



Stoichiometric Modeling of Aboveground–Belowground Interaction of Herbaceous Plant and Two Herbivores

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Received: 8 January 2020 / Accepted: 23 July 2020
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Abstract

In a grassland ecosystem, the dynamics and coexistence mechanisms of two herbivores competing for one herbaceous plant have been widely studied, while the chemical heterogeneity of herbaceous plant's aboveground and belowground parts is usually ignored in dynamic modeling. Based on the traditional two herbivore-one herbaceous plant competition model, a new stoichiometric competition model, which incorporates the chemical heterogeneity of herbaceous plants, is formulated to investigate effects of the aboveground–belowground interactions and the chemical heterogeneity on the dynamics of the two herbivore-one herbaceous plant system. We perform theoretical analysis for the stability of boundary equilibria and show that a stable coexistent equilibrium is possible with two herbivores on one herbaceous plant. Moreover, numerical simulations reveal that various light intensity and nitrogen input can also allow all populations to coexist in periodic oscillations or irregularly cyclic oscillations. Our findings further indicate that when the nitrogen input is fixed, higher light intensity leads to a dominance of the lower N-demand herbivore, while the light intensity is fixed, higher nitrogen input leads to a dominance of the higher N-demand herbivore. Moderate levels of light and nutrient could promote the coexistence of two herbivores and herbaceous plant. This study also explains the functional mechanism for the decline of species diversity in response to nitrogen enrichment.

Keywords Stoichiometry · Aboveground and belowground · Competition · N:C ratio · Species diversity

1 Introduction

A grassland ecosystem, as a key part of a terrestrial ecosystem, is composed of aboveground and belowground subsystems that contain enormous amount of species interacting at various spatial scales (Van et al. 2009). Most studies focus on aboveground parts of herbaceous plants due to sampling difficulties and limited measuring methods and less data are available of belowground parts. Plants have longer effects

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in the belowground than in the aboveground since organisms in the soil have lower mobility and higher survival rates (Van et al. 2009). In addition, many herbivores only ingest the aboveground herbaceous plants and 80–90% biomass of herbaceous plants remain in the belowground part, which contributes to the regeneration of the plant's aboveground part (Niklas 2005). Moreover, a growing body of evidence implies that above- and belowground communities and processes are intrinsically linked, and feedbacks between these two subsystems are important for community structure and ecosystem functioning (Masters et al. 1993; Van et al. 2000, 2001). Therefore, it is significant to consider the different roles and interactions of aboveground and belowground herbaceous plants.

Predation and competition are the main forces shaping food webs and ecological communities. Meanwhile, the competitive interactions affect the earth's biodiversity (Peter and Kuang 2008). The fact that two herbivores compete for one herbaceous plant and coexist is widespread in a grassland ecosystem. For example, in the steppe and deserts around Qinghai Lake on the Qinghai-Tibet Plateau, Przewalski's gazelle (*Procapra przewalskii*) and the domestic Tibetan sheep (*Ovis aries*) compete for the graminoids (Liu and Jiang 2004); In Inner Mongolica steppe, the *Ovis aries* and *Spermophilus dauricus* compete for *Stipa grandis* (Liu et al. 2013). However, the competitive exclusion principle (CEP) states that no equilibrium is possible mathematically if n species exploit fewer than n resources (Levin 1970). This principle is largely inconsistent with bio-diversity observed in nature. Although various mechanisms, such as spatial heterogeneity or chaotic fluctuations, have been proposed to explain this coexistence, none of them invalidate the principle (Armstrong and McGehee 1980; Richards et al. 2000; Chase et al. 2002; Kuang et al. 2003).

To explain the contradiction between the natural reality and competitive exclusion principle, stoichiometry has been widely employed in competition models. Loladze et al. (2004) incorporated principles of ecological stoichiometry into a standard predator-prey model and revealed that chemical heterogeneity within and among species can support species coexistence. Here, ecological stoichiometry is the study of the balance of energy and multiple chemical elements in ecological interactions (Sternern and Elser 2008). Miller et al. (2004) proposed a stoichiometric model to analyze the two-patch consumer-resource systems. They obtained that competition models incorporating stoichiometry can be meaningful in explaining biodiversity and providing a mechanism for deterministic extinction. The stoichiometric competition model of two predators and one prey established by Deng and Loladze (2007) showed that the reduction in prey quality can give rise to chaotic oscillation. Wang et al. (2009) showed that *Daphnia* species invasion model exhibited chaotic coexistence of the competing species. These studies work well for aquatic ecosystems by treating the prey (primary producer) as an integrality; however, the aboveground–belowground interaction in grassland ecosystems is much less explored (Bardgett and Wardle 2003).

Turchin formulated a herbaceous regeneration dynamic model, in which they divided the herbaceous plant into aboveground and belowground parts and considered the interactions between the two portions. The model clearly elaborated the energy flow between the aboveground and belowground (Turchin 2003). Yet, they neglected effects of nutrients on the biomass. In fact, it has been shown that variable chemical composition (i.e., stoichiometry) of prey can significantly affect competitive predator-

prey dynamics both experimentally (Sterner et al. 1998; Nelson et al. 2001; Urabe et al. 2002) and theoretically (Andersen 1997; Loladze et al. 2000; Muller et al. 2001; Wang et al. 2008; Wang 2010; Peace et al. 2014; Chen et al. 2017; Peace and Wang 2019).

Nitrogen is one of the most important limiting nutrient elements of plants and plays a vital role in plant growth. Many studies show that nitrogen enrichment can promote the aboveground growth of grassland ecosystems, and then lead to an increase in the aboveground biomass (LeBauer and Treseder 2008; Song et al. 2012). Furthermore, nitrogen enrichment can also affect species diversity and community stability in grassland ecosystems (Gough et al. 2000; Bai et al. 2004). More counter-intuitively, nitrogen enrichment can accelerate loss of rare species in the community, reduce species diversity, and ultimately lead to a decline in ecosystem stability (Suding et al. 2005; Lan and Bai 2012). The mechanism for this decline remains unclear. Most existing studies are mainly based on field observational evidence and experimental analysis while the dynamical modeling approach is lacking.

In this study, by considering the ecological stoichiometry of key nutrient elements, in Sect. 2, we formulate a new stoichiometric competition model to investigate the dynamics among two herbivore and one herbaceous plant and characterize the mechanism that nitrogen enrichment reduces species diversity in a grassland ecosystem. Here, the biomass of herbaceous plant is divided into two parts: the aboveground and the belowground. Section 3 provides the qualitative analysis of the complex dynamics of the stoichiometric competition model. Section 4 includes some numerical studies of the time series dynamics and bifurcation analyses of the model. We investigate the effects of above- and belowground interaction and food quality on the population growth and the energy flow across herbaceous plant and herbivores. Section 5 concludes this paper by presenting biological implications of our mathematical findings and computational observations.

2 Model Formulation

In this study, we focus on the interaction between two herbivores (sheep and cattle) or primary consumers exploiting one herbaceous plant or herb in a grassland system. The model construction follows an outline in Turchin (2003) and Loladze et al. (2004). We start with a conventional (MacArthur–Rosenzweig-type) model, which describes a system of two herbivores feeding on one herbaceous plant

$$\begin{cases} \frac{dS}{dt} = rS \left(1 - \frac{S}{K} \right) - f_1(S)H_1 - f_2(S)H_2, \\ \frac{dH_1}{dt} = e_1 f_1(S)H_1 - d_1 H_1, \\ \frac{dH_2}{dt} = e_2 f_2(S)H_2 - d_2 H_2. \end{cases} \quad (1)$$

In (1), S , H_1 and H_2 denote biomass densities of the herbaceous plant and two herbivores, respectively; r is the intrinsic growth rate of the herbaceous plant; d_1 and

d_2 represent specific loss rates of herbivores that include respiration and death; f_1 and f_2 are herbivores' ingestion rates, which are assumed to be monotonically increasing and bounded differentiable functions following Holling type II functional response, i.e., $f_i(S)$ satisfies following assumptions

$$f_i(0) = 0, \quad f_i'(S) > 0 \quad \text{and} \quad f_i''(S) < 0 \quad \text{for} \quad S \geq 0, \quad i = 1, 2; \quad (2)$$

e_1 and e_2 are the maximum production efficiencies of converting ingested herbaceous plant biomass into herbivore biomass. The second law of thermodynamics requires that $e_1 < 1$ and $e_2 < 1$. K is the herbaceous plant's constant carrying capacity in terms of carbon (C) and represents the light intensity.

However, herbivores usually only feed on the aboveground part of the herbaceous plants, the belowground part of herbaceous plants will be retained and the energy stored in the belowground will help the aboveground to regrow after the aboveground is ingested by herbivores (Ares and Singh 1974). Hence, it is reasonable and realistic to take into account the heterogeneity of above- and belowground herbaceous plants.

Let A be the aboveground biomass density and B be the corresponding belowground biomass of herbaceous plant. Assume that the photosynthesis rate is directly proportional to the amount of aboveground biomass and a constant proportion of fixed energy by photosynthesis is transferred belowground. Similarly, some proportion of belowground energy is mobilized for the growth of aboveground biomass, and aboveground biomass will increase because a portion of energy fixed aboveground will be allocated to growth. In Turchin (2003), based on above assumptions, Turchin reached the following dynamic model

$$\begin{cases} \frac{dB}{dt} = sA - cB \left(1 - \frac{A}{K}\right) - d_0B, \\ \frac{dA}{dt} = (rA + cB) \left(1 - \frac{A}{K}\right), \end{cases} \quad (3)$$

where K represents the carrying capacity (i.e., the maximum standing biomass) relating to light intensity, s is the constant proportion of fixed biomass by photosynthesis assigned to the belowground part, r reflects the rate at which energy is fixed by the aboveground, c denotes the rate of carbon delivered from belowground to aboveground, d_0 is the specific degraded rate of the belowground biomass.

In order to explore the impact of interactions between aboveground and belowground of herbaceous plants on the dynamics of the competitive food web, we combine (1) with (3) and then obtain

$$\begin{cases} \frac{dB}{dt} = sA - cB \left(1 - \frac{A}{K}\right) - d_0B, \\ \frac{dA}{dt} = (rA + cB) \left(1 - \frac{A}{K}\right) - f_1(A)H_1 - f_2(A)H_2, \\ \frac{dH_1}{dt} = e_1 f_1(A)H_1 - d_1H_1, \\ \frac{dH_2}{dt} = e_2 f_2(A)H_2 - d_2H_2. \end{cases} \quad (4)$$

This model characterizes energy flow through aboveground to the belowground of herbaceous plants but neglects the effect of element cycling. Since any biological populations require both energy and various mineral elements to sustain their growth, we reconstruct a new four-dimensional model that incorporates chemical heterogeneity based on the principles in ecological stoichiometry. We deliberately focus on the two key chemical elements C and N, since C comprises the bulk of the dry weight of the most organisms and N plays a vital role in the plant growth and decomposition (Manzoni et al. 2008).

In addition, organisms have inherent stability, that is, biological organisms have the ability to maintain a relatively constant chemical composition in a changing environment (Koojiman 1995). Therefore, the N:C ratio in plants cannot be infinitely increased. Nitrogen in plants is mainly contained in proteins and chloroplasts, while chloroplasts are found in the leaves of aerial parts of the limbs. Hence, nitrogen content in different organs of plants is considerably different. For example, many experiments show that nitrogen content of stems and roots of herbs are about 4–5% while the nitrogen content in leaves is about 10–15% (Zhou et al. 2018), the N:C in leaves or stems is greater than that in roots (Zhang et al. 2019). In reality, nitrogen is absorbed from the soil by plants mainly through the roots (Bouldin 1961). Moreover, plant stoichiometry has lower levels of variation than soil and/or bedrock stoichiometry (Castle and Neff 2009; Neff et al. 2006). Moreover, this tendency influences the capacity of sequestration of C in the ecosystem, since more C will be diverted to detritus in soils and sediments when the efficiency of C use is low due to a stoichiometric imbalance (Hessen et al. 2004).

The above considerations are expressed in the following assumptions:

- (A1) All nitrogen absorbed by herbaceous plant derives from the soil.
- (A2) The system is closed for N, with a total of N (mg N/m²), which is divided into three pools: N in the herbivores, N in the aboveground plants and the rest as N potentially available for the belowground part.
- (A3) The two herbivores maintain constant N:C ratios, say θ_1 and θ_2 (mg N/mg C), respectively; in the absence of extreme scenarios (e.g., drought, flood, or chemical pollution, et al.), N:C ratio of the aboveground varies, but never falls below a minimum θ_{\min} (mg N/mg C) and never rises over a maximum θ_{\max} (mg N/mg C). We assume that the N:C within $(\theta_{\min}, \theta_{\max})$ is the “normal N:C” of the aboveground part; “the natural level” of N denotes the amount of nitrogen input when the aboveground N:C is less than θ_{\min} . The belowground part’s N:C ratio is a constant θ_0 (mg N/mg C), and $\theta_{\min} > \theta_0$.

From these three assumptions, it follows that the light intensity limits herbaceous plant’s density to K (mg C/m²) and the combination of (A2) and (A3) imposes another limit on the herbaceous plants, N/θ_{\min} . Moreover, the herbivores and belowground part contain $\theta_1 H_1$, $\theta_2 H_2$ and $\theta_0 B$ (mg N/m²) of nitrogen, respectively. Thus, nitrogen available for the aboveground herbaceous plant at any given time is $N - \theta_1 H_1 - \theta_2 H_2 - \theta_0 B$ (mg N/m²). For convenience, denote $Q = N - \theta_1 H_1 - \theta_2 H_2 - \theta_0 B$. Recalling that N:C in the aboveground should be at least θ_{\min} (mg N/mg C), one obtains that the aboveground part’s density cannot exceed Q/θ_{\min} (mg C/m²). Therefore, the density of aboveground plant (mg C/m²) at any time is given by

$$\min \left(K, Q/\theta_{\min} \right). \tag{5}$$

If the aboveground plant’s N:C ratio is greater than θ_i , then the i -th herbivore can convert the energy content of the plant with the maximal (in C terms) efficiency e_i , $i = 1, 2$. If the aboveground plant’s N:C ratio is less than θ_i , then the plant is poor quality food for herbivores, and the i -th herbivore wastes excess carbon to maintain its constant N:C ratio. The waste is assumed to be proportional to the ratio of aboveground plant’s N:C to i -th herbivore’s N:C, which reduces the growth efficiency in C terms. The following minimum function provides the simplest way to capture such effects of variable herbaceous plant quality on herbivores’ growth efficiencies

$$e_i \min \left(1, \frac{Q/A}{\theta_i} \right), \quad i = 1, 2. \tag{6}$$

By (A3), the aboveground part’s N:C ratio varies while the N:C ratio of belowground part remains constant, because plants can maintain a dynamic balance of N: C through internal mechanisms (Sterner and Elser 2002). If $Q/A \geq \theta_{\max}$, then it implies the nitrogen content in plant is sufficient, so the absorption of nitrogen may be reduced, then the herbaceous aboveground part increases the absorption of carbon by intense photosynthesis to reduce N:C ratio. If $\theta_{\min} < Q/A < \theta_{\max}$, then the aboveground part of the plant absorbs C from the belowground at rate c . If $Q/A < \theta_{\min}$, then it indicates that the aboveground part’s N: C is lower than the minimum ratio required to ensure its normal growth. In this case, the aboveground does not absorb carbon from the belowground, but transfers carbon to roots to increase the aboveground N:C ratio, and helps to accumulate biomass in the belowground portion for absorbing more nutrition from soil (Zhou et al. 2018). Furthermore, if $\theta_0 < Q/A < \theta_{\min}$, then the belowground part absorbs all carbon transferred from aboveground herbaceous plant (assuming the absorption rate is still c); while $Q/A < \theta_0 < \theta_{\min}$, because the N:C ratio of belowground part is constant, the belowground part wastes excess carbon that transferred from aboveground, and the absorption rate is $\frac{Q/A}{\theta_0} c$. Therefore, the transfer of C between the aboveground and the belowground is

$$\min \left(\frac{Q/A}{\theta_0}, 1 \right) c B \left(1 - \frac{A}{\min \left(K, Q/\theta_{\min} \right)} \right). \tag{7}$$

Incorporating (5), (6) and (7) into (4) leads to

$$\begin{cases} \frac{dB}{dt} = sA - \min\left(\frac{Q}{A}, 1\right)cB\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0B, \\ \frac{dA}{dt} = (rA + cB)\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - f_1(A)H_1 - f_2(A)H_2, \\ \frac{dH_1}{dt} = e_1 \min\left(1, \frac{Q}{A}\right)f_1(A)H_1 - d_1H_1, \\ \frac{dH_2}{dt} = e_2 \min\left(1, \frac{Q}{A}\right)f_2(A)H_2 - d_2H_2. \end{cases} \tag{8}$$

Here all parameters are positive and their biological significance, default values (when available), and reference resources are summarized in Table 1.

Remark 1 When $H_1 = H_2 = 0$ and $Q/A < \theta_0 < \theta_{\min}$, $A' + B'$ in system (8) is

$$A' + B' = sA - d_0B + rA \left(1 - \frac{A\theta_{\min}}{Q}\right) + \left(1 - \frac{Q}{A\theta_0}\right) \left(1 - \frac{A\theta_{\min}}{Q}\right),$$

where $1 - A\theta_{\min}/Q < 0$. Then the third and fourth terms are negative. The negative terms imply that the whole plant will expel carbon out of its body when the N:C aboveground is low.

3 Qualitative Analysis

3.1 Boundedness and Invariance

In this section, we investigate the primary dynamics of (8). The boundedness and positive invariance of the solutions of the system are assured by the following theorem.

Theorem 1 *The open set*

$$\Delta \equiv \{(B, A, H_1, H_2) : B > 0, 0 < A < k, \\ A + B < (s + r + d_0)k/d_0, H_1 > 0, H_2 > 0, \theta_{\min}A + \theta_1H_1 + \theta_2H_2 < N\}$$

is positively invariant with respect to (8), where $k = \min(K, N/\theta_{\min})$.

Proof Consider the solution $S(t) = (B(t), A(t), H_1(t), H_2(t))$ of (8) with $S(0) \in \Delta$. Let $t_1 > 0$ be the first time at which $S(t)$ touches or crosses the boundary of Δ . We prove the claim by contradiction arguments and the discussion is divided into seven cases.

Case 1. $B(t_1) = 0$. Let $A_1 = \min_{t \in [0, t_1]} A(t)$. If $Q/A \geq \theta_0$, then one has

$$\frac{dB}{dt} = sA - cB\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0B$$

Table 1 Model parameters

Parameter	Description	Value l	Units	Source
K	Resource carrying capacity determined by light	0.01–4	(mg C)/m ²	Set
N	Total nitrogen in the system	0.02–0.1	(mg N)/m ²	Set
r	Intrinsic growth rate of aboveground part	0.93	day ⁻¹	Loladze et al. (2004)
s	Proportion of fixed biomass by photosynthesis assigned to the belowground part	0.93	day ⁻¹	Ping et al. (2007)
c	Ratio of energy delivered by the belowground part to the aboveground part	0.2	day ⁻¹	Li (2008)
d_0	Loss rate of the belowground part	0.3	day ⁻¹	Sterner and Elser (2002)
d_1	Loss rate of the higher N-demand herbivore	0.08	day ⁻¹	Jorgensen and Bendoricchio (2001)
d_2	Loss rate of the lower N-demand herbivore	0.1	day ⁻¹	Jorgensen and Bendoricchio (2001)
θ_0	N:C of the belowground plant	0.004	(mg N)/(mg C)	Jorgensen and Bendoricchio (2001)
θ_{\min}	Minimal possible N:C of the aboveground plant	0.005	(mg N)/(mg C)	Muller et al. (2001)
θ_{\max}	Maximal possible N:C of the aboveground plant	0.15	(mg N)/(mg C)	Muller et al. (2001)
θ_1	Constant N:C of the higher N-demand herbivore	0.05	(mg N)/(mg C)	Muller et al. (2001)
θ_2	Constant N:C of the lower N-demand herbivore	0.032	(mg N)/(mg C)	Muller et al. (2001)
e_1	Maximal conversion rate of the higher N-demand herbivore	0.57	–	Mazumaer et al. (2006)
e_2	Maximal conversion rate of the lower N-demand herbivore	0.55	–	Myjius et al. (2001)
c_1	Maximal ingestion rate of the higher N-demand herbivore	0.8	day ⁻¹	Loladze et al. (2004)
c_2	Maximal ingestion rate of the lower N-demand herbivore	0.7	day ⁻¹	Loladze et al. (2004)
a_1	Half-saturation constant of the higher N-demand herbivore	0.45	(mg C)/m ²	Loladze et al. (2004)
a_2	Half-saturation constant of the lower N-demand herbivore	0.36	(mg C)/m ²	Loladze et al. (2004)

$$\begin{aligned} &\geq -cB\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0B \\ &\geq -cB\left(1 - \frac{A_1}{K}\right) - d_0B := \alpha_1B, \quad t \in [0, t_1]. \end{aligned}$$

The standard argument yields that $B(t) \geq B(0)e^{\alpha_1 t} > 0$ for any $t \in [0, t_1]$, which implies that $B(t_1) \geq B(0)e^{\alpha_1 t_1} > 0$.

If $Q/A < \theta_0$, then

$$\begin{aligned} \frac{dB}{dt} &= sA - \frac{Q/A}{\theta_0}cB\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0B \\ &\geq -\frac{Q/A}{\theta_0}cB\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0B \\ &\geq \frac{cB\theta_{\min}}{\theta_0} - \frac{QcB}{A\theta_0} - d_0B \\ &\geq \left(\frac{c\theta_{\min}}{\theta_0} - \frac{cN}{A_1\theta_0} - d_0\right)B := \alpha_2B. \end{aligned}$$

Hence, one has $B(t_1) \geq B(0)e^{\alpha_2 t_1} > 0$, and there is a contradiction. No trajectory can touch the boundary $B(t) = 0$.

Case 2. $A(t_1) = 0$. Since $B(t)$, $H_1(t)$ and $H_2(t)$ are continuous, let $B_1 = \max_{t \in [0, t_1]} B(t)$, $H_1^1 = \max_{t \in [0, t_1]} H_1(t)$, $H_2^2 = \max_{t \in [0, t_1]} H_2(t)$, $\bar{f}_1 = f_1'(0)$, $\bar{f}_2 = f_2'(0)$, $\bar{Q} = N - \theta_1 H_1^1 - \theta_2 H_2^2 - \theta_0 B_1$. If $A(t) > \bar{Q}/\theta_{\min}$, then $A(t_1) > 0$ holds. If $A(t) \leq \bar{Q}/\theta_{\min}$, then

$$\begin{aligned} \frac{dA}{dt} &= (rA + cB)\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - f_1(A)H_1 - f_2(A)H_2 \\ &\geq rA\left(1 - \frac{A}{\min(K, \bar{Q}/\theta_{\min})}\right) - f_1(A)H_1 - f_2(A)H_2 \\ &\geq \left[r\left(1 - \frac{k}{\min(K, \bar{Q}/\theta_{\min})}\right) - \bar{f}_1 H_1^1 - \bar{f}_2 H_2^2\right]A := \alpha_3A. \end{aligned}$$

Using the standard comparison argument, we find that $A(t) \geq A(0)e^{\alpha_3 t} > 0$ for all $t \in [0, t_1]$. Hence, $S(t)$ cannot touch the boundary $A(t) = 0$.

Case 3. $A(t_1) = k$. For all $t \in [0, t_1]$, it follows that

$$\begin{aligned} \frac{dA}{dt} &= (rA + cB)\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - f_1(A)H_1 - f_2(A)H_2 \\ &\leq (rA + cB)\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) \\ &\leq (rA + cB)\left(1 - \frac{A}{k}\right). \end{aligned}$$

Hence, one obtains $dA/dt \leq 0$, if $A(t) \geq 0$ for all $t \in [0, t_1]$. The standard comparison argument yields that $A(t) < k$ for all $t \in [0, t_1]$. This contradicts to the fact that $A(t_1) = k$. $S(t)$ cannot touch the boundary $A(t) = k$.

Case 4. $A(t_1) + B(t_1) = (s + r + d_0)k/d_0$. Since $A(t) + B(t) < (s + r + d_0)k/d_0$ for any $t \in [0, t_1]$, then $A'(t_1) + B'(t_1) \geq 0$. If $\theta_{\min} > Q/A > \theta_0$, then

$$\begin{aligned} A'(t_1) + B'(t_1) &= (rA(t_1) + cB(t_1))\left(1 - \frac{A(t_1)}{\min(K, Q(t_1)/\theta_{\min})}\right) \\ &\quad - f_1(A(t_1))H_1(t_1) - f_2(A(t_1))H_2(t_1) + sA(t_1) \\ &\quad - \frac{Q(t_1)/A(t_1)}{\theta_0}cB(t_1)\left(1 - \frac{A(t_1)}{\min(K, Q(t_1)/\theta_{\min})}\right) - d_0B(t_1) \\ &< sA(t_1) + rA(t_1) - d_0B(t_1) \\ &= sA(t_1) + rA(t_1) - d_0\left(\frac{(s + r + d_0)k}{d_0} - A(t_1)\right) \\ &= s(A(t_1) - k) + r(A(t_1) - k) + d_0(A(t_1) - k) < 0. \end{aligned}$$

By similar arguments, if $Q/A > \theta_{\min}$ or $Q/A < \theta_0$, then one has $A'(t_1) + B'(t_1) < 0$. Hence, $S(t)$ cannot touch the boundary $A(t) + B(t) = (s + r + d_0)k/d_0$.

Case 5. $H_1(t_1) = 0$. Let $P_1 = \max_{t \in [0, t_1]} P(t)$ and $\tilde{f}_2 = f'_2(0)$, then

$$\frac{dH_1}{dt} = e_1 \min\left(1, \frac{Q/A}{\theta_1}\right) f_1(A)H_1 - d_1H_1 \geq -d_1H_1, \quad t \in [0, t_1].$$

The standard comparison argument yields that $H_1(t) \geq H_1(0)e^{-d_1t}$ for all $t \in [0, t_1]$ and thus, no trajectory touches the boundary $H_1(t) = 0$.

Case 6. $H_2(t_1) = 0$. Then

$$\frac{dH_2}{dt} = e_2 \min\left(1, \frac{Q/A}{\theta_2}\right) f_2(A)H_2 - d_2H_2 \geq -d_2H_2, \quad t \in [0, t_1].$$

Hence, $H_2(t) \geq H_2(0)e^{-d_2t}$. This excludes the possibility that $S(t)$ touches the boundary $H_2(t) = 0$ as well.

Case 7. $\theta_{\min}A(t_1) + \theta_1H_1(t_1) + \theta_2H_2(t_1) = N$. Since $\theta_{\min}A(t) + \theta_1H_1(t) + \theta_2H_2(t) < N$ for any $t \in [0, t_1]$. Hence, $\theta_{\min}A'(t_1) + \theta_1H'_1(t_1) + \theta_2H'_2(t_1) \geq 0$. Since

$$\begin{aligned} A'(t_1) &= (rA(t_1) + cB(t_1))\left(1 - \frac{A(t_1)}{\min(K, Q(t_1)/\theta_{\min})}\right) \\ &\quad - f_1(A(t_1))H_1(t_1) - f_2(A(t_1))H_2(t_1) \\ &\leq -f_1(A(t_1))H_1(t_1) - f_2(A(t_1))H_2(t_1), \\ H'_1(t_1) &= e_1 \min\left(1, \frac{Q/A(t_1)}{\theta_1}\right) f_1(A(t_1))H_1(t_1) - d_1H_1(t_1) \\ &\leq e_1 \frac{\theta_{\min}}{\theta_1} f_1(A(t_1))H_1(t_1), \\ H'_2(t_1) &= e_2 \min\left(1, \frac{Q/A(t_1)}{\theta_2}\right) f_2(A(t_1))H_2(t_1) - d_2P(t_1) \end{aligned}$$

$$\leq e_2 \frac{\theta_{\min}}{\theta_2} f_2(A(t_1))H_2(t_1).$$

Then,

$$\begin{aligned} & \theta_{\min}A'(t_1) + \theta_1H_1'(t_1) + \theta_2H_2'(t_1) \\ & \leq \theta_{\min}\left[-f_1(A(t_1))H_1(t_1) - f_2(A(t_1))H_2(t_1)\right] \\ & \quad + \theta_1e_1\frac{\theta_{\min}}{\theta_1}f_1(A(t_1))H_1(t_1) + \theta_2e_2\frac{\theta_{\min}}{\theta_2}f_2(A(t_1))H_2(t_1) \\ & = (e_1 - 1)\theta_{\min}f_1(A(t_1))H_1(t_1) + (e_2 - 1)\theta_{\min}f_2(A(t_1))H_2(t_1). \end{aligned}$$

Note that $0 < e_1 < 1, 0 < e_2 < 1$, then $\theta_{\min}A'(t_1) + \theta_1H_1'(t_1) + \theta_2H_2'(t_1) < 0$. There is a contradiction. No trajectory touches the boundary $\theta_{\min}A(t) + \theta_1H_1(t) + \theta_2H_2(t) = N$.

In summary, we claim that the solution $S(t) = (B(t), A(t), H_1(t), H_2(t))$ of (8) starting in Δ stays in Δ for any $t \geq 0$. The proof is complete. □

3.2 Equilibria

To facilitate the discussion below, we rewrite system (8) in the following form

$$\begin{aligned} \frac{dB}{dt} &= BF_1(B, A, H_1, H_2), \\ \frac{dA}{dt} &= AF_2(B, A, H_1, H_2), \\ \frac{dH_1}{dt} &= H_1G_1(B, A, H_1, H_2), \\ \frac{dH_2}{dt} &= H_2G_2(B, A, H_1, H_2), \end{aligned} \tag{9}$$

where

$$\begin{aligned} F_1(B, A, H_1, H_2) &= s\frac{A}{B} - \min\left(\frac{Q/A}{\theta_0}, 1\right)c\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0, \\ F_2(B, A, H_1, H_2) &= (r + c\frac{B}{A})\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - \frac{f_1(A)}{A}H_1 - \frac{f_2(A)}{A}H_2, \\ G_1(B, A, H_1, H_2) &= e_1\min\left(1, \frac{Q/A}{\theta_1}\right)f_1(A) - d_1, \\ G_2(B, A, H_1, H_2) &= e_2\min\left(1, \frac{Q/A}{\theta_2}\right)f_2(A) - d_2. \end{aligned} \tag{10}$$

To find equilibria of (9), we need to solve the following system of algebraic equations

$$\begin{aligned} BF_1(B, A, H_1, H_2) &= 0, \quad AF_2(B, A, H_1, H_2) = 0, \\ H_1G_1(B, A, H_1, H_2) &= 0, \quad H_2G_2(B, A, H_1, H_2) = 0. \end{aligned}$$

Note that $G_i, i = 1, 2$ denote the per capita growth rate of each herbivore. If the per capita growth rate keeps negative, then only the herbaceous plant can survive in the system. The herbivore-extinct boundary equilibrium $E_1 = (B_0, A_0, 0, 0)$ can be viewed as the internal equilibrium of the subsystem without herbivores. For simplifying, we explore the herbivores are extinct and study the stability of $E_0 = (B_0, A_0)$ of following subsystem

$$\begin{cases} \frac{dB}{dt} = sA - \min\left(\frac{Q/A}{\theta_0}, 1\right)cB\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right) - d_0B, \\ \frac{dA}{dt} = (rA + cB)\left(1 - \frac{A}{\min(K, Q/\theta_{\min})}\right). \end{cases} \tag{11}$$

Let

$$\Omega = \{(B, A) : 0 < B < N/\theta_0, 0 < A < k, A + B < (s + r + d_0)k/d_0\},$$

$$k = \min\{K, N/\theta_{\min}\},$$

$$\Phi(B, A) := \begin{cases} sA - \frac{N - \theta_0 B}{\theta_0 A} cB \left(1 - \frac{A\theta_{\min}}{N - \theta_0 B}\right) - d_0B, & A + B \geq N/\theta_0, \\ sA - cB \left(1 - \frac{A\theta_{\min}}{N - \theta_0 B}\right) - d_0B, & A + B \leq N/\theta_0, \\ & B \geq (A - \theta_{\min}K)/\theta_0, \\ sA - cB \left(1 - \frac{A}{K}\right) - d_0B, & A + B \leq N/\theta_0, \\ & B \leq (A - \theta_{\min}K)/\theta_0. \end{cases}$$

$$\Psi(B, A) := \begin{cases} (rA + cB) \left(1 - \frac{A\theta_{\min}}{N - \theta_0 B}\right), & A + B \geq N/\theta_0, \\ (rA + cB) \left(1 - \frac{A\theta_{\min}}{N - \theta_0 B}\right), & A + B \leq N/\theta_0, B \geq (A - \theta_{\min}K)/\theta_0, \\ (rA + cB) \left(1 - \frac{A}{K}\right), & A + B \leq N/\theta_0, B \leq (A - \theta_{\min}K)/\theta_0. \end{cases}$$

In the case $N/\theta_0 \leq (s + r + d_0)k/d_0$, when $k = N/\theta_{\min}$ or $k = K$, the studied regions are divided into two parts (see Fig. 1a) or three parts (see Fig. 1b). Similarly, in the case $N/\theta_0 > (s + r + d_0)k/d_0$, when $k = N/\theta_{\min}$ or $k = K$, the studied region is one part (see Fig. 1c) or is divided into two parts (see Fig. 1d). Without any loss of generality, we only consider the case when $k = K, N/\theta_0 \leq (s + r + d_0)k/d_0$ (Fig. 1b). In this case, we define

$$D_1 = \left\{ (B, A) \in \Omega, B + A \geq \frac{N}{\theta_0} \right\},$$

$$D_2 = \left\{ (B, A) \in \Omega, B + A < \frac{N}{\theta_0}, B \geq \frac{N - \theta_{\min}K}{\theta_0} \right\},$$

$$D_3 = \left\{ (B, A) \in \Omega, B + A < \frac{N}{\theta_0}, B < \frac{N - \theta_{\min}K}{\theta_0} \right\}.$$

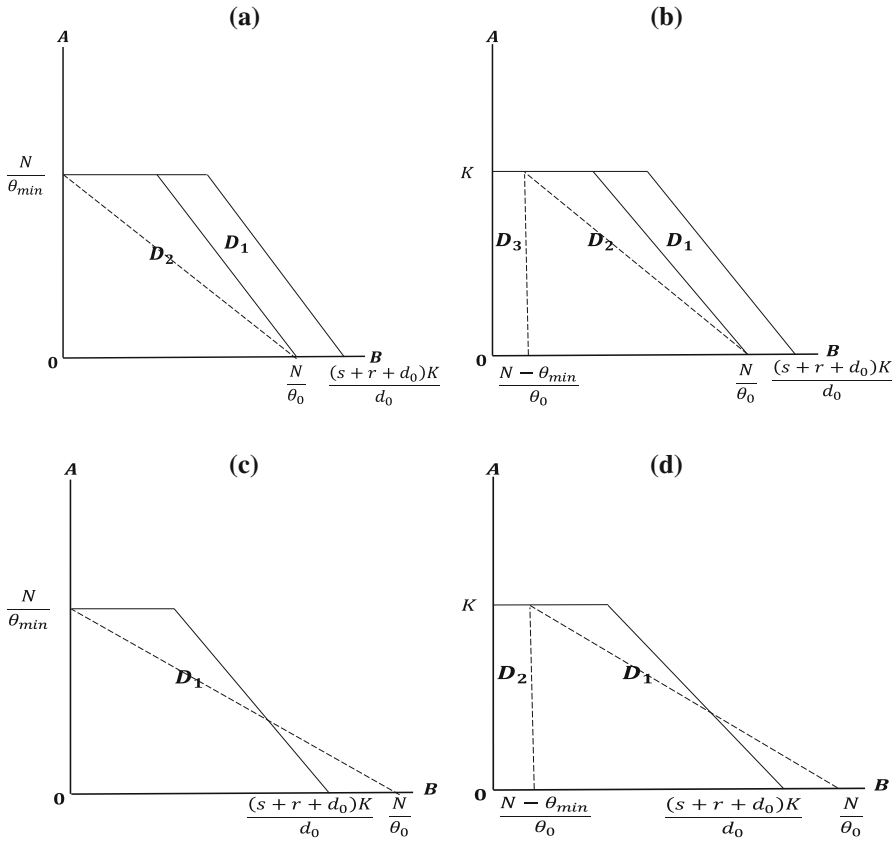


Fig. 1 The partition of studied region Ω . **a** $k = N/\theta_{\min}$, $N/\theta_0 \leq (s + r + d_0)k/d_0$. **b** $k = K$, $N/\theta_0 \leq (s + r + d_0)k/d_0$. **c** $k = N/\theta_{\min}$, $N/\theta_0 > (s + r + d_0)k/d_0$. **d** $k = K$, $N/\theta_0 > (s + r + d_0)k/d_0$

It is easy to show that, if $(B, A) \in D_1$, namely $Q/A < \theta_0 < \theta_{\min}$, then $1 - A\theta_{\min} < 0$ and there is no solution satisfying $\Psi(B, A) = 0$. We then only need to study the cases $(B, A) \in D_2, D_3$. System (11) takes the form

$$\begin{cases} \frac{dB}{dt} = sA - cB \left(1 - \frac{A\theta_{\min}}{N - \theta_0 B}\right) - d_0 B := \Phi_1(B, A), \\ \frac{dA}{dt} = (rA + cB) \left(1 - \frac{A\theta_{\min}}{N - \theta_0 B}\right) := \Psi_1(B, A), \end{cases} \tag{12}$$

$$\begin{cases} \frac{dB}{dt} = sA - cB \left(1 - \frac{A}{K}\right) - d_0 B := \Phi_2(B, A), \\ \frac{dA}{dt} = (rA + cB) \left(1 - \frac{A}{K}\right) := \Psi_2(B, A), \end{cases} \tag{13}$$

in the domains D_2, D_3 , respectively.

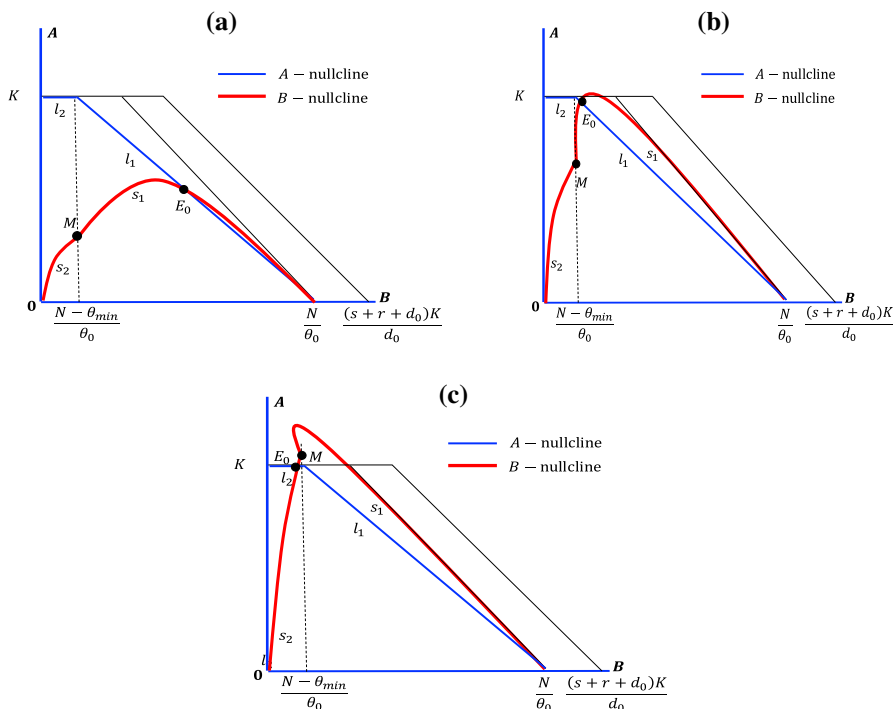


Fig. 2 (Colour figure online) The nullclines and equilibria. **a–b** $K\theta_{\min} < N \leq N_1$, the equilibrium lays on region D_2 . **c** $N > N_1$, the equilibrium lays on region D_3

Motivated by the method in Xie et al. (2016), we first analyze the nullclines of the system. Let $\Phi_1 = 0, \Phi_2 = 0$, then one has

$$sA - d_0B = cB(1 - A\theta_{\min}/(N - \theta_0B)) \quad \text{and} \quad sA - d_0B = cB(1 - A/K),$$

which denotes two curves, say s_1 and s_2 , respectively. Thus the B-nullcline in the invariant region are curves composed of s_1 and s_2 (see Fig. 2). Let $\Psi_1(B, A) = 0$, then $B = 0, A = 0$ and $B = -\theta_{\min}/\theta_0A + N/\theta_0$, denoted by l_1 the line segment $\theta_0B + \theta_{\min}A = N, B \in [0, K]$. Let $\Psi_2 = 0$, then $B = 0, A = 0$ and $A = K$, denoted by l_2 the line segment $A = K, B \in [0, (N - \theta_{\min}K)/\theta_0]$. Hence, the A-nullcline in the invariant region are the positive A-axis, B-axis, and a polygonal line composing of l_1 and l_2 (see Fig. 2). We then calculate the critical value. Let the curves s_1 and s_2 intersect at the intersection of l_1 and l_2 , i.e., $M = (K, (N - \theta_{\min})/\theta_0)$. Denote the critical value N by N_1 and directly calculation derives $N_1 = (\theta_{\min} + s\theta_0K/d_0)K$. When N passes through the critical from small to large, i.e., $N \leq N_1$ (see $(B, A) \in D_2$ in Fig. 2a–b) and $N > N_1$ (see $(B, A) \in D_3$ in Fig. 2c), we have the following theorems.

Theorem 2 *If $K\theta_{\min} \leq N \leq N_1$, then $E_0 = (B_0, A_0)$ exists and is globally asymptotically stable.*

Proof When $K\theta_{\min} \leq N \leq N_1$, $E_0 = (B_0, A_0)$ exists in D_2 and is explicitly solved from (12). Direct calculation gives

$$B_0 = \frac{sN}{\theta_0s + \theta_{\min}d_0}, \quad A_0 = \frac{d_0N}{\theta_0s + \theta_{\min}d_0}.$$

The Jacobian matrix at E_0 becomes

$$J(E_0) = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$\begin{aligned} a_{11} &= \frac{c\theta_0s}{d_0\theta_{\min}} - d_0, & a_{12} &= s + \frac{cs}{d_0} > 0, \\ a_{21} &= -\frac{\theta_0}{\theta_{\min}} \left(r + \frac{cs}{d_0} \right) < 0, & a_{22} &= -\left(r + \frac{cs}{d_0} \right) < 0. \end{aligned}$$

Then

$$\begin{aligned} \text{Det}(J(E_0)) &= d_0r + cs + \frac{rs\theta_0}{\theta_{\min}} + \frac{cs^2\theta_0}{d_0\theta_{\min}} > 0, \\ \text{Tr}(J(E_0)) &= \left(1 - \frac{\theta_0}{\theta_{\min}} \right) \frac{cs}{d_0} - d_0 - r < 0. \end{aligned}$$

Routh–Hurwitz Criterion shows that both eigenvalues of the Jacobian have negative real parts. Therefore, E_0 is locally asymptotically stable. Consider the Dulac function

$$V(B, A) = B^{-1}A^{-1}, \tag{14}$$

then

$$\begin{aligned} \frac{\partial(\Phi_1 V)}{\partial B} + \frac{\partial(\Psi_1 V)}{\partial A} &= V(B, A) \left(\frac{\partial\Phi_1}{\partial B} + \frac{\partial\Psi_1}{\partial A} \right) + \Phi_1(B, A) \frac{\partial V}{\partial B} + \Psi_1(B, A) \frac{\partial V}{\partial A} \\ &= V(B, A) \left(r \frac{A}{K} - \frac{rA\theta_{\min}}{N - \theta_0B} - rA \frac{A\theta_0\theta_{\min}}{(N - \theta_0B)^2} - \frac{sA}{B} - \frac{cB}{K} \right) \\ &\leq V(B, A) \left(r \frac{A}{K} - \frac{rA\theta_{\min}}{N - \theta_0B} \right). \end{aligned}$$

Note that $(B, A) \in D_2$, then $B > (N - \theta_{\min}K)/\theta_0$, which yields

$$\partial(\Phi_1 V)/\partial B + \partial(\Psi_1 V)/\partial A \leq rA/K - (rA\theta_{\min})/(N - \theta_0B) < 0,$$

the Dulac criterion precludes the possibility for (12) to admit any limit-cycle behavior. Therefore, from the Poincaré–Bendixson criterion, it follows that E_0 is globally asymptotically stable. □

Theorem 3 *If $N > N_1$, then $E_{01} = (sK/d_0, K)$ exists and is globally asymptotically stable.*

Proof When $N > N_1$, $E_{01} = (sK/d_0, K)$ is solved directly from (13). The Jacobian matrix at E_{01} becomes

$$J_2(E_{01}) = \begin{pmatrix} -d_0 & s + sc/d_0 \\ 0 & -(r + sc/d_0) \end{pmatrix},$$

both eigenvalues of the Jacobian have negative real parts. Therefore, E_{01} is locally asymptotically stable.

We next consider the Dulac function defined by

$$V_2(B, A) = B^{-1}A^{-1}, \tag{15}$$

then

$$\begin{aligned} \frac{\partial(\Phi_2 V_2)}{\partial B} + \frac{\partial(\Psi_2 V_2)}{\partial A} &= V_2(B, A) \left(\frac{\partial\Phi_2}{\partial B} + \frac{\partial\Psi_2}{\partial A} \right) + \Phi_2(B, A) \frac{\partial V_2}{\partial B} + \Psi_2(B, A) \frac{\partial V_2}{\partial A} \\ &= V_2(B, A) \left(-\frac{rA + cB}{K} - s\frac{A}{B} - c\frac{B}{A} \left(1 - \frac{A}{K}\right) \right) < 0 \end{aligned}$$

Dulac’s criterion precludes the possibility for (13) to admit any limit-cycle behavior. Therefore, from the Poincaré-Bendixson criterion, it follows that E_{01} is globally asymptotically stable. \square

The boundary equilibrium $E_2 = (\bar{B}, \bar{A}, \bar{H}_1, 0)$ represents the extinction of the lower N-demand herbivore (H_2), and $E_3 = (\bar{B}, \bar{A}, 0, \bar{H}_2)$ indicates the extinction of the higher N-demand herbivore (H_1). Thus E_2 or E_3 can be viewed as the internal equilibrium of the subsystem only with one consumer and one herbaceous plant. Without any loss of generality, we discuss the existence of E_2 as an example. Due to the complexity of the system (8), we analyze the existence on the plane by viewing a scenario of the phase space. It is easy to show that, if $Q/A < \theta_{\min}$, then there is no solution satisfying $F_2(\bar{B}, \bar{A}, \bar{H}_1, 0) = 0$. We only need to study the case when $Q/A > \theta_{\min}$. Rewrite F_1 as

$$F_1(\bar{B}, \bar{A}, \bar{H}_1, 0) = s\frac{\bar{B}}{\bar{A}} - c\left(1 - \frac{\bar{A}}{\min(K, \bar{Q}_2/\theta_{\min})}\right) - d_0.$$

From $F_1(\bar{B}, \bar{A}, \bar{H}_1, 0) = 0$ and $G_1(\bar{B}, \bar{A}, \bar{H}_1, 0) = 0$, it follows that

$$\bar{H}_1 = \frac{\bar{A}(sr\bar{A}/(c\bar{B}) - rd_0/c + s - d_0\bar{B}/\bar{A})}{f_1(\bar{A})}.$$

Then the boundary equilibria can be studied by degenerating the system onto the 2-dimensional $B - A$ plane by setting $H_1 = \bar{H}_1$. The equilibria can be found at the

interaction in the $B - A$ plane of the following two curves

$$\phi_1(A, B) = \frac{s\bar{A}}{\bar{B}} - c \left(1 - \frac{\bar{A}}{\min(K, \bar{Q}_2/\theta_{\min})} \right) - d_0 = 0, \tag{16}$$

$$\phi_2(A, B) = e_1 \min\left(1, \frac{\bar{Q}_2/\bar{A}}{\theta_1}\right) f_1(\bar{A} - d_1) = 0, \tag{17}$$

where $f_1(\bar{A}) = c_1\bar{A}/(a_1 + \bar{A})$, $\bar{Q}_2 = N - \theta_0B - \theta_1\bar{H}_1$. When $\bar{Q}_2/K > \theta_{\min}$ and $\bar{Q}_2/\bar{A} > \theta_1$, there is only a unique equilibrium (see Fig. 3e). Otherwise, there may exist zero to three equilibria (see Fig. 3a–d). Following proposition summarizes and lists the various possibilities for the roots of (16) and (17).

Proposition 1 *If $\bar{Q}_2/K > \theta_{\min}$ and $\bar{Q}_2/\bar{A} > \theta_1$, then system (8) has a unique boundary equilibrium; if $\bar{Q}_2/K \leq \theta_{\min}$, or $\bar{Q}_2/K > \theta_{\min}$ and $\bar{Q}_2/\bar{A} \leq \theta_1$, then system (8) may have zero to three equilibria.*

If system (9) has an internal equilibrium $E^* = (B^*, A^*, H_1^*, H_2^*)$, then its coordinates to solve the following system of algebraic equations

$$F_i(B, A, H_1, H_2) = 0, \quad G_i(B, A, H_1, H_2) = 0, \quad i = 1, 2. \tag{18}$$

From Loladze et al. (2004), it follows that (8) will never have any positive equilibrium if the herbaceous plant’s quality is good for both herbivores. However, in the case of bad quality of herbaceous plant,

$$\begin{aligned} X &:= N - \theta_1 H_1^* - \theta_2 H_2^* - \theta_0 B^* = \frac{d_1 \theta_1 A^*}{e_1 f_1(A^*)} = \frac{d_2 \theta_2 A^*}{e_2 f_2(A^*)}, \\ Y &:= (rA^* + cB^*) \left(1 - \frac{A^*}{\min(K, [d_2 \theta_2 A^*]/[\theta_{\min} e_2 f_2(A^*)])} \right) \\ &= f_1(A^*) H_1^* + f_2(A^*) H_2^*, \\ Z &:= \min\left(\frac{d_2 \theta_2}{e_2 \theta_0}, 1\right) \left(1 - \frac{A^*}{\min(K, [d_2 \theta_2 A^*]/[\theta_{\min} e_2 f_2(A^*)])} \right) = sA^*/B^* - d_0. \end{aligned}$$

Then the value of A^* is determined by

$$\frac{d_1 \theta_1 A^*}{e_1 f_1(A^*)} = \frac{d_2 \theta_2 A^*}{e_2 f_2(A^*)}, \tag{19}$$

and the values of B^* , H_1^* and H_2^* are given by

$$\begin{aligned} B^* &= \frac{sA^*}{d_0 + Z}, \\ H_1^* &= \frac{f_2(A^*)N - \theta_2 Y - (\theta_0 s A^* f_2(A^*)) / (d_0 + Z) - (d_2 \theta_2 A^*) / e_2}{\theta_1 f_2(A^*) - \theta_2 f_1(A^*)}, \end{aligned}$$

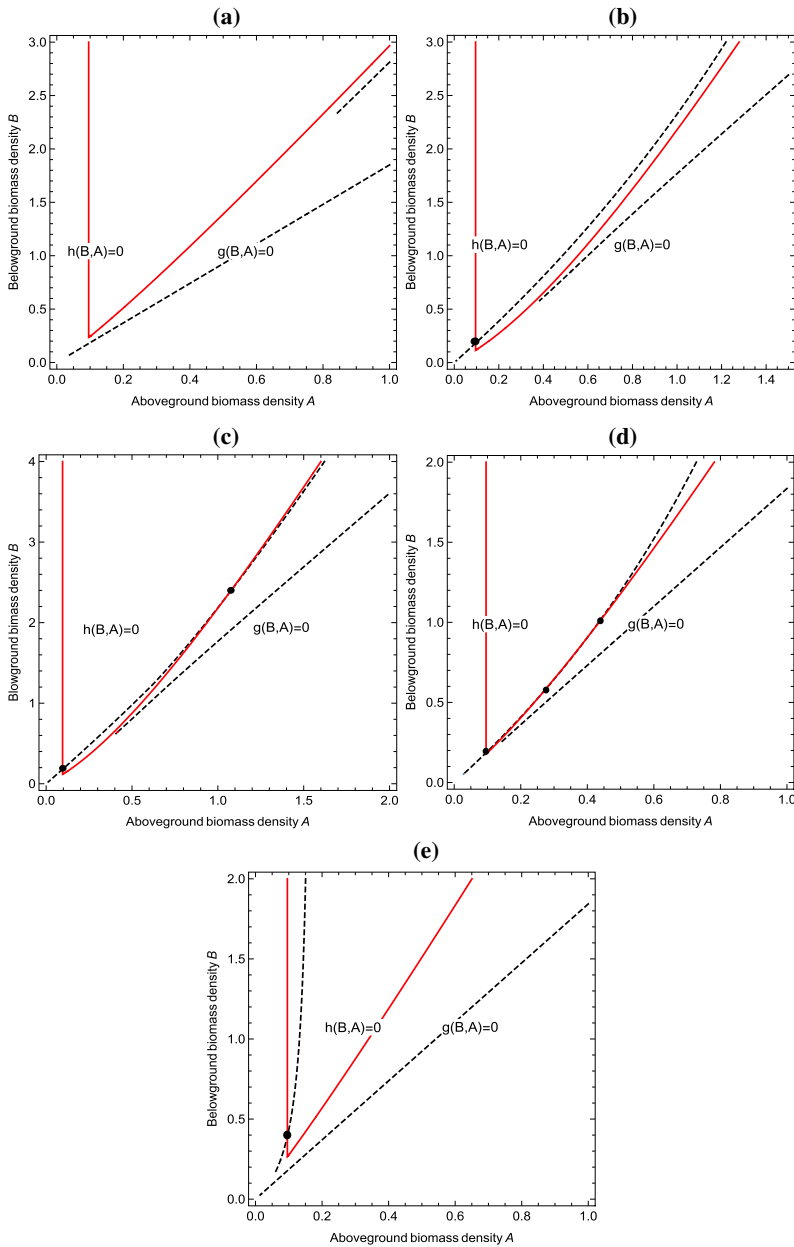


Fig. 3 Location of the equilibria in the A – B plane. The inverse peak-shaped curve is defined by $h(\bar{B}, \bar{A}) = 0$, which will never change its shape as parameters vary. The black dashed curve is defined by $g(\bar{B}, \bar{A}) = 0$ with different K , N and θ_1 values. A solid circle denotes a possible equilibrium. Here, $N = 0.1$ in **a–d**, while $N = 0.03$ in **e**, the light intensity K and θ_1 in **a–e** are 1, 2, 4, 0.9, 0.05 and 0.2, 0.05, 0.05, 0.1, 0.05, respectively

$$H_2^* = \frac{\theta_1 Y - f_1(A^*)N + (\theta_0 s A^* f_1(A^*)) / (d_0 + Z) + (d_2 \theta_2 A^* f_1(A^*)) / [e_2 f_2(A^*)]}{\theta_1 f_2(A^*) - \theta_2 f_1(A^*)}. \tag{20}$$

Thus, let $Q^* = N - \theta_1 H_1^* - \theta_2^* H_2^* - \theta_0 B^*$, we have the following proposition.

Proposition 2 *If $Q^*/A^* < \theta_i$, then system (8) has a possible positive equilibrium $E^* = (B^*, A^*, H_1^*, H_2^*)$, where (B^*, A^*, H_1^*, H_2^*) satisfies (19) and (20).*

To characterize the type of species interactions occurring at this equilibrium, it is convenient to examine the Jacobian matrix. The Jacobian matrix at E^* takes the following form

$$J(E^*) = \begin{bmatrix} B^* & 0 & 0 & 0 \\ 0 & A^* & 0 & 0 \\ 0 & 0 & H_1^* & 0 \\ 0 & 0 & 0 & H_2^* \end{bmatrix} \times M(B^*, A^*, H_1^*, H_2^*), \tag{21}$$

where

$$M = (a_{ij})_{4 \times 4} = \begin{bmatrix} \frac{\partial F_1}{\partial B} & \frac{\partial F_1}{\partial A} & \frac{\partial F_1}{\partial H_1} & \frac{\partial F_1}{\partial H_2} \\ \frac{\partial F_2}{\partial B} & \frac{\partial F_2}{\partial A} & \frac{\partial F_2}{\partial H_1} & \frac{\partial F_2}{\partial H_2} \\ \frac{\partial G_1}{\partial B} & \frac{\partial G_1}{\partial A} & \frac{\partial G_1}{\partial H_1} & \frac{\partial G_1}{\partial H_2} \\ \frac{\partial G_2}{\partial B} & \frac{\partial G_2}{\partial A} & \frac{\partial G_2}{\partial H_1} & \frac{\partial G_2}{\partial H_2} \end{bmatrix} \tag{22}$$

is the ecosystem matrix. The possible items of M are listed below:

$$\begin{aligned}
 \frac{\partial F_1}{\partial B} &= \begin{cases} \frac{c}{A} - \frac{sA}{B^2}, & \text{if } Q < A\theta_0, \\ \frac{cA\theta_0\theta_{\min}}{Q^2} - \frac{sA}{B^2}, & \text{if } A\theta_0 \leq Q < K\theta_{\min}, \\ -\frac{sA}{B^2} < 0, & \text{if } Q \geq K\theta_{\min}, \end{cases} \\
 \frac{\partial F_1}{\partial A} &= \begin{cases} \frac{cQ}{\theta_0 A^2} + \frac{s}{B} > 0, & \text{if } Q < A\theta_0, \\ \frac{c\theta_{\min}}{Q} + \frac{s}{B} > 0, & \text{if } A\theta_0 \leq Q < K\theta_{\min}, \\ \frac{c}{K} + \frac{s}{B} > 0, & \text{if } Q \geq K\theta_{\min}, \end{cases} \\
 \frac{\partial F_1}{\partial H_i} &= \begin{cases} \frac{c\theta_i}{A\theta_0} > 0, & \text{if } Q < A\theta_0, \\ \frac{cA\theta_i\theta_{\min}}{Q^2} > 0, & \text{if } A\theta_0 \leq Q < K\theta_{\min}, \\ 0, & \text{if } Q \geq K\theta_{\min}, \end{cases} \\
 \frac{\partial F_2}{\partial B} &= \begin{cases} \frac{c}{A} - \frac{c}{K} \geq 0, & \text{if } K \leq Q/\theta_{\min}, \\ \frac{c}{A} - \frac{rA\theta_0\theta_{\min}}{Q^2} \\ -\frac{c\theta_{\min}(N - \theta_1 H_1 - \theta_2 H_2)}{Q^2}, & \text{if } K > Q/\theta_{\min}, \end{cases} \tag{23} \\
 \frac{\partial F_2}{\partial A} &= \begin{cases} -\frac{r}{K} - \frac{cB}{A^2} - \left(\frac{f_1(A)}{A}\right)' H_1 \\ -\left(\frac{f_2(A)}{A}\right)' H_2 < 0, & \text{if } K \leq Q/\theta_{\min}, \\ -\frac{r\theta_{\min}}{Q} - \frac{cB}{A^2} \left(\frac{f_1(A)}{A}\right)' H_1 \\ -\left(\frac{f_2(A)}{A}\right)' H_2 < 0, & \text{if } K > Q/\theta_{\min}, \end{cases} \\
 \frac{\partial F_2}{\partial H_i} &= \begin{cases} -\frac{f_i(A)}{A} < 0 & \text{if } K \leq Q/\theta_{\min}, \\ -\frac{\theta_i\theta_{\min}(rA + cB)}{Q^2} - \frac{f_i(A)}{A} < 0 & \text{if } K > Q/\theta_{\min}, \end{cases} \\
 \frac{\partial G_i}{\partial B} &= \begin{cases} 0 & \text{if } Q/A \geq \theta_i, \\ -\frac{e_i\theta_0 f_i(A)}{A\theta_i} < 0 & \text{if } Q/A < \theta_i, \end{cases} \\
 \frac{\partial G_i}{\partial A} &= \begin{cases} e_i f_i'(A) > 0 & \text{if } Q/A \geq \theta_i, \\ -\frac{e_i Q}{\theta_i} \left(\frac{f_i(A)}{A}\right)' < 0 & \text{if } Q/A < \theta_i, \end{cases} \\
 \frac{\partial G_i}{\partial H_j} &= \begin{cases} 0 & \text{if } Q/A \geq \theta_i, \\ -\frac{e_i\theta_j f_i(A)}{A\theta_i} < 0 & \text{if } Q/A < \theta_i. \end{cases}
 \end{aligned}$$

Due to the complexity of the system (8), it seems difficult to establish explicit sufficient conditions for the stability of the equilibria by Routh–Hurwitz criteria. Instead, we explore it by the analysis of ecosystem matrix. In the ecosystem matrix, a_{ij} measures the effect of j -th species on i -th specie’s net growth rate.

According to the relations of N:C ratios Q^*/A^* , θ_1 and θ_2 , the discussion is divided into three cases.

1. If $Q^*/A^* > \theta_i$, $i = 1, 2$, that is, the herbaceous plant’s quality is good for both herbivores, then the ecosystem matrix takes the form

$$\begin{bmatrix} + / - & + & 0 / + & 0 / + \\ + / - & + / - & - & - \\ 0 & + & 0 & 0 \\ 0 & + & 0 & 0 \end{bmatrix}, \tag{24}$$

which indicates that the interaction between the herbivore and the herbaceous plant falls into the traditional predator-prey category, i.e., (+, -) type.

2. If $Q^*/A^* < \theta_i$, $i = 1, 2$, i.e., the herbaceous plant’s quality is bad for both herbivores, then the ecosystem matrix is

$$\begin{bmatrix} + / - & + & 0 / + & 0 / + \\ + / - & + / - & - & - \\ - & - & - & - \\ - & - & - & - \end{bmatrix} \tag{25}$$

which implies that the interaction between herbivore and herbaceous plant changes from (+, -) to (-, -). It means that all the three species compete with each other, and the competition lies in two species not only intraspecifically but also interspecifically due to the limited N content. The increase in the herbaceous plant with bad quality will not promote the herbivores’ growth. It has been shown that the interference among herbivores can enhance the possibility for coexistence (Kuang et al. 2003).

3. If $\theta_2 > Q^*/A^* > \theta_1$ or $\theta_1 > Q^*/A^* > \theta_2$, i.e., the quality of herbaceous plant is good for the herbivore with lower N:C ratio but is bad for the other herbivore, then the ecosystem matrix reads

$$\begin{bmatrix} + / - & + & 0 / + & 0 / + \\ + / - & + / - & - & - \\ 0 & + & 0 & 0 \\ - & - & - & - \end{bmatrix} \text{ or } \begin{bmatrix} + / - & + & 0 / + & 0 / + \\ + / - & + / - & - & - \\ - & - & - & - \\ 0 & + & 0 & 0 \end{bmatrix}.$$

In this case, the herbivore with lower N:C ratio will survive due to the relatively good food quality, while the herbivore with higher N:C ratio will go extinct due to the relatively bad food quality.

A significant and unusual property of this system is that the sign of $\partial G_i / \partial A$, $i = 1, 2$ changes from positive to negative when the herbaceous plant’s N:C ratio

is less than the N:C ratio of the i -th herbivore, θ_i . These negative derivatives mean that, all else being equal, higher herbaceous plant density reduces the growth rates of herbivores. It is because that when the quality of herbaceous plant is bad, then any further increase in the herbaceous plant's density deteriorates its quality, which neutralizes the benefit provided by higher herbaceous plant density to herbivores that has already been limited by N . This effect is in strong contrast to many conventional population dynamics. Moreover, the signs of $\partial G_i / \partial B$, $i = 1, 2$ turn from 0 to negative as herbaceous plant's quality becomes bad for the herbivores, $Q^*/A^* < \theta_i$. It means that the belowground part competes with the herbivores for N to keep the regular growth of herbaceous plant when the available nutrient is limiting. Furthermore, the sustained increase in the belowground settles more nutrient which makes the quality of plants becomes worse, then the densities of the herbivores decrease due to the bad quality of food.

4 Numerical Simulation

The principal aim of this section is to investigate the impact of variational initial states, nitrogen availability, and light intensity on the dynamics of (8). In the numerical analysis, the herbivores' ingestion rates are chosen as Monod (Michaelis–Menten) functions, i.e., $f_i(x) = c_i x / (a_i + x)$, $i = 1, 2$, and all parameters take the values listed in Table 1 if not specified.

In a grassland ecosystem, the aboveground part of herbaceous plants is usually consumed by herbivores, while the belowground is preserved. The traditional model (e.g., (1)) cannot well describe the dynamic scenarios since the belowground is not explicitly modeled in the system. Here, we use (8) to investigate the effect of the aboveground part on changing trends of population dynamics. Set $A(0) = 0.3$, Fig. 4a shows that initially the biomass density of the aboveground increases which is followed by an increase in the densities of the belowground and the two herbivores. With the increase in two herbivores, the densities of both aboveground and belowground decline while the density of the herbivore with higher N-demand $H_1(t)$ keeps growing and the herbivore with lower N-demand $H_2(t)$ shows an opposite trend due to the inferior competitiveness. In Fig. 4b, $A(0) = 0$, it is observed that the density of the aboveground could recover and regrow due to the transfer support of material from the belowground; meanwhile, the belowground conserves more biomass due to the absence or less amount of the aboveground. The densities of two herbivores first decrease due to the lack of food and then increase due to the regrowth of the aboveground plants. Then, the trend of future development in Fig. 4b is similar to that in Fig. 4a. The simulation analyses show that, in the short term, the variation of (8) is quite different when the aboveground is present or not, while, in the long run, (8) eventually stabilizes at some internal equilibrium in both cases. Therefore, (8) reasonably describes the dynamic interaction among one herbaceous plant and two herbivores, and also well characterizes the realistic scenario in a grassland ecosystem.

The light intensity (i.e., K) can change the herbaceous plant's quality (Loladze et al. 2000), and analyses in previous section suggest that plant's N:C ratio can profoundly affect predation and competition between the two herbivores. Moreover, plant's nitro-

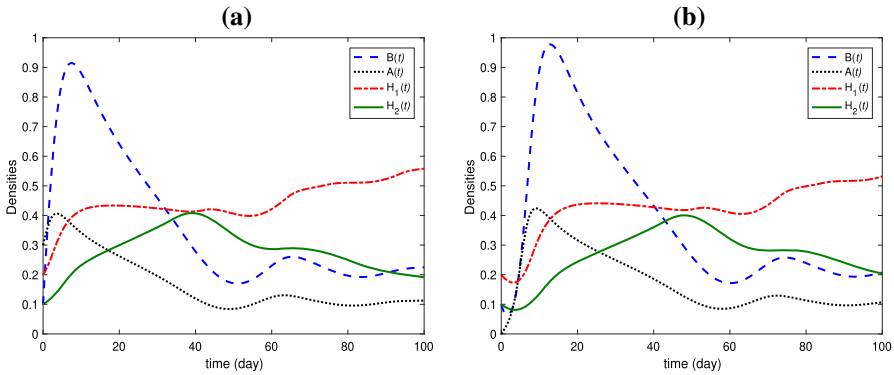


Fig. 4 Time series dynamics of (8) with different initial values of the aboveground: **a** $(B(0), A(0), H_1(0), H_2(0)) = (0.1, 0.3, 0.2, 0.1)$, **b** $(B(0), A(0), H_1(0), H_2(0)) = (0.1, 0, 0.2, 0.1)$. Here the parameter values are defined in Table 1 except $K = 0.7$ and $N = 0.03$

gen addition rates also affect the nutrient transfer between the aboveground and the belowground in grassland ecosystems. Hence, we choose K and N as bifurcation parameters to explore how (8) response to variations of light intensity K and nitrogen availability N . Figure 5 presents such bifurcation diagrams where the densities of all populations are drawn along the gradient of nitrogen and energy availabilities implicitly represented by N and K . From Fig. 5, one observes that, the aboveground and belowground herbaceous plants can only survive at very low densities with the limitation of light intensity and nitrogen availability, then grow rapidly with enhancing light and nitrogen. With further increase in light intensity and nitrogen availability, the densities of the aboveground and belowground do not increase anymore due to the ingestion of herbivores and the limitation of nutrient or energy (see Fig. 5a and b). Meanwhile, neither of the herbivores can survive due to starvation at sufficiently low light intensity and nitrogen availability. As K and N increase, all herbivores survive and coexist stably or cyclically, but all of them tend to perish with the extremely high light intensity and nitrogen (see Fig. 5c and d). In particular, the two herbivores can coexist under moderate light and nitrogen availabilities.

In order to deeply understand the characteristics of the bifurcation and to better investigate the effects of the light intensity K and the total nitrogen availability N , we present detailed discussions of some cross-profiles along the gradient of K from 0 to 4 and the gradient of N from 0.02 to 0.1 (see Figs. 6, 7, 8, 9, 10 and 11).

It follows from Figs. 6 and 7 that when the total nitrogen availability is low ($N = 0.03$) or sufficiently high ($N = 0.08$), all populations coexist in a single form, either at a steady state or at a cyclic state. That is, when $N = 0.03$, herbivores can coexist at a stable steady-state exploiting the herbaceous plant (see $0.23 < K < 0.61$ in Fig. 6); when $N = 0.08$, the populations can only coexist via cyclic oscillation (e.g., $1.79 < K < 2.55$ in Fig. 7). Dramatically, in both cases, with the further increase in light intensity, the higher N-demand herbivore becomes extinct initially which is followed by the extinction of the lower N-demand herbivore (such as $0.61 < K < 2$ in Fig. 6 and $2.55 < K < 4$ in Fig. 7). This is possible, because increasing light intensity lowers

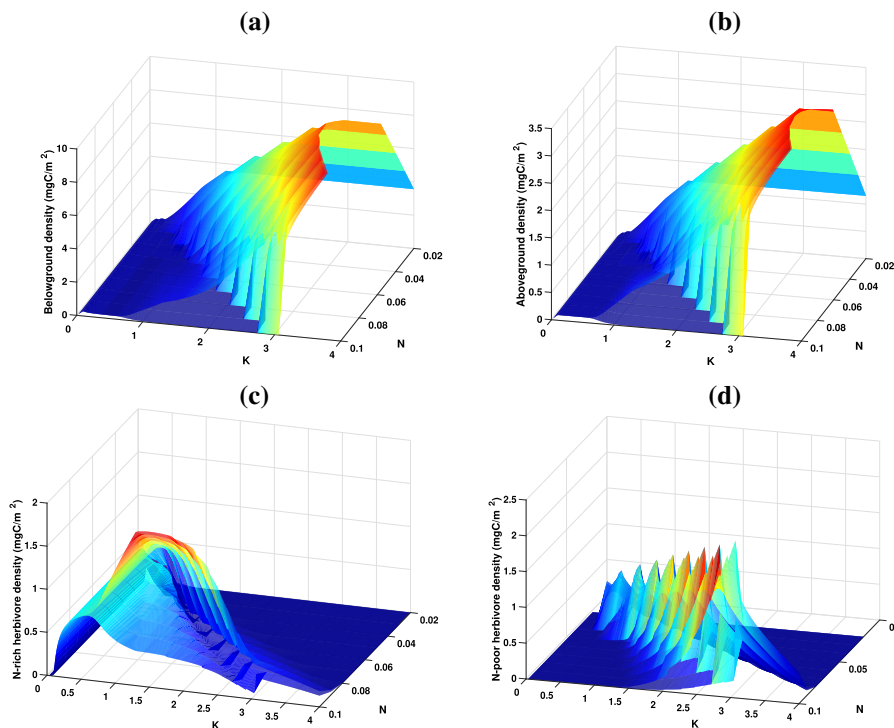


Fig. 5 Bifurcation surfaces for (8) with the light intensity K and the nitrogen availability N being the bifurcation parameters. **a–d** represent bifurcation surfaces of the equilibrium densities of the belowground herbaceous plant B , the aboveground herbaceous plant A , the higher N-demand herbivore H_1 , and the lower N-demand herbivore H_2 plotted against K and N , respectively

the herbaceous plant's quality, and extremely low food quality drives the extinction of the two herbivores in order. Furthermore, due to the extinction of herbivores, with increasing light intensity, the densities of aboveground and belowground herbaceous plants increase first and stay constant finally due to the limitation of total nitrogen availability (see Fig. 6a).

When the total nitrogen availability is at some intermediate level, we focus on a typical case with $N = 0.04$ (Fig. 8), the dynamics become more complex. When the light intensity is low (e.g., $0 < K < 0.55$ in Fig. 8), the dynamics are similar to that of the case when the total nitrogen availability is low, that is, both herbivores cannot survive due to low level of food abundance; with the increase in food abundance, the higher N-demand herbivore survives initially and then the lower N-demand herbivore survives. As the light intensity K increases further (e.g., $0.55 < K < 1.03$ in Fig. 8), compared with the previous low nutrient case, now the dynamical behaviors are quite different. In Fig. 8, at $K = 0.55$, the internal equilibrium loses its stability and undergoes a supercritical Hopf bifurcation, and all populations coexist via oscillations as K increases from 0.55 to 0.62. When K increases further (e.g., from 0.62 to 0.97 in Fig. 8), the dynamics of (8) are significantly different from that of the model in Loladze et al.

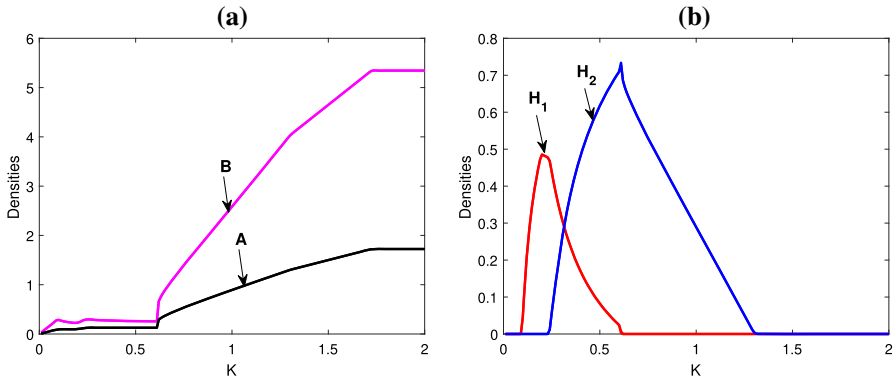


Fig. 6 Bifurcation diagrams of the equilibrium densities of (8) plotted against the light intensity K . Here $N = 0.03$ and the values of other parameters are defined in Table 1

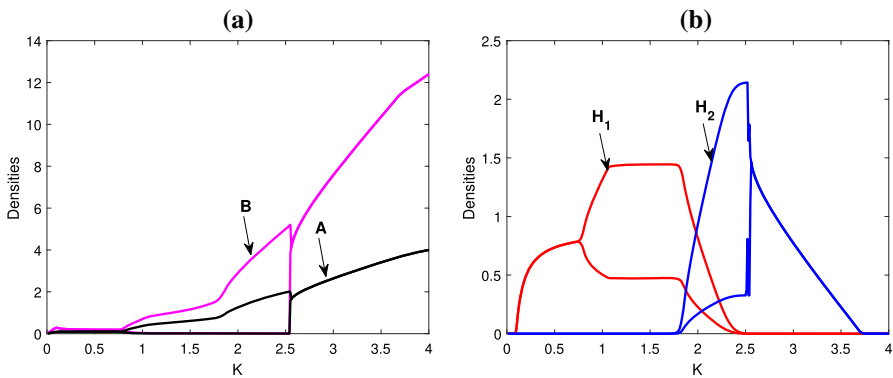


Fig. 7 (Colour figure online) Bifurcation diagrams of equilibrium densities with respect to light intensity K for the scenario of $N = 0.08$ in Fig. 5

(2004) due to the explicit consideration of the belowground. In fact, with K increasing from 0.62 to 0.97, system (8) admits oscillatory dynamics and all populations coexist with irregularly cyclic oscillations. Similar to Wang et al. (2009), we plot the spectrum of maximum Lyapunov exponent (MLE) of (8) against K in Fig. 8e which shows that there is no chaotic orbit since the maximum Lyapunov exponent $\lambda < 0$ for $0 < K < 2.5$. When the light intensity increases through an intermediate threshold value (e.g., $K = 0.97$ in Fig. 8), the dynamics of (8) change abruptly, the irregularly periodic behavior disappears via a supercritical Hopf bifurcation once again. When K increases from 0.97 to 1.03, all populations oscillate periodically. When K increases further, the above- and belowground plants grow rapidly with sufficient light intensity but the density of the higher N-demand herbivore H_1 cannot survive and the density of the lower N-demand herbivore H_2 declines due to worse and worse food quality (for $1.03 < K < 1.8$). Finally, extremely high light intensity ($1.8 < K < 2.5$) leads to extinction of both herbivores.

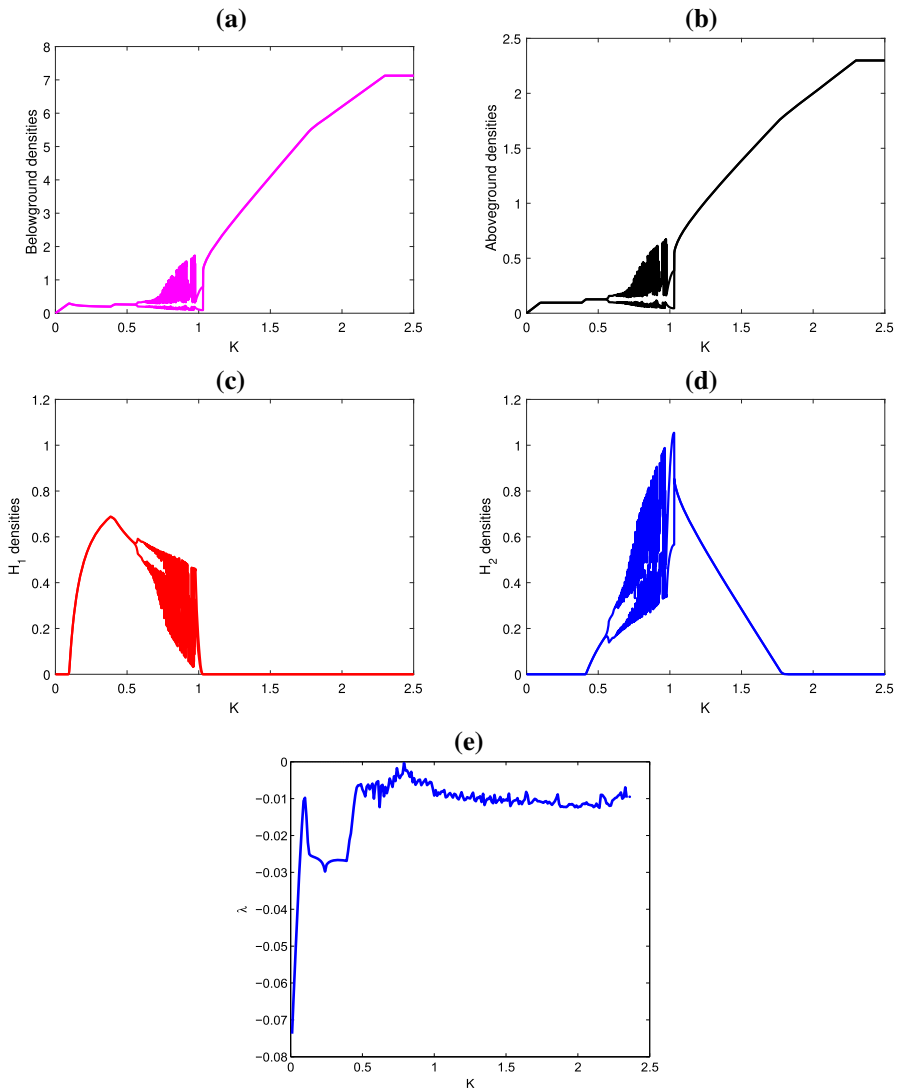


Fig. 8 Bifurcation diagrams of equilibrium densities for system (8) with respect to light intensity K varying from 0 to 2.5. **a** and **b** are bifurcation diagrams of the equilibrium densities of the belowground herbaceous plant and the aboveground herbaceous plant for the scenario of $N = 0.04$ in Fig. 5a and b. **c–d** Represent bifurcation diagrams of the equilibrium densities of the higher N-demand herbivore H_1 and lower N-demand herbivore H_2 for the scenario of $N = 0.04$ in Fig. 5c and d. **e** Spectrum of the maximum Lyapunov exponent (λ) against K of system (8). The MLE is negative for $0 < K < 2.5$, which implies that there is no chaotic orbit

In conclusion, for the effect of variations of light intensity, if the total nitrogen availability N is fixed, high light intensity leads to an increase in herbaceous plant abundance and hence deteriorates the herbaceous plant's quality, whence the herbivore with lower N-demand will have a competitive advantage. Due to the limitation of nitrogen, the biomass of herbaceous plant does not continuously increase with the increase in light intensity. Meanwhile, because of the poor food quality (small N:C ratio), both herbivores go extinct despite of a sufficient food quantity (e.g., $3.75 < K \leq 4$ in Fig. 7b), which is consistent with the explanation of the paradox of nutrient enrichment proposed in Loladze et al. (2000). In addition, for different nitrogen availabilities increasing from low to high, the densities of aboveground and belowground biomasses increase as light intensity increases (e.g., Figs. 6, 7 and 8). The range of parameter K for the survival of herbivores expands with the increase in nitrogen availability N .

Next, we discuss the effect of varying total nitrogen availability N on the dynamics of (8), and we expound the details for low, intermediate, and high levels of light intensity with $K = 0.2$, $K = 0.7$, and $K = 1$, respectively. For $K = 0.2$ (Fig. 9), the light intensity is at a low level, all populations can only coexist when the nitrogen availability is also very low ($0.02 < N < 0.032$), this is because the N:C of the aboveground is relatively high, the quality of herbaceous plant is good for both herbivores. Furthermore, with the increase in N ($0.02 < N < 0.08$), the density of the higher N-demand herbivore is always higher than that of the lower N-demand herbivore. The reason is that, the low light intensity limits the abundance of herbaceous plants and the herbivore having higher growth rate (H_1) takes advantage in the low food abundance.

For $K = 0.7$, we observe from Fig. 10 that, when N increases, the system experiences a dynamic path with the switch pattern: H_2 -existence equilibrium ($0.02 \leq N < 0.032$) \rightarrow coexistence equilibrium ($0.032 \leq N < 0.037$) \rightarrow irregular oscillation ($0.037 \leq N < 0.045$) \rightarrow H_1 -existence equilibrium ($0.045 \leq N < 0.08$). So, when the light intensity is at intermediate level, large N will facilitate the existence of the higher N-demand herbivore and stabilize the system to an H_2 -existence equilibrium.

For $K = 1$, we can see from Fig. 11 that, when N increases, the dynamic path of the system with respect to N has a different pattern of switches: None-herbivore equilibrium ($0.02 \leq N < 0.023$) \rightarrow H_2 -existence equilibrium ($0.023 \leq N < 0.039$) \rightarrow cyclic ($0.039 \leq N < 0.06$) \rightarrow H_1 -existence cyclic ($0.06 \leq N < 0.08$). Whence, if the light intensity is high, then large N will lead the system to a cyclic state. Particularly, when $0.071 < N < 0.08$, the densities of the aboveground and belowground herbaceous plants oscillate between 0 and 0.38 in Fig. 11, which implies that the plants have a potential extinction trend with the increase in total nitrogen availability. High nitrogen availability improves the food quality of the herbaceous plant and then increases the biomass of the higher N-demand herbivore, while the excessive predation of herbivores leads to a potential extinction of the herbaceous plant. This finding is consistent with the experimental results in Suding et al. (2005), Lan and Bai (2012) that nitrogen enrichment can promote the loss of rare species in the community and further reduce species diversity.

In summary, when the light intensity and nitrogen availability are low, the herbivores can coexist at low densities; when the light is fixed, the increase in nitrogen can lead to the extinction of the lower N-demand herbivore. In addition, increasing both light and nutrient make all populations coexist via stable state, periodic or irregularly

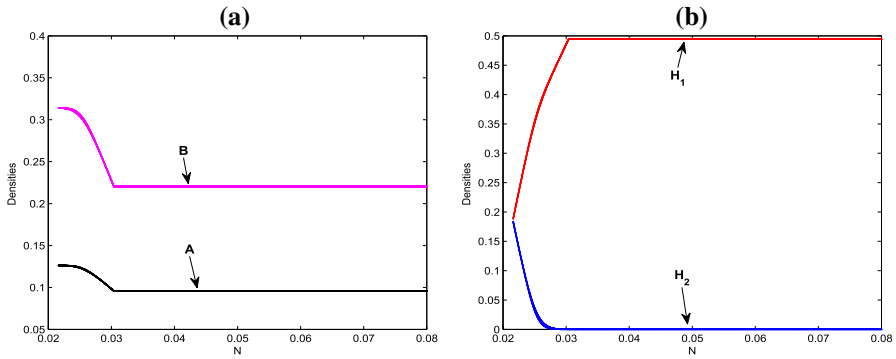


Fig. 9 Bifurcation diagrams of equilibrium densities with respect to nitrogen availability N for the scenario of $K = 0.2$ in Fig. 5

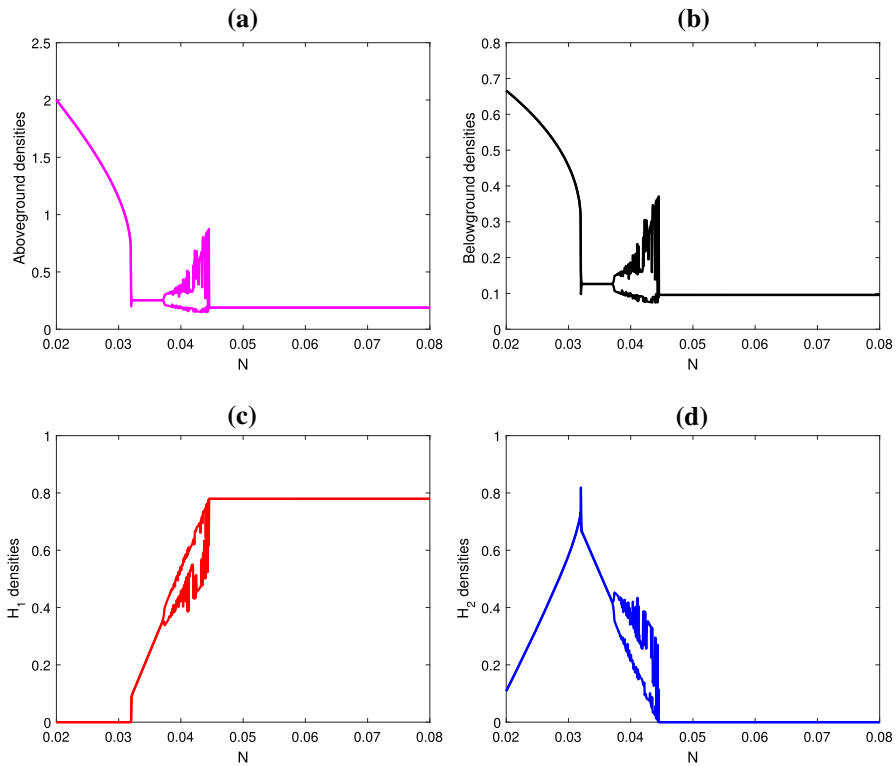


Fig. 10 Bifurcation diagrams of all populations densities with respect to nitrogen availability N varying from 0.02 to 0.08 for the scenario of $K = 0.7$ in Fig. 5

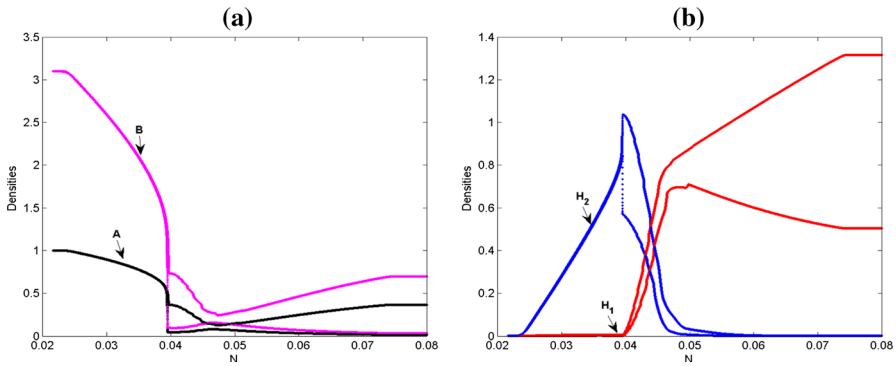


Fig. 11 Bifurcation diagrams of all populations densities with respect to nitrogen availability N varying from 0.02 to 0.08 for the scenario of $K = 1$ in Fig. 5

cyclic oscillations, i.e., moderate levels of light and nitrogen availabilities contribute to species diversity. It is more interesting that extremely high level of nitrogen can cause overeating of herbivores on the herbaceous plant, and then may lead to extinction of the herbaceous plant.

5 Discussion

In this study, we formulate a new ecological stoichiometric model of two competing herbivores on one herbaceous plant in a grassland ecosystem, where the heterogeneity of herbaceous plant and the effect of food quality are explicitly incorporated. The interaction between the aboveground and belowground of herbaceous plant is well identified. The effects of light intensity and nitrogen availability on the model's dynamics are systematically explored. Both analytical and simulation findings expound the importance of the aboveground–belowground interaction and chemical heterogeneity. As shown in Fig. 4, the model (8) reasonably describes the dynamics among two herbivores exploring one herbaceous plant and can also well characterize the realistic scenarios in a grassland ecosystem. Our study shows that aboveground and belowground interaction can facilitate the coexistence of four populations. All populations can coexist either in a stable equilibrium or in oscillations, even in irregularly cyclic oscillations (Figs. 5, 8 and 10).

The results of numerical experiments reveal that, both light intensity and nitrogen availability play important roles in the growth and coexistence of the four populations. When the total nitrogen availability N is fixed (Figs. 6, 7 and 8), the increased light intensity could increase the amount of herbaceous plant and hence deteriorate the herbaceous plant's quality, and both herbivores coexist first, then the lower N -demand herbivore excludes the higher N -demand herbivore finally. It implies that intermediate levels of light intensity and nitrogen availability promote the coexistence of two herbivores, and a higher light intensity can help the lower N -demand herbivore to win. With the further increase in light intensity, the densities of the aboveground and belowground plants do not increase anymore due to the ingestion of herbivores and

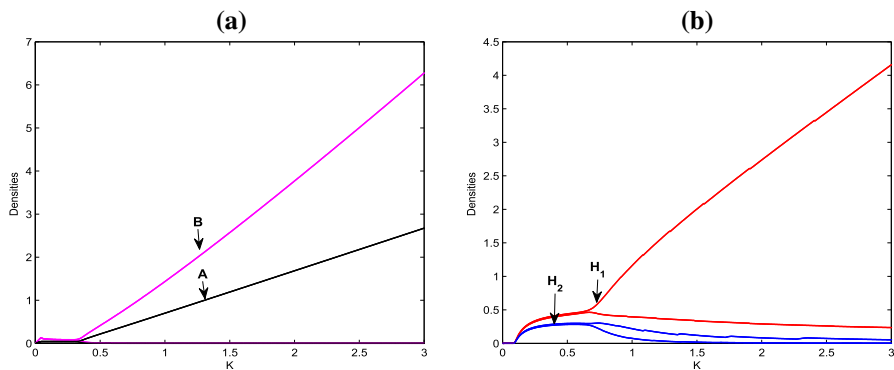


Fig. 12 (Colour figure online) Bifurcation diagrams of (4) with light intensity K being the bifurcation parameter. Other parameters are defined in Table 1

the limitation of nitrogen. Meanwhile, the quality of the herbaceous plant becomes too bad for both herbivores, initially the higher N-demand herbivore tends to die out which is followed by the extinction of lower N-demand herbivore despite of a sufficient food quantity (e.g., $1.35 < K < 2$ in Fig. 6b, $3.75 < K \leq 4$ in Fig. 7b and $1.8 < K < 2.5$ in Fig. 8b). The above facts expound the paradox of nutrient enrichment and are consistent with the findings in Loladze et al. (2000). In addition, for different nitrogen availabilities, the biomass densities of the aboveground and belowground plants can reach higher levels with the increase in light intensity. The range of parameter K for the survival of herbivores expands with the increase in total nitrogen availability N . It is concluded that, when the light intensity and nitrogen availability are both at high levels, the herbaceous plant will grow well, which is in good agreement with the reality.

When the light intensity is fixed (Figs. 9, 10 and 11), the increase in nitrogen availability improves the herbaceous plant's quality and thus satisfies the need of lower N-demand herbivore first, and further becomes good for both herbivores. The higher N-demand herbivore will occupy more nutrient resources and the amount of the lower N-demand herbivore will decline. It suggests again that, the light and nitrogen availability at intermediate levels facilitate the coexistence of herbivores. Different from the scenarios in Figs. 6, 7 and 8, when the nitrogen availability is high, the higher N-demand herbivore keeps at a stable state or at a periodic oscillation instead of going perish (e.g., $0.028 < N < 0.08$ in Fig. 9, $0.044 < N < 0.08$ in Fig. 10 and $0.06 < N < 0.08$ in Fig. 11). It implies that high nitrogen availability can lead to the domination of the higher N-demand herbivore in the competition. Note that, when the light intensity is at an intermediate level, extremely high nitrogen may lead to the extinction of herbaceous plant (see $0.071 < N < 0.08$ in Fig. 11), which suggests that the nutrient enrichment can reduce the species diversity.

Figure 12 represents the bifurcation diagrams of system (4) and elucidates the dynamic evolution of (4) with K increasing from 0 to 3 mg C/m^2 . The values of parameters are the same as those in system (8). Note that system (4) shows simple oscillatory dynamics, the densities of the aboveground and belowground plants as

well as the higher N-demand herbivore increase as light intensity increases, while the density of lower N-demand herbivore keeps decreasing (see $0.65 < K < 3$ in Fig. 12). In particular, the higher N-demand herbivore is always dominant. However, the stoichiometric model (8) shows something quite different. With the enhancement of the light intensity, the higher N-demand herbivore density declines while the lower N-demand herbivore starts to survive and its density keeps increasing. In addition, when the light intensity is at high level, the densities of plants tend to a stable state rather than continuously increasing due to the limitation of nitrogen availability. It is distinct that the two herbivores in system (8) may perish when the light intensity is extremely high, which is more reasonable and realistic.

In summary, we reach the following conclusions:

- First, the stoichiometric competition model, which incorporates the aboveground–belowground interactions, provides a more realistic illustration of the competition of two herbivores on one herbaceous plant in a grassland ecosystems.
- Second, when the food quality of herbaceous plant is good, the new model admits similar dynamics to that of the traditional one. Whereas, when the food quality of herbaceous plant is poor, the stoichiometric competition model provides more realistic and reasonable mechanisms for the deterministic extinction of two herbivores.
- Third, the aboveground and belowground interaction and stoichiometry within or among species can considerably change the existence states of herbaceous plant and herbivores.
- Finally, the moderate levels of light intensity and nitrogen availability contribute to species diversity (i.e., it guarantees the coexistence of all populations), while extremely high nitrogen may lead to the extinction of the herbaceous plant due to the excessive predation of herbivores. This finding answers the question why nitrogen enrichment results in reduced species diversity.

In addition, plant biologists often discuss the root-to-shoot ratio of plants (Aikio and Markkola 2002; Grechi et al. 2007), which is super interesting to investigate. The model (8), which characterizes the above- and belowground parts of the plant separately and allows varying stoichiometric ratios, can also be applied to investigate the biomass ratio between these two plant parts. Figure 13 depicts that the predicted root-to-shoot ratio varies under different nitrogen and light gradients. In particular, the numerical result also indicates that the root-to-shoot ratio of the plant tends to a cyclic state with the increasing of both nitrogen input and light intensity. Moreover, the values of B/A when $N = 0.02$, $K \in (0.2, 0.8)$ ($B/A > 2.5$) are always greater than that when $K = 0.2$, $N \in (0.02, 0.08)$ ($B/A < 2.4$). This implies that plants grown under low nitrogen have a higher root-to-shoot ratio than plants grown under low light. The result is consistent with the experimental finding in Aikio and Markkola (2002) that the plant will regulate the biomass of shoot when light is limited and will regulate the biomass of root when nitrogen is restricted.

In this work, it is assumed that the N:C ratio of the belowground herbaceous plant is constant (called the “strict homeostasis” assumption). The ideas for relaxing the “strict homeostasis” assumption have been presented in some recent studies (Wang et al. 2012, 2018). However, in natural setting, the belowground can also store nutrient

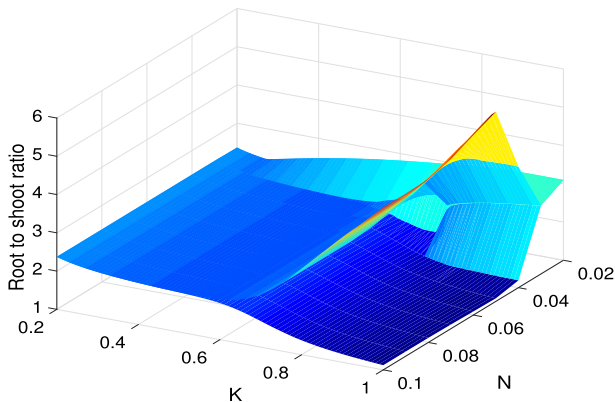


Fig. 13 (Colour figure online) Bifurcation surfaces for the root-to-shoot ratio with the light intensity K and the nitrogen availability N being the bifurcation parameters. Other parameters are defined in Table 1

and change its N:C ratio. Therefore, it is reasonable and important to understand the dynamics of stoichiometric competition model with the belowground having a variable N:C ratio. In ecology, it has been long recognized that the temporal fluctuations in the physical environment are a major driver of population fluctuations. The light intensity and nitrogen availability as well as other abiotic or biotic factors are usually subject to seasonality and vary greatly over time. Whence, the competition process will be more complicated and challenging to study with seasonal forcing. The comprehensive consideration of the above issues may shed new insights on the studied topic. We leave these as future work and open questions.

Acknowledgements The research was partially supported by National Natural Science Foundation of People's Republic of China (Nos. 11671072, 11271065).

References

- Aikio S, Markkola AM (2002) Optimality and phenotypic plasticity of shoot-to-root ratio under variable light and nutrient availabilities. *Evol Ecol* 16(1):67–76
- Ares J, Singh JS (1974) A model of the root biomass dynamics of a shortgrass prairie dominated by blue grama (*Bouteloua gracilis*). *J Appl Ecol* 11(2):727–728
- Armstrong RA, McGehee R (1980) Competitive exclusion. *Am Nat* 115:151–170
- Andersen T (1997) Grazers as sources and sinks for nutrients: conclusions, limitations, and speculations. In: *Pelagic nutrient cycles*, vol 129. Springer, Berlin, pp 207–213
- Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431:181–184
- Bardgett RD, Wardle DA (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–2268
- Bouldin DR (1961) Mathematical description of diffusion process in the soil-plant system. *Soil Sci Soc Am J* 25:476–480
- Castle SG, Neff JG (2009) Plant response to nutrient availability across variable bedrock geologies. *Ecosystems* 12:101–113
- Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002) The interaction between predation and competition: a review and synthesis. *Ecol Lett* 5:302–315

- Chen M, Fan M, Kuang Y (2017) Global dynamics in a stoichiometric food chain model with two limiting nutrients. *Math Biosci* 289:9–19
- Deng B, Loladze I (2007) Competitive coexistence in stoichiometric chaos. *Chaos* 17(3):113–136
- Grechi I, Vivin Ph, Hilbert G, Milin S, Robert T, Gaudillère JP (2007) Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. *Environ Exp Bot* 59:139–149
- Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos* 89:428–439
- Hessen DO, Agren GI, Anderson TR, Elser JJ, de Ruiter PC (2004) Carbon sequestration in ecosystems: the role of stoichiometry. *Ecology* 85:1179–1192
- Jørgensen SE, Bendoricchio G (2001) Fundamentals of ecological modelling. Elsevier, Amsterdam
- Koojiman S (1995) The stoichiometry of animal energetics. *J Theor Biol* 177(2):139–149
- Kuang Y, Fagan WF, Loladze I (2003) Biodiversity, habitat area, resource growth rate and interference competition. *Bull Math Biol* 65:497–518
- Lan ZC, Bai YF (2012) Testing mechanisms of N-enrichment-induced species loss in a semiarid Inner Mongolia grassland: critical thresholds and implications for long-term ecosystem responses. *Philos Trans R Soc B* 367:3125–3134
- LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89:371–379
- Levin SA (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *Am Nat* 104:413–423
- Li CJ (2008) Advanced nutritional botany Beijing. Chinese Agricultural University Press, Beijing
- Liu BW, Jiang ZG (2004) Dietary overlap between Przewalski's gazelle and domestic sheep in the Qinghai lake region and implication for rangeland management. *J Wildlife Manage* 68(2):241–246
- Liu GH, Gui H, Wang GJ, Wang SP, Zang YJ, Shao XQ, Wan XR, Hao SG (2013) Diet composition and trophic niche of main herbivores in the typical Steppe of Inner Mongolia. *Acta Agrestia Sinica* 21(3):439–445 (in Chinese)
- Loladze I, Kuang Y, Elser JJ (2000) Stoichiometry in producer-grazer systems: linking energy flow with element cycling. *Bull Math Biol* 62:1137–1162
- Loladze I, Kuang Y, Elser J (2004) Competition and stoichiometry: coexistence of two predators on one prey. *Theor Popul Biol* 65(1):1–15
- Masters GJ, Brown VK, Gange AC (1993) Plant mediated interactions between aboveground and below-ground insect herbivores. *Oikos* 66:148–151
- Manzoni S, Jackson RB, Troymow JA, Porporato A (2008) The global stoichiometry of litter nitrogen mineralization. *Science* 321:684–686
- Mazumaer M, Rahman A, Kumagai H (2006) Analyses of factors affecting dry matter intake of lactating dairy cows. *Anim Sci J* 77(1):53–62
- Miller CR, Kuang Y, Fagan WF, Elser JJ (2004) Modeling and analysis of stoichiometric two-patch consumer-resource systems. *Math Biosci* 189(2):153–184
- Muller EB, Nisbet RM, Koojiman SALM, Elser JJ, McCauley E (2001) Stoichiometric food quality and herbivore dynamics. *Ecol Lett* 4:519–529
- Mylius SD, Klumpers K, de Roos AM, Persson L (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am Nat* 158(3):259–276
- Neff JC, Reynolds R, Sanford RL, Fernandez D, Lamothe P (2006) Controls of bedrock geochemistry on soil and plant nutrients in southern Utah. *Ecosyst* 9:879–889
- Nelson WA, McCauley E, Wrona FJ (2001) Multiple dynamics in a single predator-prey system: experimental effects of food quality. *Proc R Soc Lond* 268:1223–1230
- Niklas KJ (2005) Modelling below-and above-ground biomass for non-woody and woody plants. *Ann Botlondon* 95(2):315–321
- Peace A, Wang H (2019) Compensatory foraging in stoichiometric producer-grazer models. *Bull Math Biol* 81(12):4932–4950
- Peace A, Wang H, Kuang Y (2014) Dynamics of a producer-grazer model incorporating the effects of excess food nutrient content on grazer's growth. *Bull Math Biol* 76(9):2175–2197
- Peter C, Kuang JJ (2008) The interaction between predation and competition. *Nature* 456(7219):235–238
- Ping XY, Jia BR, Yuan WP (2007) Dynamic simulation of the biomass of *Ichinensis*. *J Appl Ecol* 18(12):2699–2704 (in Chinese)

- Richards SA, Nisbet RM, Wilson WG, Possingham HP (2000) Grazers and diggers: exploitation competition and coexistence among foragers with different feeding strategies on a single resource. *Am Nat* 155:266–279
- Song L, Ba XM, Liu XJ, Zhang FS (2012) Impact of nitrogen addition on plant community in a semi-arid temperate steppe in China. *J Arid Land* 4:3–10
- Sterner RW, Clasen J, Lampert W, Weisse T (1998) Carbon: phosphorus stoichiometry and food chain production. *Ecol Lett* 1:146–150
- Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to biosphere. Princeton University Press, Princeton, pp 1–15
- Sterner RW, Elser JJ (2008) Encyclopedia of ecology II ecological stoichiometry: overview. *Encycl Ecol* 2008:1101–1116
- Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL, Milchunas DG, Pennings S (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc Natl Acad Sci USA* 102:4387–4392
- Turchin P (2003) Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton
- Urabe J, Elser JJ, Kyle M, Yoshida T, Sekino T, Kawabata Z (2002) Herbivorous animals can mitigate unfavourable ratios of energy and material supplies by enhancing nutrient recycling. *Ecol Lett* 5:177–185
- Van der Wal R, Egas M, Van der Veen A, Bakker JE (2000) Vectors of resource competition and herbivory on plant performance along a natural productivity gradient. *J Ecol* 88:317–330
- Van der Putten WH, Vet LEM, Harvey JA, Wäkers FL (2001) Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists trends. *Ecol Evol* 16:547–554
- Van der Putten WH, Bardgett RD, De Ruiter PC, Hol WHG, Meyer KM, Bezemer TM, Bradford MA, Christense S, Eppinga MB, Fukami T, Hemerik L, Molofsky J, Schädler M, Scherber C, Strauss SY, Vos M, Wardle DA (2009) Empirical and theoretical challenges in aboveground–belowground ecology. *Oecologia* 161(1):1–14
- Wang H, Kuang Y, Loladze I (2008) Dynamics of a mechanically derived stoichiometric producer–grazer model. *J Biol Dyn* 2(3):286–296
- Wang H, Dunning K, Elser JJ, Kuang Y (2009) *Daphnia* species invasion, competitive exclusion, and chaotic coexistence. *DCDS-B* 12(2):481–493
- Wang H (2010) Revisit brown lemming population cycles in Alaska: examination of stoichiometry. *IJNAM-B* 2010 1(1):93–108
- Wang H, Sterner RW, Elser JJ (2012) On the “strict homeostasis” assumption in ecological stoichiometry. *Ecol Model* 243:81–88
- Wang H, Lu Z, Raghavan A (2018) Weak dynamical threshold for the “strict homeostasis” assumption in ecological stoichiometry. *Ecol Model* 384:233–240
- Xie T, Yang X, Li X, Wang H (2016) Complete global and bifurcation analysis of a stoichiometric predator–prey model. *J Dyn Differ Equ* 30(2):447–472
- Zhang Y, Li C, Wang M (2019) Linkages of C:N:P stoichiometry between soil and leaf and their response to climatic factors along altitudinal gradients. *J Soil Sediment* 19(4):1820–1829
- Zhou XR, Rong XM, Fan M, Nescolarde-Selva JA (2018) Stoichiometric modeling of aboveground–belowground interaction of herbaceous plant. *Math Biosci Eng* 16(1):25–55

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