable estimated herbivore respiration rate, as this type of parameter is extremely difficult to measure [5].

The detritus pool contains both plant and herbivore biomass, due to death and inefficient grazing. It is assumed that once producer or herbivore biomass enters the detritus pool, it is well-mixed and not discriminated by decomposers. Most loss from the detritus compartment is due to decomposition to the decomposer pool; however, we account for a small amount of general loss from both detritus and decomposers that exits the system completely [6]. We do not consider decomposer death to detritus, as it would complicate the model unnecessarily; the biomass cycles back into the decomposer compartment through detritus easily, and becomes a negligible term [6].

The inorganic nitrogen pool gains biomass from herbivore excretion and from mineralization from decomposers when present in a C-limited environment. There is general input from outside the system, as well as general loss that leaves the system; however, most inorganic mass is lost to producer uptake.

There is also movement between the decomposer and inorganic X pools, making the decomposer compartment the most complex portion of the model. Decomposers take in biomass from the detritus, and either mineralize excess nitrogen to the inorganic pool, or immobilize nitrogen from the inorganic pool in order to supplement nutrient requirements [3]. The direction of this flux depends on several factors. We need to consider the decomposer TER and its relation to the detritus C:X ratio, as well as the ability of the inorganic X pool to supplement any extra nitrogen to the decomposer. In this model, the growth efficiency of decomposers is held constant, so the decomposer C:X ratio directly determines the TER. In X-limitation, an immobilization rate is established, and determines the decomposition rate. In C-limitation, a decomposition rate is first
established. Depending on the differential between detritus C:X and decomposer C:X ratios, decomposers interact with the inorganic pool by either mineralizing excess nitrogen or immobilizing needed supplementary nitrogen.

Model Equations and Derivations

We assume the system is donor controlled, with the exception of herbivory. In a donor controlled system, uptake rates are determined entirely by the biomass of the ‘donor’ compartment. In this model, herbivory is the only rate that is not donor controlled. In most ecosystems, including our forest/shrubland setting, the producer biomass available for consumption greatly outweighs the needs of the herbivores. This allows for a mass action term for herbivory, where herbivory is determined by both the producer biomass as well as herbivore biomass. Table 2 in Appendix A contains variable and parameter definitions along with parameter values.

The mass balance equation for nitrogen in the producer pool is given by

\[
\frac{dX_P}{dt} = \text{inorganic X uptake - herbivory - death} = u_I X_I - h X_H X_P - d_P X_P, \tag{1}
\]

where \( u_I \) is the producer inorganic nitrogen uptake rate, \( h \) is the herbivory rate, and \( d_P \) is the producer death rate. Because C and X are in ratio,

\[
\frac{dC_P}{dt} = \alpha \frac{dX_P}{dt},
\]

where \( \alpha \) is the producer C:X ratio. The mass balance equations for carbon in the producer pool is

\[
\frac{dC_P}{dt} = \text{fixation - herbivory - death} = \alpha (u_I X_I - h X_H X_P - d_P X_P). \tag{2}
\]

The mass balance equation for herbivore nitrogen is

\[
\frac{dX_H}{dt} = \text{herbivory - death - excretion} = e h X_H X_P - d_H X_H - \text{excretion}, \tag{3}
\]

where \( e \) is the herbivore efficiency and \( d_H \) is the herbivore death rate. We now formulate the equation for herbivore carbon in order to derive the herbivore excretion term. First,
because C and X are in ratio for the herbivores, we have \( \frac{dC_H}{dt} = \gamma \frac{dX_H}{dt} \) where \( \gamma \) is the herbivore C:X ratio. Then

\[
\frac{dC_H}{dt} = \gamma (e h X_H X_P - d_H X_H - \text{excretion}) \\
= \gamma e h X_H X_P - \gamma d_H X_H - \gamma (\text{excretion}).
\] (4)

From the model, we also have

\[
\frac{dC_H}{dt} = \text{herbivory} - \text{death} - \text{respiration}.
\]

Because herbivory is associated with the producer compartment and herbivore death is associated with the herbivore compartment,

\[
\frac{dC_H}{dt} = \alpha e h X_H X_P - \gamma d_H X_H - \gamma r_H X_H.
\]

We establish the respiration term, where \( r_H \) represents the herbivore respiration rate as

\[
\frac{dC_H}{dt} = \alpha e h X_H X_P - \gamma d_H X_H - r_H C_H \\
= \alpha e h X_H X_P - \gamma d_H X_H - \gamma r_H X_H.
\] (5)

Setting Eqs. (4) and (5) equal,

\[
\gamma e h X_H X_P - \gamma d_H X_H - \gamma (\text{excretion}) = \alpha e h X_H X_P - \gamma d_H X_H - \gamma r_H X_H.
\]

Solving for excretion, we find that

\[
\text{excretion} = \frac{\gamma - \alpha}{\gamma} e h X_H X_P + r_H X_H,
\]

which leads to the following equation for herbivore nitrogen

\[
\frac{dX_H}{dt} = e h X_H X_P - d_H X_H - \left[ \frac{\gamma - \alpha}{\gamma} e h X_H X_P + r_H X_H \right].
\] (6)

The movement of biomass between the detritus, decomposer, and inorganic nitrogen pools are more complex. In order to derive the mass balance equations for the remaining
pools, we first discuss decomposer mineralization and immobilization [3]. We denote the flux of C and X from detritus to decomposers as $\phi_{MC}$ and $\phi_{MX}$ respectively, and the flux from the inorganic X pool to the decomposer pool as $\phi_I$. Note that $\phi_{MC}$ and $\phi_{MX}$ are always positive, but $\phi_I$ can be positive (indicating immobilization) or negative (indicating mineralization). The decomposer C:X ratio $\beta = C_D/X_D$, and the decomposer demand ratio $\delta = \beta/c$ where $c$ is the decomposer growth efficiency. We also note that $\phi_{MC} = \mu \phi_{MX}$, where $\mu$ is the decomposer C:X ratio, as decomposition is associated with the detritus compartment.

The mass balance equation for decomposer nitrogen is

\[
\frac{dX_D}{dt} = \text{decomposition + mineralization/immobilization - loss} = \phi_{MX} + \phi_I - lDX_D,
\]  

(7)

where $l_D$ is the decomposer loss rate. The mass balance equation for decomposer carbon is

\[
\frac{dC_D}{dt} = \text{decomposition - respiration - loss} = \phi_{MC} - (1-c)\phi_{MC} - lDC_D = c\phi_{MC} - lDC_D.
\]  

(8)

Because $\frac{dX_D}{dt}$ and $\frac{dC_D}{dt}$ must be in ratio with each other, we have $\frac{dC_D}{dt} = \beta \frac{dX_D}{dt}$. Substituting in Eqs. (7) and (8) for $\frac{dX_D}{dt}$ and $\frac{dC_D}{dt}$ respectively,

\[
c\phi_{MC} - lDC_D = \beta[\phi_{MX} + \phi_I - lDX_D],
\]

\[
c\phi_{MC} - lDC_D = \beta\phi_{MX} + \beta\phi_I - lD\beta X_D.
\]

Because $C_D = \beta X_D$, we have $lDC_D = lD\beta X_D$ and these terms cancel so that

\[
c\phi_{MC} = \beta\phi_{MX} + \beta\phi_I.
\]
Noting that \( \frac{\beta}{c} = \delta \), one has

\[
\phi_{MC} = \delta \phi_{MX} + \delta \phi_I.
\]

The fluxes \( \phi_{MC} \) and \( \phi_{MX} \) both come from the detritus compartment, and so are in ratio as \( \phi_{MC} = \mu \phi_{MX} \). Therefore, we have \( \mu \phi_{MX} = \delta \phi_{MX} + \delta \phi_I \) so that

\[
\phi_{MX} = \frac{\delta}{\mu - \delta} \phi_I. \tag{9}
\]

Solving Eq. (9) for \( \phi_I \) gives

\[
\phi_I = \frac{\mu - \delta}{\delta} \phi_{MX}. \tag{10}
\]

If decomposers are carbon limited (C-limited), decomposer growth will be determined by their uptake from the detritus. We set \( \phi_{MX} = m_X X_M \), where \( m_X \) is the uptake rate. Substitution into Eq. (10) gives

\[
\phi_I = \frac{\mu - \delta}{\delta} m_X X_M. \tag{11}
\]

If decomposers are nitrogen limited (X-limited), their uptake of inorganic nitrogen will determine their growth. We set \( \phi_I = r_I X_I \), where \( r_I \) is the inorganic X uptake rate. Substitution into Eq. (9) gives

\[
\phi_{MX} = \frac{\delta}{\mu - \delta} r_I X_I. \tag{12}
\]

By Liebig’s Law of the Minimum, decomposer growth depends only on the availability of detrital carbon when \( m_X X_M < \frac{\delta}{\mu - \delta} r_I X_I \), and depends on the availability of inorganic X when \( m_X X_M > \frac{\delta}{\mu - \delta} r_I X_I \). The decomposition term in the mass balance equations is then given by

\[
\text{decomposition} = \text{Min} \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right]. \tag{13}
\]
and the mineralization/immobilization term is

\[
\text{mineralization/immobilization} = \text{Min} \left[ \frac{\mu - \delta}{\delta} m_X X_M, r_I X_I \right].
\] (14)

The mass balance equation for decomposer nitrogen is therefore

\[
\frac{dX_D}{dt} = \text{Min} \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right] + \text{Min} \left[ \frac{\mu - \delta}{\delta} m_X X_M, r_I X_I \right] - l_D X_D.
\] (15)

Consider again Eq. (8) where \( \frac{dC_D}{dt} = c\phi_{MC} - l_D C_D \). Since \( C_D \) and \( X_D \) are in ratio in the decomposer compartment, then \( C_D = \beta X_D \). Also, \( \phi_{MC} \) and \( \phi_{MX} \) are in ratio in the detritus compartment, so that \( \phi_{MC} = \mu \phi_{MX} \). This gives

\[
\frac{dC_D}{dt} = c\mu \phi_{MX} - \beta l_D X_D
\]

\[
= c\text{Min} \left[ \mu m_X X_M, \frac{\delta\mu}{\mu - \delta} r_I X_I \right] - \beta l_D X_D
\] (16)

The mass balance equation for detritus is given by

\[
\frac{dX_M}{dt} = \text{producer death} + \text{herbivore death} + \text{herbivory inefficiency} - \text{decomposition} - \text{loss}
\]

\[
= d_P X_P + d_H X_H + (1 - \epsilon) h X_P X_H - \text{Min} \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right] - l_M X_M.
\] (17)

Producer death and herbivory are associated with the producer compartment, herbivore death is associated with the herbivore compartment, and the decomposition and loss are associated with the detritus compartment. Therefore, since in all of these compartments \( C \) and \( X \) are in ratio (\( \alpha \) for producers, \( \gamma \) for herbivores, and \( \mu \) for detritus),

\[
\frac{dC_M}{dt} = \text{producer death} + \text{herbivore death} + \text{herbivory inefficiency} - \text{decomposition} - \text{loss}
\]

\[
= \alpha d_P X_P + \gamma d_H X_H + \alpha (1 - \epsilon) h X_P X_H - \mu \text{Min} \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right] - \mu l_M X_M.
\] (18)
Finally, the mass balance equation for the inorganic nitrogen compartment is:

$$\frac{dX_I}{dt} = \text{input} + \text{excretion} - \text{loss} - \text{producer uptake} - \text{mineralization/immobilization}$$

$$= I_I + \left[ \frac{\gamma - \alpha}{\gamma} \varepsilon hX_HX_P + r_HX_H \right] - l_I X_I - u_I X_I - \text{Min} \left[ \frac{\mu - \delta}{\delta} m_X X_M, r_I X_I \right].$$

(19)

In conclusion, the mass balance nitrogen equations for each compartment of our model are as follows:

$$\frac{dX_P}{dt} = u_I X_I - hX_HX_P - d_P X_P$$

(20)

$$\frac{dX_H}{dt} = \varepsilon hX_HX_P - d_H X_H - \left[ \frac{\gamma - \alpha}{\gamma} \varepsilon hX_HX_P + r_HX_H \right]$$

(21)

$$\frac{dX_M}{dt} = d_P X_P + d_H X_H + (1 - \varepsilon) hX_HX_P - \text{Min} \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right] - l_M X_M$$

(22)

$$\frac{dX_D}{dt} = \text{Min} \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right] + \text{Min} \left[ \frac{\mu - \delta}{\delta} m_X X_M, r_I X_I \right] - l_D X_D$$

(23)

$$\frac{dX_I}{dt} = I_I + \left[ \frac{\gamma - \alpha}{\gamma} \varepsilon hX_HX_P + r_HX_H \right] - l_I X_I - u_I X_I - \text{Min} \left[ \frac{\mu - \delta}{\delta} m_X X_M, r_I X_I \right]$$

(24)

**Methods**

We parameterized this model with data from temperate deciduous forests. As plants move through the seasons, their stoichiometric quality oscillates [2]. At the beginning of summer, plant quality is at its highest, which means that plant C:X ratio is at its lowest. Herbivore efficiency is at a high, as the majority of plant matter is edible to herbivores, and herbivores will avoid sloppy grazing because they benefit the most from healthy, nutritious plants. During this time, the detritus C:X ratio will be at a low, as the percentage of detritus C:X from the producer compartment is at its lowest, and the larger percentage of biomass from the herbivore compartment has a constant C:X ratio that is significantly lower than plant biomass regardless of the season. We posit that the decomposer pool should be bacterially dominated during the summer [7], as a low detritus C:X ratio generally translates to a lower decomposer C:X ratio.

As we move through summer into fall, the quality of the plant declines, meaning the plant C:X ratio rises. As a result herbivore efficiency will decline [8], largely due to plant matter becoming inedible to herbivores. Detritus C:X ratio rises, and the
decomposer pool should be fungally dominated [7].

These seasonal changes in plant quality and herbivore efficiency and their resultant effects on decomposition and mineralization [6] trigger a shift in the C:X ratio of the decomposer compartment, reflecting a shift between bacterial and fungal dominance [7]. In our model, we employ a sinusoidal function to simulate seasonal change in plant quality and herbivore efficiency, with a period of one calendar year beginning on June 21st. In this model, producer C:X ratio ranges from 20 to 40 [4, 5], and herbivore efficiency ranges from 0.3 to 0.8 [5].

To study these effects on the type of decomposer present in the system, we hold the decomposer biomass constant. Then \( \frac{dX_D}{dt} = 0 \), so from Eq. (23) one has

\[
0 = \text{Min} \left[ \frac{\delta}{\mu - \delta} r_I X_I \right] + \text{Min} \left[ \frac{\mu - \delta}{\delta} m_X X_M, r_I X_I \right] - l_D X_D. \tag{25}
\]

We isolate the decomposer demand ratio, \( \delta \), to form a new equation for the system. For a C-limited decomposer pool, Eq. (25) becomes

\[
0 = m_X X_M + \frac{\mu - \delta}{\delta} m_X X_M - l_D X_D.
\]

Solving for \( \delta \), we find that

\[
\delta = \frac{\mu}{l_D} \frac{m_X X_M}{X_D}. \tag{26}
\]

Note that in decomposer C-limitation, the demand ratio is a function of detritus C:X ratio and detrital biomass.

For an X-limited decomposer pool, Eq. 25 becomes

\[
0 = \frac{\delta}{\mu - \delta} r_I X_I + r_I X_I - l_D X_D.
\]

Solving for \( \delta \), we find that

\[
\delta = \mu - \frac{\mu r_I X_I}{l_D X_D}. \tag{27}
\]

Note that in X-limitation, \( \delta \) is a function of detritus C:X ratio and inorganic nitrogen biomass.
We now have a four equation ordinary differential equation (ODE) model, with ODEs for the producer, herbivore, detritus, and inorganic X compartments, as well as an equation to determine the decomposer demand ratio, which gives the decomposer C:X ratio:

\[
\frac{dX_P}{dt} = u_I X_I - h_X X_P - d_P X_P, \\
\frac{dX_H}{dt} = e h X_H X_P - d_H X_H - \left[ \frac{\gamma}{\delta} e h X_H X_P + r_H X_H \right], \\
\frac{dX_M}{dt} = d_P X_P + d_H X_H + (1 - e) h X_P X_H - Min \left[ m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right] - L_M X_M, \\
\frac{dX_I}{dt} = I_I + \left[ \frac{\gamma}{\delta} e h X_H X_P + r_H X_H \right] - L_I X_I - u_I X_I - Min \left[ \frac{\mu}{\delta} m_X X_M, r_I X_I \right], \\
\delta = \begin{cases} 
\frac{\mu m_X X_M}{L_D X_D} & \text{in C-limitation,} \\
\mu - \frac{\mu r_I X_I}{L_D X_D} & \text{in X-limitation.}
\end{cases}
\]

The decomposer C:X ratio is typically about 4 in a bacterially dominated system, and closer to 10 or more in a fungally dominated system [9]. In our model, this range of decomposer C:X values corresponds to a range of demand ratios of approximately 13 to 33.

To analyze our system, we must determine the decomposer biomass and initial conditions for the system. First, numerical steady states were found for the original five equation model in a C-limited state (Eqs. (20)-(24)). A carbon limited state was chosen because while C-limited, it is possible for decomposers to mineralize nitrogen to the inorganic pool or immobilize needed nitrogen from the inorganic pool. In contrast, X-limited decomposers can only immobilize nitrogen, which could unnecessarily limit our system. We used the midpoint values for plant C:X, herbivore efficiency, and decomposer C:X, ($\alpha = 30$, $e = 0.55$, and $\beta = 7$), and herbivore respiration rate $r_H = 0.014$ [5]. Herbivore C:X ratios can reasonably vary between 7 and 10 in a forest setting [5, 6], so a midpoint herbivore C:X ratio of $\gamma = 8.5$ was used. The numerical steady state for the decomposer pool gives $X_D = 7.480$.

For this value of $X_D$ and our starting conditions on Jun 21st ($\alpha = 20$ and $e = 0.8$), the steady states of Eqs.(28)-(31) were found numerically. These numerical steady states,
shown in Table 1, are used as the initial values for the system given by Eqs. (28)-(32) which is solved numerically using MATLAB’s adaptive-step size Runge-Kutta solver ODE45. In order to optimally adapt our model, we amended the herbivore C:X ratio and respiration rate to $\gamma = 7$ [5] and $r_h = 0.0165$.

Results and Discussion

Figure 2 shows the numerical solution for producer biomass, herbivore biomass, detritus biomass, inorganic X biomass, detritus C:X ratio, and decomposer demand ratio for $t = 0$ to 20,000 days. After an initial transient period, the system stabilized, showing a regularly oscillating decomposer C:X ratio range from 3.7 to 10.2 (corresponding to a demand ratio range from 12.3 to 34.0) indicating a shift from a bacterially dominated

<table>
<thead>
<tr>
<th>Variable</th>
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</tr>
</thead>
<tbody>
<tr>
<td>$X_P$</td>
<td>301.04</td>
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<td>$X_M$</td>
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</tr>
<tr>
<td>$X_I$</td>
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Figure 2: Numerical solution of Eqs. 28 – 32 showing producer biomass, herbivore biomass, detritus biomass, inorganic X biomass, detritus C:X ratio, and decomposer demand ratio for $t = 0$ to 20,000 days.
decomposer pool in the summer to a fungally dominated pool in the winter. Figure 3 shows the relative change of the decomposer C:X ratio, producer C:X ratio, and herbivore efficiency to each of their initial values. We see clearly that an increase in plant C:X ratio and drop in herbivore efficiency results in a rise of decomposer C:X ratio, and therefore a shift to a fungally dominated decomposer pool as expected [10, 7].

Figure 4 shows a polar plot of the relationship between the producer C:X ratio and the decomposer demand ratio; it is clear from the plot that as plant quality lowers
and the C:X ratio rises, the demand ratio is forced to rise with it as an effect.

It is important to note that while producer biomass does decrease in the late fall, the decrease is quite small; the range of producer biomass across the entire year is less than 2g/m². For this reason, the graph of herbivory over the course of one year has essentially the same shape as herbivore biomass (See Figure 5). When producer C:X ratio is at a high, plant quality is lowest, and herbivores compensate with an increase in overall herbivory; we therefore see that increased herbivory in the fall leads to an overall decrease in primary production (producer biomass) in the winter. Because both herbivore and producer biomass is at a low during the winter months in our model, herbivory is at a low during the winter. Also at this time, inorganic X biomass is at a high, as plants require less inorganic nutrient at a high C:X ratio. (See Fig.6)

In the summer months, with plant C:X ratio low and herbivore efficiency at a high, the detritus C:X ratio will be at a low, as detritus biomass C:X from the producer compartment is low (see Fig.6). We see that the decomposer pool is bacterially dominated during the summer, as a low detritus C:X ratio translates to a low decomposer C:X ratio.

![Figure 5: Producer biomass, herbivore biomass and herbivory across a calendar year](image)

In our forest setting, producer C:X ratios are consistently and significantly higher than herbivore C:X ratios [4], meaning that plant quality is relatively lower, and herbivore efficiency plays a larger role in nutrient cycling [4]. Specifically, as plant quality and inefficiency of herbivory rises, the flux of plant biomass to the detrital pool increases, causing a rise in the detrital C:X ratio. During this time, therefore, we should see an increase in fungal population throughout the fall, shifting to a fungally dominated
Figure 6: Producer biomass, herbivore biomass, detritus biomass, inorganic X biomass, detritus C:X ratio, and decomposer C:X ratio across a calendar year.

decomposer pool by the winter months. This reflects the notion that fungally dominated decomposer pools mineralize more nitrogen than bacteria [8].

In a standard producer-herbivore-decomposer food web, bacteria will immobilize supplemental inorganic X while fungi will mineralize excess X [2]. While this is the case in our model as well, we do note an interesting characteristic of our model specifically: once we reach stability, throughout the calendar year, we do not enter into an X-limited environment. Our decomposer is C-limited throughout the entire year. Recall that decomposers become X-limited only when the detritus C:X ratio is significantly larger than the decomposer demand ratio, and when the inorganic pool is not large enough to adequately supplement needed X. Figure 6 shows that during the summer months when the demand ratio is at its lowest and we could enter X-limitation, we have a local maximum of inorganic X biomass, keeping the system in C-limitation. This phenomenon could be due to numerous factors. It is likely that our choice to find steady state values in a C-limited environment could have contributed to this, as well as the specific values we chose to use as initial conditions.

Figure 7 shows decomposition on the left, and the flux between the microbial pool and the inorganic nitrogen pool on the right. Decomposers are immobilizing when the graph is above 0 (a positive flux towards the decomposer compartment) and are mineralizing excess nitrogen when the graph is below 0 (a negative flux away from the
decomposer pool). We see that decomposition is at an all time low towards the end of summer. Consequently, at this time we see a short period of immobilization by the bacterially dominated decomposer pool. Decomposition is at a maximum in the winter, resulting in a maximum of mineralization of excess nitrogen into the inorganic pool from the fungally dominated decomposer pool. We expect to see this type of nutrient cycling, as microbes immobilize nitrogen in preparation for the winter, when they retain what they need and mineralize any excess [2].

Decomposer communities, unlike herbivores and many plants, are capable of adapting to surroundings quickly [7], so we can expect to realistically see this kind of seasonal change. This capability of such rapid change allows us to more closely examine these types of ecosystems on a much smaller time scale, and can highlight the importance of decomposers in any ecological system. The shift in the decomposer pool between bacteria and fungi during the calendar year highlights their role in not only decomposition, but also nutrient cycling and primary production [2].

Conclusion

In this thesis we presented a producer-herbivore-decomposer soil food web model and employed two important seasonal changes to analyze how these changes affect the decomposer pool. As seasons change, plant quality oscillates and this oscillation greatly
affects herbivore efficiency; these parameters help drive nutrient cycling [5] as well as whether the decomposer pool is bacterially or fungally dominated. We see that the seasonal shift in the decomposer population has a profound effect on nutrient cycling and primary production.

In models such as these, there is an extremely complicated relationship between above and belowground communities because they exist at a range of spatial and temporal scales [2]. Our model is important because it is the first of its kind to consider seasonal changes in both plant quality and herbivore efficiency and their effects on the microbial pool. In addition, our model can be adapted to and parameterized for many different systems with realistic seasonal changes and their effects on the overall ecosystem. Further analysis could explain seasonal patterns of soil respiration, and could give a hypothesis on how available nitrogen is both retained and lost from the system [7].

A potential next step could be to add an outside perturbation, or ‘noise’ to the system, such as disease outbreak or rapid deforestation. We could also keep decomposer biomass as a varying variable rather than a constant value, because decomposer biomass has been shown to reach its peak under snow; the release of nitrogen during snowmelt is a major contributor to primary production in the spring [10].
References


Table 2: Variables and Parameter Values

<table>
<thead>
<tr>
<th>Type</th>
<th>Symbol</th>
<th>Value</th>
<th>Units</th>
<th>Definition</th>
<th>Citation</th>
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<td>g/m²</td>
<td>Inorganic X mass</td>
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</tbody>
</table>

Units for the ecosystem parameters were derived using the fact that all variables must have units of $g/m^2$ and all stoichiometric parameters must have units of $g/g$. 
Appendix B: Supplemental Derivations

Respiration Rate, \( r_H \)

Given that the excretion term \( \frac{\gamma - \alpha}{\gamma}ehX_HX_P + r_HX_H \) must clearly be positive at all times, there are two potential scenarios. If the herbivore C:X ratio is greater than the producer C:X ratio \( (\gamma > \alpha) \), excretion is always positive. However, this is not the case in our setting. We can find the allowable values for respiration rate \( r_H \) by using a simple inequality:

\[
\frac{\gamma - \alpha}{\gamma}ehX_HX_P + r_HX_H > 0
\]

\[
r_H > \frac{\alpha - \gamma}{\gamma}ehX_P
\]

The respiration rate \( r_H \) must satisfy the above inequality at all times to keep excretion positive.

Detritus C:X ratio, \( \mu \)

The detritus C:X ratio, \( \mu \), is a function of producer C:X ratio \( \alpha \) and herbivore C:X ratio \( \gamma \). It is given that the detritus C:X ratio \( \mu = C_M/X_M \), so \( \mu X_M = C_M \). We then have

\[
\mu \left[ d_PX_P + d_HX_H + (1 - e)hX_HX_P - l_MX_M - \min \left( m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right) \right] = \alpha d_PX_P + \gamma d_HX_H + \alpha(1 - e)hX_HX_P - \mu l_M X_M - \mu \min \left( m_X X_M, \frac{\delta}{\mu - \delta} r_I X_I \right)
\]

Canceling like terms on both sides of the equation,

\[
\mu [d_PX_P + d_HX_H + (1 - e)hX_HX_P] = \alpha d_PX_P + \gamma d_HX_H + \alpha(1 - e)hX_HX_P
\]

Solving for \( \mu \),

\[
\mu = \frac{\alpha d_PX_P + \gamma d_HX_H + \alpha(1 - e)hX_HX_P}{d_PX_P + d_HX_H + (1 - e)hX_HX_P}
\]

We can express \( \mu \) in terms of \( \alpha \) and \( \gamma \) to represent the detritus C:X ratio as a weighted average of the producer and herbivore mass. The coefficient of \( \alpha \) represents the percentage of detritus coming from the producers, while the coefficient of \( \gamma \) represents the percentage
coming from the herbivores.

\[
\mu = a \left( \frac{d_p X_P + (1 - e)h X_H X_P}{d_p X_P + d_H X_H + (1 - e)h X_H X_P} \right) + \gamma \left( \frac{d_H X_H}{d_p X_P + d_H X_H + (1 - e)h X_H X_P} \right)
\]

**C-Limited Decomposer Detritus Uptake Rate, \( m_X \)**

The uptake rate \( m_X \) is based on the equation for \( \mu \):

\[
m_X = a \left( \frac{d_p X_P + (1 - e)h X_H X_P}{d_p X_P + d_H X_H + (1 - e)h X_H X_P} \right) + j \left( \frac{d_H X_H}{d_p X_P + d_H X_H + (1 - e)h X_H X_P} \right)
\]

Here, \( a \) is the C-limited decomposer uptake rate of plant detritus, while \( j \) is the C-limited decomposer uptake rate of herbivore detritus. Because the model is already so complex, a fixed value of \( m_X \) was used [6].

**Steady States and Jacobian**

Analytical steady states and the corresponding Jacobian matrix can be found for the original five equation model using Mathematica. However, because our model is so complex, the analytical steady states and Jacobian are extremely long and complicated. As the equations would take up many pages, and since they are not illuminating, they are not included in this thesis.
Appendix C: Sensitivity Testing

The sensitivity of a variable $u$ that depends on a parameter $p$ is given by the following equation:

$$\tau_p^u = \frac{\partial u}{\partial p} \times \frac{p}{u}$$

evaluated at baseline parameter values. This formula calculates the relative change of the variable $u$ as a result of a change in parameter $p$ [11].

We tested the sensitivity of each variable in our model to producer C:X ratio, $\alpha$, and herbivore efficiency, $e$. To do this, we found analytical steady states for the model, found the partial derivatives with respect to producer C:X and herbivore efficiency, and evaluated these at our baseline parameter values. For simplicity, we used the midpoint parameter values, $\alpha = 30$ and $e = 0.55$.

Table 3: Sensitivity of Model Variables to Producer C:X Ratio and Herbivore Efficiency

<table>
<thead>
<tr>
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<th>$\alpha$</th>
<th>$e$</th>
</tr>
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<td>-1</td>
</tr>
<tr>
<td>$X_H$</td>
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<td>1.305</td>
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<tr>
<td>$X_M$</td>
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<td>-0.002</td>
</tr>
<tr>
<td>$X_I$</td>
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<td>0.260</td>
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<tr>
<td>$\delta$</td>
<td>0.578</td>
<td>-0.552</td>
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</table>
Appendix D: MATLAB Codes

Function Code

The following is the code used to numerically solve the system of differential equations that describe our model. Note that while we allow the system to move into decomposer X-limitation, we stay in C-limitation for the chosen initial conditions, so for simplicity, we include in the code only the C-limited definition of the decomposer demand ratio, $\delta$.

```matlab
function [dxdt] = deltamodel(t,x)

dxdt = zeros(4,1);

% the following are using alpha = 30 and e = 0.55
Xd = 7.480; % rh = 0.014, gamma = 8.5
ui = 0.34;
dp = 4.8*10^-6;
h = 3*10^-5;
dh = 0.003;

lm = 8.4*10^-4;
ld = 3.3*10^-3;
mx = 4.34*10^-3;
Ii = 0.03;
li = 3*10^-4;
ri = 0.09;

rh = 0.0165;
gamma = 7;

alpha = -10*cos((2*pi/365)*t) + 30;
e = .25*cos((2*pi/365)*t) + .55;

Xp = x(1);
Xh = x(2);
Xm = x(3);
Xi = x(4);

mu = (alpha*(dp*Xp + (1-e)*h*Xh.*Xp) + gamma*dh*Xh)./(dp*Xp +...
(1-e)*h*Xh.*Xp + dh*Xh);

delta = (mu*mx*Xm)/(ld*Xd);

a= mx*Xm;
b= (delta/(mu - delta))*ri*Xi;
c= ((mu - delta)./delta).*mx*Xm;
d= ri*Xi;

if a>0 && b>0
M1 = min(a,b);
```

24
if M1 == a
    M2 = c;
else
    M2 = d;
end

else
    M1 = a;
    M2 = c;
end

dxdt(1) = ui*Xi - h*Xh.*Xp - dp*Xp;
dxdt(2) = e*h*Xh.*Xp - dh*Xh - (((gamma - alpha)/gamma)*e*h*Xh.*Xp + rh*Xh);
dxdt(3) = dp*Xp + dh*Xh + (1-e)*h*Xh.*Xp - M1 - lm*Xm;
dxdt(4) = Ii + (((gamma - alpha)/gamma)*e*h*Xh.*Xp + rh*Xh) - li*Xi - ui*Xi - M2;
end

ODE45 Code

The following is the code for the ODE45 program to find numerical solutions to the system of differential equations given initial conditions for each variable. Similarly to the function code, here we use only the C-limited definition of the decomposer demand ratio, δ.

%ODE45
clear
clc
close all

%the following are using alpha = 30 and e = 0.55
Xd = 7.480; %rh = 0.014, gamma = 8.5

ui = 0.34;
dp = 4.8*10^-6;
h = 3*10^-5;
dh = 0.003;

lm = 8.4*10^-4;
ld = 3.3*10^-3;
mx = 4.34*10^-3;
li = 0.03;
ri = 0.09;

rh = 0.0165;
gamma = 7;
yfinal = 40000;
\[ \text{ode45('deltamodel', [0, yfinal], [301.04, 6.45, 6.27, 0.18])} \]

\[ T = \text{numel}(t); \] %length of vector \( t \)

\%delta, \( \mu \), \( \alpha \), \( e \), abcd values
for i = 1:T
  \( X_p(i) = x(i,1); \)
  \( X_h(i) = x(i,2); \)
  \( X_m(i) = x(i,3); \)
  \( X_i(i) = x(i,4); \)
  \( \alpha(i) = -10*\cos((2*\pi/365)*t(i)) + 30; \)
  \( e(i) = .25*\cos((2*\pi/365)*t(i)) + .55; \)
  \( \mu(i) = (\alpha(i) \times (d_p \times X_p(i) + (1-e(i)) \times h \times X_h(i) \times X_p(i)) + \gamma \times d_h \times X_h(i)) / (d_p \times X_p(i) + (1-e(i)) \times h \times X_h(i) \times X_p(i) + d_h \times X_h(i)); \)
  \( \delta(i) = (\mu(i) \times m_x \times X_m(i)) / (d_l \times X_d); \)
  \( a(i) = m_x \times X_m(i); \)
  \( b(i) = (\delta(i) / (\mu(i) - \delta(i))) \times r_i \times X_i(i); \)
  \( c(i) = ((\mu(i) - \delta(i)) / \delta(i)) \times m_x \times X_m(i); \)
  \( d(i) = r_i \times X_i(i); \)
end

for i = 1:T
  if \( a(i) > 0 \) \&\& \( b(i) > 0 \)
    \( M_1(i) = \text{min}(a(i), b(i)); \)
    if \( M_1(i) = a(i) \)
      \( M_2(i) = c(i); \)
    else \( M_2(i) = d(i); \)
  end
elseif \( b(i) < 0 \)
  \( M_1(i) = a(i); \)
  \( M_2(i) = c(i); \)
else
  \( M_1(i) = b(i); \)
  \( M_2(i) = d(i); \)
end
end

\( \beta = \delta \times 0.3; \)