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Modelling tree-grass coexistence in water-limited ecosystems

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ABSTRACT

Tree-grass coexistence is commonly observed in arid and semi-arid ecosystems. Many of these ecosystems are undergoing a shift from grassland to tree dominance or the opposite. Therefore, exploring the mechanism of tree-grass coexistence and studying how ecosystems respond to environmental change are critical to understanding such shift. We construct a tree-grass-water model by considering the Walter's two layer hypothesis, i.e., the grass species only access to the shallow soil water, while the tree can uptake both the shallow and deep soil water. Results show that the tree-grass coexistence region increases with increasing their niche separation. Hence, the vertical niche separation between trees and grass with respect to limiting water resources might be one of mechanisms for tree-grass coexistence. Besides, both tree and grass display positive responses to precipitation, but surprisingly, there exists a catastrophe that the mean vegetation density first rapidly increases, but then quickly decreases as precipitation increases in the tree-grass-water model with infiltration feedback. Most likely, this catastrophe is due primarily to the periodical fluctuation of vegetation density and water caused by its intrinsic infiltration feedback. Overall, our study provides new insights into the dynamics of tree-grass in arid and semi-arid ecosystems.

Keywords: dynamic model; niche separation; periodic fluctuation; Walter's two layer hypothesis

1. Introduction

Water-limited ecosystems (so-called drylands), including arid, semiarid and sub-humid regions, occupy approximately 50% of the global land area (Parsons and Abrahams, 1994). However, these ecosystems are undergoing a transition from grasslands dominance to tree dominance or the opposite (Briggs et al., 2005; Ratajczak et al., 2012; Ratajczak et al., 2014; Sala and Maestre, 2014). The state-transition can affect community pattern, ecosystem functioning and long-term biodiversity maintenance (Ward, 2005; Knapp et al., 2008; Eldridge et al., 2011; Ratajczak et al., 2012). Consequently, understanding the shift between grassland and woodland can provide theoretical support for biodiversity conservation and management.

Exploring the mechanism of tree-grass coexistence could improve our understanding of the aforementioned shift. Many studies have conducted to identify the general mechanism of tree-grass coexistence in both arid and semi-arid ecosystems (Higgins et al., 2000; Jeltsch et al., 2000; Sankaran et al., 2004; Baudena and Rietkerk, 2013; February et al., 2013; Holdo, 2013; Priyadarshini et al., 2015). The root niche separation model proposed by Walter (1971) is a classic one to explain the mechanism of tree-grass coexistence (Cable, 1969; Knoop and Walker, 1985; Kambatuku et al., 2013), which assuming that trees and grasses display differential access to the limited resources (i.e., water) because of their spatial difference in rooting distributions. For instance, trees and grasses can coexist steadily when woody and herbaceous niches do not overlap, trees are able to persist because of exclusive access to deeper water. However, it is also disputed that the lack of obvious difference in maximum rooting depth between these two functional groups has caused this hypothesis to fall out of favor (Lawson et al., 1968; Higgins et al., 2000). For example, the roots of the existing tree and grass were concentrated in the upper 30 cm in Ghana at a mean annual precipitation of 1,000 mm (Lawson et al., 1968). Until now, the general contribution of the Walter's two-layer model to the coexistence of grass and tree is still vaguely understood.

Numerous factors (e.g., climate change, herbivory, human induced landscape

fragmentation, disease, and harvest) are underlying driving forces of the increase in tree and/or grass abundance (Brown and Archer, 1999; Beschta, 2003; Briggs et al., 2005; Sankaran et al., 2005; Briggs et al., 2007; Kjelland et al., 2007; Knapp et al., 2008; Van Auken, 2009; Ripple and Beschta, 2011; Staver and Levin, 2012; Kukavskaya et al., 2013; Dantas et al., 2016; Afanador et al., 2016). Among these factors, precipitation is the critical environmental factor that can affect vegetation biomass in water-limited ecosystems (Sankaran et al., 2005; Hirota et al., 2011; Kulmatiski and Beard, 2013). Sankaran et al. (2005) showed that the arid and semi-arid savannas can be considered as stable ecosystems when the mean annual precipitation (MAP) is less than 650mm, in those ecosystems water constrains woody cover and permits grass species to coexist. In contrast, when MAP is above 650mm, savannas are ‘unstable’ systems, where MAP is sufficient for woody canopy closure, and disturbances (fire, herbivory) are required for the coexistence of trees and grass. In these arid and semi-arid areas, where water is a limited resource for plant growth and the main resource that plants compete for, future climate change in precipitation should be considered in the distribution and dynamics of tree-grass.

Many experiments have studied how ecosystems shifted under precipitation change (Fang et al., 2001; Knapp and Smith, 2001; Weltzin et al., 2003; Bai et al., 2008; Carlyle et al., 2014). It has been generally recognized that the aboveground net primary production (ANPP) was strongly correlated with annual precipitation (AP) at a continental scale. However, the relationship between interannual variability in ANPP and in AP remains debated (e.g., Knapp and Smith, 2001; Fang et al., 2001; Yang et al., 2008). Knapp and Smith (2001) revealed that interannual variability in ANPP was not related to variability in AP with analyzing the data from 11 Long-Term Ecological Research sites across North America. However, using a remote-sensing approach, Fang et al. (2001) found an opposite trend by studying the relationship between interannual variability in net primary production (NPP) and precipitation across China. Yang et al. (2008) also demonstrated a positive relationship between variation in ANPP and AP by reanalyzing the long-term data from 118 grassland sites across the world. All these results show that most ecosystems

are sensitive to precipitation change. However, the quantitatively potential consequences of these sensitivities are still largely unknown.

Therefore, we are aiming to explore the underlying mechanism of Walter's two-layer hypothesis on the tree-grass coexistence in the water-limited ecosystems without considering herbivory, disease, or harvest, and to explain the conflicting relationships between interannual variability in ANPP and AP. Specially, (1) a tree-grass-water model is constructed to explore the effect of different vertical roots overlap between grasses and trees (no overlap, partial overlap, full overlap) on their coexistence. This model includes the feedback between plant and surface water (as seen in HilleRisLambers et al., 2001; Gilad et al., 2007a; Baudena and Rietkerk, 2013) and the Walter's two-layer hypothesis. (2) The responses of vegetation (grass and/or tree) to precipitation in the water-controlled systems are explored by simulating the dynamics of plant-water model under different parameters of precipitation.

2. Model

2.1 The tree-grass-water model

Since rooting depths generally increase with the plant growth forms as their size and life span increase, so the values are greatest in trees and smallest in annual grasses (Schenk et al. 2002). Grasses with their shallow root system are proposed to use shallow soil water, while trees are assumed to uptake both shallow and deep soil water (i.e., the Walter's two-layer hypothesis). In water-limited ecosystems, both grasses and trees compete for this limited resource (i.e. water). The plant densities of both tree and grass are assumed to linearly increase with increasing the content of obtained water (e.g., Baudena and Rietkerk, 2013). At the same time, plant density can affect water distribution, e.g., grass density is a critical factor to determine the rate and amount of infiltration (HilleRisLambers et al., 2001; Gilad et al., 2007a; Baudena and Rietkerk, 2013). The higher grass density leads to more water infiltrating into the soil from the surface profile. Accordingly, the tree-grass-water model can be described as follows:

$$\frac{dB_g}{dt} = c_g \cdot \gamma_1^g \cdot W_1 \cdot B_g - m_g \cdot B_g, \quad (1.1)$$

$$\frac{dB_t}{dt} = c_t \cdot (\gamma_1^t \cdot W_1 + \gamma_2^t \cdot W_2) \cdot B_t - m_t \cdot B_t, \quad (1.2)$$

$$\frac{dW_{sf}}{dt} = P_i - \alpha_{sf} \cdot \frac{B_g + k \cdot w_0}{B_g + k} \cdot W_{sf}, \quad (1.3)$$

$$\frac{dW_1}{dt} = \alpha_{sf} \cdot \frac{B_g + k \cdot w_0}{B_g + k} \cdot W_{sf} - \alpha_1 \cdot W_1 - E_1 \cdot W_1 - (\gamma_1^t \cdot B_t + \gamma_1^g \cdot B_g) \cdot W_1, \quad (1.4)$$

$$\frac{dW_2}{dt} = \alpha_1 \cdot W_1 - E_2 \cdot W_2 - \gamma_2^t \cdot B_t \cdot W_2. \quad (1.5)$$

All variables and parameters are interpreted in Table 1. Equation (1.1) represents the dynamics of grass density (B_g), which increases linearly with the soil water consumption ($\gamma_1^g \cdot W_1$) from the shallow soil $c_g \cdot \gamma_1^g \cdot W_1 \cdot B_g$, and grass species mortality is also assumed to be linear ($m_g \cdot B_g$).

Table 1 List of variables and parameters and their interpretations

Variables and Parameters	Descriptions (units and values)
B_t	Tree density (g m ⁻²)
B_g	Grass density (g m ⁻²)
W_{sf}	Surface water (mm)
W_1	Shallow soil water (mm)
W_2	Deep soil water (mm)
c_g	Conversion of water uptake into grass growth of grass (10 g mm ⁻¹ m ⁻²)
γ_1^g	Grass maximum specific water uptake from shallow root layer (0.05 mm g ⁻¹ m ² d ⁻¹)
m_g	Mortality of grass (0.3 d ⁻¹)
c_t	Conversion of water uptake into tree growth of tree (7 g mm ⁻¹ m ⁻²)
γ_1^t	Tree maximum specific water uptake from shallow root layer (0.03, 0.05 mm g ⁻¹ m ² d ⁻¹)
γ_2^t	Tree maximum specific water uptake from deep root layer (0.03, 0.05 mm g ⁻¹ m ² d ⁻¹)
m_t	Mortality of tree (0.3 d ⁻¹)
P_i	Precipitation per day (0.1-0.65 mm d ⁻¹)
α_{sf}	Proportion of surface water available for infiltration (0.3 d ⁻¹)
k	Rate at which infiltration increases with specific plant density (5 g m ⁻²)
w_0	Infiltration rate in the surface layer without grass (0.1, 0.2)
α_1	Infiltration rate in the shallow soil water layer (0.1, 0.2 d ⁻¹)
E_1	Shallow soil water loss due to evaporation or drainage (0.1 d ⁻¹)
E_2	Deep soil water loss due to evaporation or drainage (0.15 d ⁻¹)

Similarly, equation (1.2) represents the dynamics of tree density (B_t), which is linearly related with increasing water consumption from both the shallow soil and the deep soil ($c_t \cdot (\gamma_1^t \cdot W_1 + \gamma_2^t \cdot W_2) \cdot B_t$). Tree density may decrease due to intrinsic mortality ($m_t \cdot B_t$).

Equation (1.3) expresses the dynamics of surface water content (W_{sf}), and rainfall and infiltration are the surface water input and output, respectively. Infiltration rate depends on the surface water content, grass density and soil characteristics, since there is a positive feedback between grass density and water (i.e., the presence of vegetation increasing infiltration capacity) (Greene, 1992; Thompson et al., 2010). Thus, the infiltration is defined as $\alpha_{sf} \cdot (B_g + k \cdot w_0) / (B_g + k) \cdot W_{sf}$ (HilleRisLambers et al., 2001; Gilad et al., 2007b; Pueyo et al., 2010).

Equation (1.4) shows the dynamics of shallow soil water (W_1), where infiltration from the surface is the water input from shallow soil ($\alpha_{sf} \cdot (B_g + k \cdot w_0) / (B_g + k) \cdot W_{sf}$), and the water from the shallow soil water decreases due to the infiltration into the deep layer soil ($\alpha_1 \cdot W_1$), evaporation ($E_1 \cdot W_1$) and plant's uptake ($\gamma_1^t \cdot B_t + \gamma_1^g \cdot B_g$) $\cdot W_1$).

In equation (1.5), it reveals the dynamics of deep soil water (W_2), in which infiltration is the input. Evaporation and the loss of deep soil water by drainage is a linear function of water availability in the deep layer soil ($E_2 \cdot W_2$). Besides, trees can exploit the deep soil water, and the water uptake rate increases with the increasing of tree density ($\gamma_2^t \cdot B_t \cdot W_2$).

2.2 The tree-water model

The tree-water model is constructed based on the following two assumptions: (1) trees are able to extract the deep soil water as well as the shallow soil water. (2) There is no positive infiltration feedback between trees and surface water. Thus, trees absorb water from both layers, and the infiltration rate of surface water is the minimum water infiltration in the absence of grasses. According to the above tree-grass-water model, tree-water model can be expressed as follows:

$$\frac{dB_t}{dt} = c_t \cdot (\gamma_1^t \cdot W_1 + \gamma_2^t \cdot W_2) \cdot B_t - m_t \cdot B_t, \quad (2.1)$$

$$\frac{dW_{sf}}{dt} = P_i - \alpha_{sf} \cdot w_0 \cdot W_{sf}, \quad (2.2)$$

$$\frac{dW_1}{dt} = \alpha_{sf} \cdot w_0 \cdot W_{sf} - \alpha_1 \cdot W_1 - E_1 \cdot W_1 - \gamma_1^t \cdot B_t \cdot W_1, \quad (2.3)$$

$$\frac{dW_2}{dt} = \alpha_1 \cdot W_1 - E_2 \cdot W_2 - \gamma_2^t \cdot B_t \cdot W_2. \quad (2.4)$$

2.3 The grass-water model

Similarly, the grass-water model is built by assuming that: (1) there is a positive feedback between grass density and infiltration capacity of surface water. (2) Grass root can only absorb water from the shallow soil. Similar with the above tree-grass-water model, the grass-water model can be showed as follows:

$$\frac{dB_g}{dt} = c_g \cdot \gamma_1^g \cdot W_1 \cdot B_g - m_g \cdot B_g, \quad (3.1)$$

$$\frac{dW_{sf}}{dt} = P_i - \alpha_{sf} \cdot \frac{B_g + k \cdot w_0}{B_g + k} \cdot W_{sf}, \quad (3.2)$$

$$\frac{dW_1}{dt} = \alpha_{sf} \cdot \frac{B_g + k \cdot w_0}{B_g + k} \cdot W_{sf} - \alpha_1 \cdot W_1 - E_1 \cdot W_1 - \gamma_1^g \cdot B_g \cdot W_1, \quad (3.3)$$

$$\frac{dW_2}{dt} = \alpha_1 \cdot W_1 - E_2 \cdot W_2. \quad (3.4)$$

3. Results

3.1 Mathematical analysis

We make a mathematical analysis of the above three models. The results are summarized in Table 2 and more details can be found in Appendix A. For simplicity, the expressions of B_0 , B_1 , B_2 , C_0 , C_1 , C_2 , C_3 , C_4 are shown in Appendix A.

Table 2 Stable equilibria analysis of the tree-water model, the grass-water model and the tree-grass-water model

Equilibria	Stable conditions
Tree-water model	
Bare soil x_T^1	$(\gamma_1^t + \gamma_2^t \cdot \frac{\alpha_1}{E_2}) \cdot \frac{c_t \cdot P_i}{\alpha_1 + E_1} < m_t$
Woodland x_T^2	$(\gamma_1^t + \gamma_2^t \cdot \frac{\alpha_1}{E_2}) \cdot \frac{c_t \cdot P_i}{\alpha_1 + E_1} > m_t$
Grass-water model	
Bare soil x_G^1	$\frac{c_g \cdot \gamma_1^g \cdot P_i}{\alpha_1 + E_1} < m_g$
Grassland x_G^2	$\frac{c_g \cdot \gamma_1^g \cdot P_i}{\alpha_1 + E_1} > m_g$ and $B_2 \cdot B_1 - B_0 > 0$
Tree-grass-water model	
Bare soil x_C^1	$\frac{c_g \cdot \gamma_1^g \cdot P_i}{\alpha_1 + E_1} < m_g$ and $(\gamma_1^t + \gamma_2^t \cdot \frac{\alpha_1}{E_2}) \cdot \frac{c_t \cdot P_i}{\alpha_1 + E_1} < m_t$
Woodland x_C^2	$(\gamma_1^t + \gamma_2^t \cdot \frac{\alpha_1}{E_2}) \cdot \frac{c_t \cdot P_i}{\alpha_1 + E_1} > m_t$ and $\frac{c_g \cdot \gamma_1^g \cdot P_i}{\alpha_1 + E_1 + \gamma_1^t \cdot B_t^2} < m_g$

$$\begin{array}{ll}
\text{Grassland } x_C^3 & \frac{c_g \gamma_1^g \cdot P_i}{\alpha_1 + E_1} > m_g \text{ and } \frac{c_g \gamma_1^g}{m_g} > \frac{c_t}{m_t} \cdot \left(\gamma_1^t + \gamma_2^t \cdot \frac{\alpha_1}{E_2} \right) \text{ and } B_2 \cdot B_1 - B_0 > 0 \\
\text{Coexistence } x_C^4 & \frac{c_t}{m_t} \cdot \left(\gamma_1^t + \gamma_2^t \cdot \frac{\alpha_1}{E_2} \right) > \frac{c_g \gamma_1^g}{m_g} > \frac{c_t \gamma_1^t}{m_t} \text{ and } \frac{c_g \gamma_1^g}{m_g} > \frac{\alpha_1 + E_1 + \gamma_1^t \cdot B_t^4}{P_i} \text{ and } \frac{c_g \gamma_1^g}{m_g} > \\
& \frac{\alpha_1 + E_1 + \gamma_1^t \cdot B_t^2}{P_i} \text{ and } C_1 > 0, C_3 C_2 > C_4 C_1 \text{ and } C_3 C_2 C_1 > C_4 C_1^2 + C_0 C_3^2
\end{array}$$

The bare soil x_T^1 in the tree-water model has the stable state if $(\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot c_t \cdot P_i/(\alpha_1 + E_1) < m_t$, while the bare state x_G^1 in the grass-water model is stable if $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) < m_g$ (Table 2). When $(\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot c_t \cdot P_i/(\alpha_1 + E_1) < m_t$ and $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) < m_g$, then both the grass and the tree will go extinct in the tree-grass-water model. Both abiotic (e.g., P_i , α_1 , E_1 etc.) and biotic factors (e.g., c_t , c_g , γ_1^g etc.) determine species persistence. Plants with larger conversion of water uptake into biomass, maximum specific water uptake from root or small mortality can tolerate harsher environment, e.g., less precipitation. Note that Table 2 does not include all the possible results in the grass-water model and tree-grass-water model. For example, both x_G^1 and x_G^2 are unstable when $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) > m_g$ and $B_2 \cdot B_1 - B_0 < 0$ in the grass-water model. There is a stable periodic solution when the parameters do not satisfy the stable conditions listed in Table 2 with the following numerical simulations.

3.2 Effect of vertical root overlap on tree-grass coexistence

Effect of vertical root overlap (i.e., full overlap, partial overlap and no overlap) between tree plants and grass on competitive outcomes is explored through conducting the theoretical analysis of tree-grass-water model. In Fig. 1, from left to right, it displays the competitive outcome when the root niches for both the grass and the tree are fully overlapped ($\gamma_2^t = 0$), partially overlapped ($\gamma_1^t \neq 0, \gamma_2^t \neq 0$), and not overlapped ($\gamma_1^t = 0$), respectively. In the case with full niche overlap, the competitive outcome is determined by their difference in the increasing of plant density/decrease of plant density (i.e., $c \cdot \gamma/m$, where c is the conversion of water uptake into plant growth, γ is the maximum specific water uptake from soil and m

is plant density loss due to mortality) when both trees and grasses can survive without competition. If $c_t \cdot \gamma_1^t / m_t > c_g \cdot \gamma_1^g / m_g$, trees outcompete grasses, whereas grasses outcompete trees if $c_t \cdot \gamma_1^t / m_t < c_g \cdot \gamma_1^g / m_g$. Furthermore, grass and tree can coexist if $c_t \cdot \gamma_1^t / m_t = c_g \cdot \gamma_1^g / m_g$. When there is a partial vertical root overlap between grass and tree, the competitive outcome can be either tree outcompeting grass, grass outcompeting tree or tree-grass coexistence if both grasses and trees can survive without competition (i.e., $c_g \cdot \gamma_1^g / m_g > (\alpha_1 + E_1) / P_i$ and $(c_t \cdot \gamma_1^t + c_t \cdot \gamma_2^t \cdot \alpha_1 / E_2) / m_t > (\alpha_1 + E_1) / P_i$). If the difference in $c \cdot \gamma / m$ between grass and tree is relatively small, trees and grasses can coexist since they compete both directly with the water from the same layer and indirectly with the water from the different layers. When there is no vertical root overlap between grasses and trees, they can coexist with a relatively large difference in $c \cdot \gamma / m$. The condition of coexistence (in terms of the parameters) becomes larger as the niche difference increases.

Fig. 1. The stable state in the parameter space of the tree-grass-water model. γ_i^j means tree (i.e., $j = t$) or grass (i.e., $j = g$) maximum specific water uptake from shallow root layer (i.e., $i = 1$) or deep root layer (i.e., $i = 2$). P_i , α_1 , E_1 and E_2 represent precipitation, infiltration rate in the shallow soil water layer, shallow soil water loss rate, and deep soil water loss rate, respectively.

3.3 Numerical Simulations

We simulate the above system of ordinary differential equations using Matlab Ode45

to demonstrate the impact of precipitation and infiltration feedback on vegetation and water dynamics.

First, we test how precipitation affects the dynamics of tree-water system at steady state (Fig. 2). Fig. 2a shows the tree density (average, maximum and minimum) at steady state along a precipitation gradient (Fig. 2a). Examples of the dynamics of the tree-water system with different P_i ($=0.05, 0.35, 0.65$) are given in Fig. 2b-d, respectively. These dynamical curves suggest that the ordinary differential equations of the tree-water model achieve the steady state after $t > 100$, and tree density and water content are constant. Besides, curves of tree density (average, maximum and minimum) are overlapped (Fig. 2a). These results confirm the theoretical analysis. As expected, there is a threshold of precipitation ($P_i = P_0 = 1.08$), below which tree species go extinct as there is little precipitation. Otherwise, tree species can survive once precipitation exceeds this threshold, and the average tree density increases as precipitation increases.

Fig. 2. Dynamics of tree-water model. (a) Curves of the average, maximum and minimum tree density at steady state along a precipitation (P_i) gradient are overlapped. The red rectangle ($P_i=1.08$) is the precipitation threshold of tree persistence. (b, c, d) The dynamics of tree density in the tree-water model at $P_i=0.05$, $P_i=0.35$ and $P_i=0.65$ (i.e., the value of blue dots in the curve), respectively. Other parameters: infiltration ratio of surface water $\alpha_{sf} = 0.3$, infiltration rate of shallow soil water $a_1 = 0.2$, shallow soil water loss $E_1 = 0.1$, deep soil water loss $E_2 =$

0.15, infiltration rate in the surface layer without grass $w_0 = 0.3$, conversion of water uptake into tree growth of tree $c_t = 7$, mortality of tree $m_t = 0.3$, tree maximum specific water uptake from shallow root layer $\gamma_1^t = 0.05$, tree maximum specific water uptake from deep root layer $\gamma_2^t = 0.05$.

Then we explore the effect of precipitation interacting with infiltration feedback on the dynamics of grass-water system (Fig. 3). Likewise, the average, maximum and minimum grass density along a rainfall gradient under different soil property (i.e., infiltration rate in the surface layer without grass $w_0=0.2$ or 0.1 , due to different soil property lead to different values of w_0) at steady state are plotted (Fig. 3a,b), and examples with different P_i ($=0.1, 0.22, 0.35$) are shown in Fig. 3c-h, respectively. When $w_0=0.2$, there is one threshold (P_0) (Fig. 3a). Grass species become extinct as $P_i < P_0$. Once $P_i > P_0$, increasing precipitation leads to an increment of the mean grass density. Examples of the dynamical curves suggest that the ordinary differential equations of grass-water model can reach the steady state, and a constant grass density and water content is the final state (Fig. 3c-e). In contrast, when $w_0=0.1$, there are two thresholds (P_1, P_2) (Fig. 3.b). One is the persistent threshold, i.e., no grass exists as $P_i < P_1$ (Fig. 3f). The other one P_2 divides the parameter region into two parts: one is the stable periodic solution (Fig. 3g), and the other is the asymptotical stable state (Fig. 3h). As expected, grass density shows a gradual increase with increasing precipitation when $P_i > P_2$. Yet, the average grass density increases firstly but then decreases slightly with increasing precipitation under the condition of $P_1 < P_i < P_2$. Fig. 3g gives an example in this region that the grass density fluctuates periodically.

Fig. 3. System dynamics of the grass-water model. (a) The mean, maximum and minimum grass density at steady state along a precipitation (P_i) gradient when infiltration rate in the surface layer without grass (w_0) = 0.2. Curves of the average, maximum and minimum grass density at steady state along P_i gradient are overlapped. (b) The mean, maximum and minimum grass density at steady state along a precipitation (P_i) gradient when w_0 = 0.1. The green dot dash line, cyan dash line and black line depict the maximum, minimum and average values of grass density during the periodic fluctuation, respectively. Graph (c, d, e, f, g, h): The dynamics of grass density in the grass-water model with different w_0 (=0.2. or 0.1) and different P_i (=0.1, 0.22 or 0.35). Other parameters: infiltration ratio of surface water $\alpha_{sf} = 0.3$, infiltration rate of shallow soil water $a_1 = 0.2$, shallow soil water loss $E_1 = 0.1$, deep soil water loss $E_2 = 0.15$, rate at which infiltration increases with specific plant density $k = 5$, conversion of water uptake into tree growth of grass $c_g = 10$, mortality of grass $m_g = 0.3$, grass maximum specific water uptake from shallow root layer $\gamma_1^g = 0.05$.

Finally, we explore the effect of precipitation (P_i) interacting with the conversion of water uptake to tree density (c_t) on the dynamics of the tree-grass-water system (Fig. 4), by varying P_i and c_t . At low value of P_i , both trees and grasses become extinct. When P_i further increases, grasses can persist at low c_t , while trees can survive at high c_t . At both high P_i and high c_t , both trees and grasses can co-occur. Besides, decreasing P_i can lead to the shifts of heterogeneous vegetation (mix of grassland and trees) towards homogeneous tree type, while increasing c_t leads to the shifts from heterogeneous vegetation to homogeneous tree type.

Fig. 4. Dynamics of the tree-grass-water system by varying both precipitation (P_i) and

conversion of water uptake to tree density (c_t). (a) Species coexistence. The blue, the cyan, the deep red, the yellow, the orange red and the green regions represent the bare soil state, homogeneous tree state, tree-grass coexistence with their density fluctuating, tree-grass coexistence, homogeneous grass state with its density fluctuating, and homogeneous grass state,; (b, c) The mean grass density and tree density with increasing both P_i and c_t . Other parameters: infiltration ratio of surface water $\alpha_{sf} = 0.1$, infiltration rate of shallow soil water $a_1 = 0.2$, shallow soil water loss $E_1 = 0.1$, deep soil water loss $E_2 = 0.15$, infiltration rate in the surface layer without grass $w_0 = 0.1$, rate at which infiltration increases with specific plant density $k = 5$, conversion of water uptake into tree growth of grass $c_g = 10$, mortality rate of grass $m_g = 0.3$, grass maximum specific water uptake from shallow root layer $\gamma_1^g = 0.05$, mortality of tree $m_t = 0.3$, tree maximum specific water uptake from shallow root layer $\gamma_1^t = 0.03$, tree maximum specific water uptake from deep root layer $\gamma_2^t = 0.03$.

Discussion

By modifying the integro-differential models (HilleRisLambers et al., 2001; Gilad et al., 2007a; Baudena and Rietkerk, 2013), a spatially implicit extended model, i.e. tree-grass-water model, is developed to study arid or semiarid ecosystems. With this model, almost all possible outcomes in the parameter space through mathematical analysis and numerical simulations are found. Comparing with the spatially explicit

integro-differential models (Von Hardenberg et al., 2001), our model reveals similar dynamical patterns along precipitation gradient, i.e. the general trend of average biomass increases with increasing of precipitation.

First, the competitive outcome between the grass and the tree is explored by taking all the three possibilities of their vertical root overlap: full overlap, partial overlap or no overlap in tree-grass-water ecosystems into account separately. We find that tree-grass coexistence region increases as the niche separation increases (Fig. 1), which theoretically confirm that the vertical niche separation between the tree and the grass with respect to limited water is one of the mechanisms for tree-grass coexistence. In other words, our modelling results support the Walter's two-layer hypothesis that the grass and the tree with differential access to soil water can coexist. And this is also in line with other empirical observations (Walker et al., 1981; Walker and Noy-Meir, 1982; Van Langevelde et al., 2003). For example, Ward et al. (2013) demonstrated that the Walter's two-layer hypothesis worked remarkably well within the scope of Walter's original intentions by surveying the global savanna literature for the records of the vertical niche partitioning by grasses and trees. According to Walter's original intentions, this rainfall-controlled tree-grass equilibrium worked in dry savannas but not in mesic and humid savannas which were controlled by biotic factors and disturbances. However, many studies conducted in savannas did not support the two-layer hypothesis (Scholes and Archer, 1997; Higgins et al., 2000; Jeltsch et al., 2000; Scheiter and Higgins, 2007; Kulmatiski et al., 2010). Most likely, studies that are against this two-layer hypothesis may be due primarily to the potential effects of the source of disturbance (e.g., fire, herbivory). Studies found that physical soil disturbance could be the primary limiting factors (Higgins et al., 2000; Sankaran et al., 2005; Higgins et al., 2010; Staver and Levin, 2012), i.e., water is not the only one limited factor in such systems. For example, Higgins et al. (2010) mentioned that fire can prevent grasses from exclusion and can induce a stable savanna state. More generally, we can conclude that the Walter's two-layer hypothesis would lead to the coexistence of the grass and the tree in water-limited ecosystems without disturbance, but may not do

so effectively in moist areas or areas with disturbances such as grazing and fire.

Then, the response of ecosystems to precipitation is simulated. Intuitively, the vegetation density decreases generally with decreasing precipitation as the precipitation exceeds the critical threshold, but it becomes a desert regime (no vegetation or vegetation density is very low) as the precipitation is less than the critical threshold (Figs. 2-4). Many theoretical or experimental studies had the similar finding. For example, through long-term and/or larger-scale observation, it has been generally recognized that the aboveground net primary production is strongly correlated with annual precipitation in water-limited ecosystems (Knapp and Smith, 2001; Meron et al., 2004). Surprisingly, there exists a catastrophe, i.e., the sudden change of the curve (Figs 3-4), in grass-water model and tree-grass-water model. In the region of catastrophe, the average vegetation density first increases rapidly but then decreases rapidly (Fig. 3b and Fig.4). The catastrophe is caused by the periodic fluctuation of vegetation density. Yet, the positive feedback between vegetation and surface water leads to the periodic fluctuation of vegetation density. Comparing these three models by assuming that grass affects the infiltration (i.e., the tree-water dynamics does not include the positive infiltration feedback, but there is a positive feedback in both the grass-water and tree-grass-water dynamic systems), we find that the density periodic fluctuation does not occur in the tree-water dynamic model (Fig. 2), but it may occur in the grass-water system or the tree-grass-water system (Fig. 3). Besides, the condition of the tree-grass-water dynamical system shows a periodic fluctuation, which is almost the same as the region in the single grass-water system (Fig. 4). Once positive infiltration feedback does not exist, there is no periodic fluctuation of vegetation density.

Vegetation increases or decreases due to its intrinsic stable fluctuation caused by the positive feedback between vegetation and the surface water in some ecosystems, rather than the effect of change in one or more abiotic or biotic factors, e.g., sheep grazing and anthropogenic disturbance, fire frequency and long-term climate change (Scholes and Archer, 1997; Coetzee et al., 2008; Liu et al., 2013; Lehmann et al., 2014). It suggests that studies of ecosystem responses to disturbance

or global change should consider the variability of plant biomass, which caused by
 its intrinsic fluctuation in a constant environment. Without taking this into account, it
 may lead to a vague understanding of the ecosystem or debate (Goward and Prince,
 1995; Fang et al., 2001; Knapp and Smith, 2001; Fang et al., 2005; Yang et al.,
 2008). For example, Knapp and Smith (2001) found that interannual variability in
 ANPP was not related to temporal variability in precipitation by summarizing ANPP
 data from 11 Long Term Ecological Research (LTER) sites across North America,
 with average sampling period of 12 years. However, using time-series remote
 sensing data over China, Fang et al. (2001) demonstrated that interannual variability
 in production increased with that in precipitation. In addition, Yang et al. (2008) also
 showed that variation in ANPP was positive related to AP by reanalyzing the
 long-term data from 118 grassland sites across the world. Our modelling results thus
 may provide a theoretical explanation for this debate. In the intrinsic stable
 fluctuation region (see Fig. 3b), although the precipitation is unchangeable, the
 interannual variability in plant biomass always exists. Then, it may exhibit different
 relationships between ANPP and precipitation, e.g., positive, negative or no
 relationship, when analyzing data from different area with different precipitations. In
 contrast, in the asymptotically stable region (see Fig. 2, 3a), larger precipitation leads
 to a higher biomass or density, which implies that larger variability in precipitation
 may lead to a larger variability in plant biomass. Thus the interannual variability in
 production increases with variability in precipitation. Besides, the findings of the
 intrinsic stable fluctuation in this study offer one possible explanation for the
 extensive nature of catastrophic shifts in ecosystems, such as bush encroachment
 problems (Van Vegten 1984; Scholes and Archer, 1997; Van Auken 2000; Moleele
 and Mainah, 2003). Our results demonstrated that the bush encroachment may be
 due to its intrinsic stable fluctuation without disturbance or due to the environmental
 change (e.g., precipitation) (Fig. 4). If the former one is true, it means that the
 ecosystem most likely have not been disrupted or disturbed and it is just in stable
 fluctuation state.

Woody plant encroachment (i.e. an increasing density of woody plants often

unpalatable to domestic livestock) into semiarid and arid systems is a global phenomenon with important ecological consequences (Knapp et al. 2008, Van Auken 2009, Eldridge et al. 2011). Our results show that woody plant encroachment facilitated by decreasing precipitation (P_i) when woody plants with a relative larger the conversion of water uptake to tree density (c_t), or by increasing c_t (Fig. 4). This is justified since the tree with a relative larger c_t (other parameters keep the same, essentially when the $c \cdot \gamma/m$ is relative larger) is a superior species in water competition. Thus, decreasing P_i may lead to the shifts of heterogeneous vegetation (mixed with grassland and trees) towards the homogeneous tree due to the grass is outcompeted by the tree. Overgrazing can be considered as an important factor to promote woody plant encroachment, and reducing grazing pressure can control woody plant encroachment (Fig. 4), which has been verified (Moleele and Perkins 1998, Van Auken 2009). The parameters of $c \cdot \gamma/m$ for native woody species can be considered as constant since most woody species that have been increasing in density are native species and have been present in these communities for thousands of years. High and constant levels of grass herbivory by domestic animals can decrease parameters of $c \cdot \gamma/m$ for native grass species, indirectly increasing parameters of $c \cdot \gamma/m$ for native woody species comparing with grass species, and thus leading to increasing of the woody plant encroachment.

In summary, our results have important implications for understanding water-limited ecosystems, and theoretically demonstrate that the Walter's two-layer hypothesis can lead to species coexistence of grass and trees in water-limited ecosystems. In addition, modelling the effect of precipitation on the dynamics of tree-grass-water ecosystems gives new insights into the relationship between interannual variability in ANPP and in precipitation.

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624

Appendix A

A.1 The feasibility and stability conditions of the equilibria in the tree-water model

The tree-water model has two possible equilibria: one is the bare soil without vegetation (x_T^1) and the other is the homogeneous tree cover equilibrium (x_T^2) which can be obtained by solving the equations of the tree-water model at steady states.

The bare soil without vegetation equilibrium is $x_T^1(B_t^{T1}, W_{sf}^{T1}, W_1^{T1}, W_2^{T1})$, where

$$B_t^{T1} = 0, \quad W_{sf}^{T1} = P_i/(\alpha_{sf} \cdot w_0), \quad W_1^{T1} = P_i/(\alpha_1 + E_1) \quad \text{and} \quad W_2^{T1} = \alpha_1 \cdot$$

W_1^{T1}/E_2 . While the homogeneous tree cover equilibrium is $x_T^2(B_t^{T2},$

$W_{sf}^{T2}, W_1^{T2}, W_2^{T2})$, where B_t^{T2} satisfies $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/(E_2 + \gamma_2^t \cdot B_t^{T2})) \cdot P_i -$

$m_t \cdot (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2}) = 0$, and $W_{sf}^{T2} = P_i/(\alpha_{sf} \cdot w_0)$, $W_1^{T2} = P_i/(\alpha_1 + E_1 +$

$\gamma_1^t \cdot B_t^{T2})$, $W_2^{T2} = \alpha_1 \cdot W_1^{T2}/(E_2 + \gamma_2^t \cdot B_t^{T2})$.

Theorem A.1

(1) The equilibrium x_T^1 is locally asymptotically stable if $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) < m_t$ and it is unstable if $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) > m_t$;

(2) In contrast, if $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) > m_t$, x_T^2 exists and it is locally asymptotically stable.

Proof

(1) It is easy to see that the equilibrium x_T^1 is always feasibility.

The Jacobian matrix of the tree-water model at x_T^1 is given by

$$J_T^1(x_T^1) =$$

$$\begin{pmatrix} c_t \cdot (\gamma_1^t \cdot W_1^{T1} + \gamma_2^t \cdot W_2^{T1}) - m_t & 0 & 0 & 0 \\ 0 & -\alpha_{sf} \cdot w_0 & 0 & 0 \\ -\gamma_1^t \cdot W_1^{T1} & \alpha_{sf} \cdot w_0 & -\alpha_1 - E_1 & 0 \\ -\gamma_2^t \cdot W_2^{T1} & 0 & \alpha_1 & -E_2 \end{pmatrix}.$$

Apparently, all characteristic roots of $J_T^1(x_T^1)$ are $\lambda_1 = c_t \cdot (\gamma_1^t \cdot W_1^{T1} + \gamma_2^t \cdot$

$W_2^{T1}) - m_t$, $\lambda_2 = -\alpha_{sf} \cdot w_0$, $\lambda_3 = -\alpha_1 - E_1$ and $\lambda_4 = -E_2$. All the roots of

650 $f_{J_T^1(x_T^1)}(\lambda) = 0$ are negative if $c_t \cdot (\gamma_1^t \cdot W_1^{T1} + \gamma_2^t \cdot W_2^{T1}) - m_t < 0$, i.e., $c_t \cdot$

651 $(\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) < m_t$.

652 (2) In contrast, we can achieve easily that x_T^2 is feasible if $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot$

653 $\alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) > m_t$ by analyzing the following equation

654
$$c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/(E_2 + \gamma_2^t \cdot B_t^{T2})) \cdot P_i - m_t \cdot (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2}) = 0.$$

655 The Jacobian matrix of the tree-water model at x_T^2 is as follows:

656
$$J_T^2(x_T^2) =$$

657
$$\begin{pmatrix} 0 & 0 & c_t \cdot \gamma_1^t \cdot B_t^{T2} & c_t \cdot \gamma_2^t \cdot B_t^{T2} \\ 0 & -\alpha_{sf} \cdot w_0 & 0 & 0 \\ -\gamma_1^t \cdot W_1^{T2} & \alpha_{sf} \cdot w_0 & -\alpha_1 - E_1 - \gamma_1^t \cdot B_t^{T2} & 0 \\ -\gamma_2^t \cdot W_2^{T2} & 0 & \alpha_1 & -E_2 - \gamma_2^t \cdot B_t^{T2} \end{pmatrix}.$$

658 The characteristic polynomial of $J_T^2(x_T^2)$ is $f_{J_T^2(x_T^2)}(\lambda) = (\alpha_{sf} \cdot w_0 + \lambda) \cdot |A|$,

659 in which $A = \begin{pmatrix} -\lambda & c_t \cdot \gamma_1^t \cdot B_t^{T2} & c_t \cdot \gamma_2^t \cdot B_t^{T2} \\ -\gamma_1^t \cdot W_1^{T2} & -\alpha_1 - E_1 - \gamma_1^t \cdot B_t^{T2} - \lambda & 0 \\ -\gamma_2^t \cdot W_2^{T2} & \alpha_1 & -E_2 - \gamma_2^t \cdot B_t^{T2} - \lambda \end{pmatrix}.$

660 $|A| = -\lambda \cdot (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2} + \lambda) \cdot (E_2 + \gamma_2^t \cdot B_t^{T2} + \lambda) - c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_1^t \cdot$

661 $W_1^{T2} \cdot \alpha_1 - c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_2^t \cdot W_2^{T2} \cdot (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2} + \lambda) - \gamma_1^t \cdot W_1^{T2} \cdot c_t \cdot$

662 $\gamma_1^t \cdot B_t^{T2} \cdot (E_2 + \gamma_2^t \cdot B_t^{T2} + \lambda) = -\lambda^3 - A_2 \lambda^2 - A_1 \lambda - A_0 = 0$, where $A_2 = \alpha_1 +$

663 $E_1 + \gamma_1^t \cdot B_t^{T2} + E_2 + \gamma_2^t \cdot B_t^{T2}$, $A_1 = (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2}) \cdot (E_2 + \gamma_2^t \cdot B_t^{T2}) + c_t \cdot$

664 $\gamma_2^t \cdot B_t^{T2} \cdot \gamma_2^t \cdot W_2^{T2} + \gamma_1^t \cdot W_1^{T2} \cdot c_t \cdot \gamma_1^t \cdot B_t^{T2}$ and $A_0 = c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_1^t \cdot$

665 $W_1^{T2} \cdot \alpha_1 + c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_2^t \cdot W_2^{T2} \cdot (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2}) + \gamma_1^t \cdot W_1^{T2} \cdot c_t \cdot \gamma_1^t \cdot$

666 $B_t^{T2} \cdot (E_2 + \gamma_2^t \cdot B_t^{T2}).$

667 $A_2 \cdot A_1 - A_0 = (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2} + E_2 + \gamma_2^t \cdot B_t^{T2}) \cdot (\alpha_1 + E_1 + \gamma_1^t \cdot$

668 $B_t^{T2})(E_2 + \gamma_2^t \cdot B_t^{T2}) + (E_2 + \gamma_2^t \cdot B_t^{T2}) \cdot c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_2^t \cdot W_2^{T2} + (\alpha_1 + E_1 + \gamma_1^t \cdot$

669 $B_t^{T2}) \cdot \gamma_1^t \cdot W_1^{T2} \cdot c_t \cdot \gamma_1^t \cdot B_t^{T2} - c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_1^t \cdot W_1^{T2} \cdot \alpha_1 > c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_2^t \cdot$

670 $W_1^{T2} \cdot \alpha_1 + (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{T2}) \cdot \gamma_1^t \cdot W_1^{T2} \cdot c_t \cdot \gamma_1^t \cdot B_t^{T2} - c_t \cdot \gamma_2^t \cdot B_t^{T2} \cdot \gamma_1^t \cdot$

671 $W_1^{T2} \cdot \alpha_1 \geq 0.$

672 Due to Routh–Hurwitz criterion, all the eigenvalues of A have negative real part

673 if $A_2 \cdot A_1 > A_0$. Thus, x_T^2 is locally asymptotically stable if it is feasible.

674 Hence the theorem.

A.2 The feasibility and stability conditions of the equilibria in the grass-water model

The grass-water model has two possible equilibria: the bare soil without vegetation equilibrium $x_G^1(B_g^{G1}, W_{sf}^{G1}, W_1^{G1}, W_2^{G1})$ and the homogeneous grass cover equilibrium $x_G^2(B_g^{G2}, W_{sf}^{G2}, W_1^{G2}, W_2^{G2})$, where $B_g^{G1} = 0$, $W_{sf}^{G1} = P_i/(\alpha_{sf} \cdot w_0)$, $W_1^{G1} = P_i/(\alpha_1 + E_1)$, $W_2^{G1} = \alpha_1 \cdot W_1^{G1}/E_2$, $B_g^{G2} = (P_i - \alpha_1 \cdot W_1^{G2} - E_1 \cdot W_1^{G2})/(\gamma_1^g \cdot W_1^{G2})$, $W_{sf}^{G2} = P_i \cdot (B_g^{G2} + k)/[\alpha_{sf} \cdot (B_g^{G2} + k \cdot w_0)]$, $W_1^{G2} = m_g/c_g \cdot \gamma_1^g$, and $W_2^{G2} = \alpha_1 \cdot W_1^{G2}/E_2$.

Theorem A.2

- (1) The equilibrium x_G^1 is locally asymptotically stable if $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) < m_g$ and it is unstable if $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) > m_g$;
- (2) While the equilibrium x_G^2 is locally asymptotically stable if $B_1 \cdot B_2 > B_0$ and $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) > m_g$, but it is unstable if $B_2 \cdot B_1 < B_0$ and $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) > m_g$. ($B_1 = \alpha_{sf} \cdot (B_g^{G2} + k \cdot w_0) \cdot (\alpha_1 + E_1 + \gamma_1^g \cdot B_g^{G2})/(B_g^{G2} + k) - c_g \cdot \gamma_1^g \cdot B_g^{G2} \cdot [k \cdot (1 - w_0) \cdot \alpha_{sf} \cdot W_{sf}/(B_g^{G2} + k)^2 - \gamma_1^g \cdot W_1^{G2}]$, $B_2 = \alpha_{sf} \cdot (B_g^{G2} + k \cdot w_0)/(B_g^{G2} + k) + \alpha_1 + E_1 + \gamma_1^g \cdot B_g^{G2}$ and $B_0 = c_g \cdot \gamma_1^g \cdot B_g^{G2} \cdot \alpha_{sf} \cdot (B_g^{G2} + k \cdot w_0) \cdot \gamma_1^g \cdot W_1^{G2}/(B_g^{G2} + k)$)

Proof

- (1) It is easy to see that the equilibrium x_G^1 is always feasibility.

The Jacobian matrix of the grass-water model at x_G^1 is given by

$$J_G^1(x_G^1) = \begin{pmatrix} c_g \cdot \gamma_1^g \cdot W_1 - m_g & 0 & 0 & 0 \\ \frac{(1-w_0)}{k} \cdot \alpha_{sf} \cdot W_{sf} & -\alpha_{sf} \cdot w_0 & 0 & 0 \\ \frac{(1-w_0)}{k} \cdot \alpha_{sf} \cdot W_{sf} - \gamma_1^g \cdot W_1^{G1} & \alpha_{sf} \cdot w_0 & -\alpha_1 - E_1 & 0 \\ 0 & 0 & \alpha_1 & -E_2 \end{pmatrix}.$$

The characteristic polynomial of $J_G^1(x_G^1)$ is $f_{J(x_G^1)}(\lambda) = (-c_g \cdot \gamma_1^g \cdot W_1 + m_g + \lambda) \cdot (\alpha_{sf} \cdot w_0 + \lambda) \cdot (\alpha_{sf} \cdot w_0 + \lambda) \cdot (\alpha_1 + E_1 + \lambda) \cdot (E_2 + \lambda)$.

Therefore, all the roots $f_{J_G^2(x_G^1)}(\lambda) = 0$ are negative if $c_g \cdot \gamma_1^g \cdot P_i / (\alpha_1 + E_1) < m_g$.

(2) In contrast, the feasibility conditions of x_G^2 is given by $x_G^2 > 0$, i.e., $c_g \cdot \gamma_1^g \cdot P_i / (\alpha_1 + E_1) > m_g$.

The Jacobian matrix of the grass-water model at x_G^2 is given by

$$J_G^2(x_G^2) = \begin{pmatrix} 0 & 0 & c_g \cdot \gamma_1^g \cdot B_g^{G2} & 0 \\ -\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g^{G2}+k)^2} & -\alpha_{sf} \cdot \frac{B_g^{G2}+k \cdot w_0}{B_g^{G2}+k} & 0 & 0 \\ \frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g^{G2}+k)^2} & -\gamma_1^g \cdot W_1^{G2} & \alpha_{sf} \cdot \frac{B_g^{G2}+k \cdot w_0}{B_g^{G2}+k} & -\alpha_1 - E_1 - \gamma_1^g \cdot B_g^{G2} \\ 0 & 0 & \alpha_1 & -E_2 \end{pmatrix}.$$

The characteristic polynomial of $J_G^2(x_G^2)$ is $f_{J_G^2(x_G^2)}(\lambda) = (-E_2 - \lambda) \cdot |B - \lambda E|$,

where

$$B - \lambda E = \begin{pmatrix} -\lambda & 0 & c_g \cdot \gamma_1^g \cdot B_g^{G2} \\ -\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g^{G2}+k)^2} & -\alpha_{sf} \cdot \frac{B_g^{G2}+k \cdot w_0}{B_g^{G2}+k} - \lambda & 0 \\ \frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g^{G2}+k)^2} & -\gamma_1^g \cdot W_1^{G2} & \alpha_{sf} \cdot \frac{B_g^{G2}+k \cdot w_0}{B_g^{G2}+k} \\ -\alpha_1 - E_1 - \gamma_1^g \cdot B_g^{G2} - \lambda \end{pmatrix}.$$

By calculating, we can achieve that $|B - \lambda E| = -\lambda^3 - B_2 \lambda^2 - B_1 \lambda - B_0$.

Based on Routh–Hurwitz criterion, all the eigenvalues of B have negative real part if $B_2 \cdot B_1 > B_0$.

Hence the theorem.

A.3 The feasibility and stability conditions of the equilibra in the grass-water model

The tree-grass-water model has four possible equilibria: the bare soil without vegetation equilibrium $x_C^1(B_g^{C1}, B_t^{C1}, W_{sf}^{C1}, W_1^{C1}, W_2^{C1})$, and the homogeneous tree cover equilibrium $x_C^2(B_g^{C2}, B_t^{C2}, W_{sf}^{C2}, W_1^{C2}, W_2^{C2})$, the homogeneous grass cover equilibrium $x_C^3(B_g^{C3}, B_t^{C3}, W_{sf}^{C3}, W_1^{C3}, W_2^{C3})$ and tree and grass coexistence equilibrium $x_C^4(B_g^{C4}, B_t^{C4}, W_{sf}^{C4}, W_1^{C4}, W_2^{C4})$. where $B_g^{C1} = 0$, $B_t^{C1} = 0$, $W_{sf}^{C1} =$

$$\begin{aligned}
720 \quad & P_i/(\alpha_{sf} \cdot w_0), \quad W_1^{C1} = P_i/(\alpha_1 + E_1), \quad W_2^{C1} = \alpha_1 \cdot W_1^{C1}/E_2, \quad B_g^{C2} = 0, \quad W_{sf}^{C2} = \\
721 \quad & P_i/(\alpha_{sf} \cdot w_0), \quad W_1^{C2} = P_i/(\alpha_1 + E_1 + \gamma_1^t \cdot B_t^{C2}), \quad W_2^{C2} = \alpha_1 \cdot W_1^{C1}/(E_2 + \gamma_2^t \cdot B_t^{C2}), \\
722 \quad & B_g^{C3} = (P_i - \alpha_1 \cdot W_1^3 - E_1 \cdot W_1^3)/(\gamma_1^g \cdot W_1^{C3}), \quad B_t^{C3} = 0, \quad W_{sf}^{C3} = P_i/\alpha_{sf} \cdot (B_g^{C3} + \\
723 \quad & k)/(B_g^{C3} + k \cdot w_0), \quad W_1^{C3} = m_g/(c_g \cdot \gamma_1^g), \quad W_2^{C3} = \alpha_1 \cdot W_1^{C3}/E_2, \quad W_1^{C4} = \\
724 \quad & m_g/(c_g \cdot \gamma_1^g), \quad W_2^{C4} = (m_t - c_t \cdot \gamma_1^t \cdot W_1^{C4})/(c_t \cdot \gamma_2^t), \quad B_t^{C4} = (\alpha_1 \cdot W_1^{C4} - E_2 \cdot \\
725 \quad & W_2^{C4})/(\gamma_2^t \cdot W_2^{C4}), \quad B_g^{C4} = (P_i - \alpha_1 \cdot W_1^{C4} - E_1 \cdot W_1^{C4} - \gamma_1^t \cdot B_t^{C4} \cdot W_1^{C4})/(\gamma_1^g \cdot W_1^{C4}), \\
726 \quad & W_{sf}^{C4} = P_i/\alpha_{sf} \cdot (B_g^{C4} + k)/(B_g^{C4} + k \cdot w_0). \text{ and the } B_t^{C2} \text{ satisfies the equation: } \gamma_1^t \cdot \\
727 \quad & \gamma_2^t \cdot B_t^{C2} \cdot B_t^{C2} + \left[\gamma_2^t \cdot (\alpha_1 + E_1) + \gamma_1^t \cdot E_2 - c_t \cdot P_i \cdot \frac{\gamma_1^t \gamma_2^t}{m_t} \right] \cdot B_t^{C2} + (\alpha_1 + E_1) \cdot E_2 - \\
728 \quad & c_t \cdot P_i \cdot (\gamma_1^t \cdot E_2 + \alpha_1 \cdot \gamma_2^t)/m_t = 0.
\end{aligned}$$

729 **Theorem A.3**

- 730 (1) The equilibrium x_c^1 is locally asymptotically stable if $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 +$
731 $E_1) < m_g$ and $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) < m_t$, vice it is unstable;
- 732 (2) If $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2) \cdot P_i/(\alpha_1 + E_1) > m_t$ and $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1 +$
733 $\gamma_1^t \cdot B_t^2) < m_g$, then x_c^2 is locally asymptotically stable, vice it is unstable;
- 734 (3) If $c_g \cdot \gamma_1^g \cdot P_i/(\alpha_1 + E_1) > m_g$ and $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2)/m_t \leq$
735 $c_g \cdot \gamma_1^g/m_g$ and $B_2 \cdot B_1 > B_0$, x_c^3 is locally asymptotically stable, vice it is
736 unstable;
- 737 (4) The feasibility conditions of x_c^4 is $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1/E_2)/m_t > c_g \cdot \gamma_1^g/$
738 $m_g > c_t \cdot \gamma_1^t/m_t$ and $c_g \cdot \gamma_1^g/m_g > (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^4)/P_i$. If $C_1 > 0$, $C_3 C_2 >$
739 $C_4 C_1$ and $C_3 C_2 C_1 > C_4 C_1^2 + C_0 C_3^2$, then x_c^4 is locally asymptotically stable, vice it
740 is unstable. (The C_1, C_2, C_3, C_4 is seen below)

741 **Proof**

742 (1) It is easy to see that the equilibrium x_c^1 is always feasibility.

743 The Jacobian matrix of the tree-grass-water model at x_c^1 is given by

$$\begin{aligned}
744 \quad & J(x_C^1) = \\
745 \quad & \begin{pmatrix} c_g \cdot \gamma_1^g \cdot W_1^{C1} - m_g & 0 & 0 & 0 & 0 \\ 0 & c_t \cdot (\gamma_1^t \cdot W_1^{C1} + \gamma_2^t \cdot -\gamma_2^t \cdot W_1^{C2}) - m_t & 0 & 0 & 0 \\ -\frac{(1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{k} & 0 & -\alpha_{sf} \cdot w_0 & 0 & 0 \\ \frac{(1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{k} - \gamma_1^t \cdot W_1^{C1} & -\gamma_1^t \cdot W_1^{C1} & \alpha_{sf} \cdot w_0 & -\alpha_1 - E_1 & 0 \\ 0 & -\gamma_2^t \cdot W_1^{C2} & 0 & \alpha_1 & -E_2 \end{pmatrix} \\
746 \quad & .
\end{aligned}$$

747 The characteristic roots of $J(x_C^1)$ is $\lambda_1 = c_g \cdot \gamma_1^g \cdot W_1^{C1} - m_g$, $\lambda_2 = c_t \cdot$
748 $(\gamma_1^t \cdot W_1^{C1} + \gamma_2^t \cdot -\gamma_2^t \cdot W_1^{C2}) - m_t$, $\lambda_3 = -\alpha_{sf} \cdot w_0$, $\lambda_4 = -\alpha_1 - E_1$, $\lambda_5 = -E_2$.

749 All the roots are negative if $c_g \cdot \gamma_1^g \cdot P_i / (\alpha_1 + E_1) < m_g$ and $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot$
750 $\alpha_1 / E_2) \cdot P_i / (\alpha_1 + E_1) < m_t$.

751 (2) If $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1 / E_2) \cdot P_i / (\alpha_1 + E_1) > m_t$, the equilibrium x_C^2 is
752 feasibility.

753 The Jacobian matrix of the tree-grass-water model at x_C^2 is given by

$$\begin{aligned}
754 \quad & J_C^2(x_C^2) = \\
755 \quad & \begin{pmatrix} c_g \cdot \gamma_1^g \cdot W_1 - m_g & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & c_t \cdot \gamma_1^t \cdot B_t & c_t \cdot \gamma_2^t \cdot B_t \\ -\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g+k)^2} & 0 & -\alpha_{sf} \cdot w_0 & 0 & 0 \\ \frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g+k)^2} - \gamma_1^g \cdot W_1 & -\gamma_1^t \cdot W_1 & \alpha_{sf} \cdot w_0 & -\alpha_1 - E_1 - \gamma_1^t \cdot B_t & 0 \\ 0 & -\gamma_2^t \cdot W_2 & 0 & \alpha_1 & -E_2 - \gamma_2^t \cdot B_t \end{pmatrix} \\
756 \quad & .
\end{aligned}$$

757 The characteristic polynomial of $J_C^2(x_C^2)$ is $f_{J_C^2(x_C^2)}(\lambda) = (c_g \cdot \gamma_1^g \cdot W_1 - m_g -$
758 $\lambda) \cdot |J_T^2(x_T^2) - \lambda E|$.

759 Thus all the roots are negative if $c_g \cdot \gamma_1^g \cdot P_i / (\alpha_1 + E_1) < m_g$ and $c_t \cdot$
760 $(\gamma_1^t + \gamma_2^t \cdot \alpha_1 / E_2) \cdot P_i / (\alpha_1 + E_1) > m_t$.

761 (3) The equilibrium x_C^3 is feasibility if $c_g \cdot \gamma_1^g \cdot P_i / (\alpha_1 + E_1) > m_g$.

762 The Jacobian matrix of the tree-grass-water model at x_C^3 is given by

$$763 \quad J_C^3(x_C^3) =$$

$$\begin{pmatrix}
0 & 0 & 0 & c_g \cdot \gamma_1^g \cdot B_g & 0 \\
0 & c_t \cdot (\gamma_1^t \cdot W_1 + \gamma_2^t \cdot W_2) - m_t & 0 & 0 & 0 \\
-\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g+k)^2} & 0 & -\alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} & 0 & 0 \\
\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g+k)^2} - \gamma_1^g \cdot W_1 & -\gamma_1^t \cdot W_1 & \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} & -\alpha_1 - E_1 - \gamma_1^g \cdot B_g & 0 \\
0 & -\gamma_2^t \cdot W_2 & 0 & \alpha_1 & -E_2
\end{pmatrix}$$

The characteristic polynomial of $J_C^3(x_C^3)$ is $f_{J_C^3(x_C^3)}(\lambda) = (c_t \cdot (\gamma_1^t \cdot W_1 + \gamma_2^t \cdot W_2) - m_t - \lambda) \cdot |J_G^2(x_G^2) - \lambda E|$.

Thus all the roots are negative if $c_g \cdot \gamma_1^g \cdot P_i / (\alpha_1 + E_1) > m_g$ and $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1 / E_2) / m_t \leq c_g \cdot \gamma_1^g / m_g$ and $B_2 \cdot B_1 > B_0$.

(4) The feasibility conditions of x_C^4 is $c_t \cdot (\gamma_1^t + \gamma_2^t \cdot \alpha_1 / E_2) / m_t > c_g \cdot \gamma_1^g / m_g > c_t \cdot \gamma_1^t / m_t$ and $c_g \cdot \gamma_1^g / m_g > (\alpha_1 + E_1 + \gamma_1^t \cdot B_t^4) / P_i$.

The Jacobian matrix of the tree-grass-water model at x_C^4 is given by

$$J_C^4(x_C^4) = \begin{pmatrix}
0 & 0 & 0 & c_g \cdot \gamma_1^g \cdot B_g & 0 \\
0 & 0 & 0 & c_t \cdot \gamma_1^t \cdot B_t & c_t \cdot \gamma_2^t \cdot B_t \\
-\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g+k)^2} & 0 & -\alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} & 0 & 0 \\
\frac{k \cdot (1-w_0) \cdot \alpha_{sf} \cdot W_{sf}}{(B_g+k)^2} - \gamma_1^g \cdot W_1 & -\gamma_1^t \cdot W_1 & \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} & -\alpha_1 - E_1 - \gamma_1^g \cdot B_g - \gamma_1^t \cdot B_t & 0 \\
0 & -\gamma_2^t \cdot W_2 & 0 & \alpha_1 & -E_2 - \gamma_2^t \cdot B_t
\end{pmatrix}$$

$$f_{J_C^4(x_C^4)}(\lambda) = \lambda \cdot \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot$$

$$\begin{vmatrix}
-\lambda & c_t \cdot \gamma_1^t \cdot B_t^{C4} & c_t \cdot \gamma_2^t \cdot B_t^{C4} \\
-\gamma_1^t \cdot W_1^{C4} & -\alpha_1 - E_1 - \gamma_1^g \cdot B_g^{C4} - \gamma_1^t \cdot B_t^{C4} - \lambda & 0 \\
-\gamma_2^t \cdot W_2^{C4} & \alpha_1 & -E_2 - \gamma_2^t \cdot B_t^{C4} - \lambda
\end{vmatrix} + c_g \cdot$$

$$\gamma_1^g \cdot B_g^{C4} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C4} \cdot$$

$$\begin{vmatrix}
-\frac{k \cdot (1-w_0)}{(B_g^{C4}+k)^2} \cdot \alpha_{sf} \cdot W_{sf}^{C4} & 0 & -\alpha_{sf} \cdot \frac{B_g^{C4}+k \cdot w_0}{B_g^{C4}+k} - \lambda \\
\frac{k \cdot (1-w_0)}{(B_g^{C4}+k)^2} \cdot \alpha_{sf} \cdot W_{sf}^{C4} - \gamma_1^g \cdot W_1^{C4} & -\gamma_1^t \cdot W_1^{C4} & \alpha_{sf} \cdot \frac{B_g^{C4}+k \cdot w_0}{B_g^{C4}+k} \\
0 & -\gamma_2^t \cdot W_2^{C4} & 0
\end{vmatrix} = -\lambda \cdot \alpha_{sf} \cdot$$

$$\begin{aligned}
780 & \frac{B_g+k \cdot w_0}{B_g+k} \cdot \lambda \cdot (\alpha_1 + E_1 + \gamma_1^g \cdot B_g^{C^4} + \gamma_1^t \cdot B_t^{C^4} + \lambda) \cdot (E_2 + \gamma_2^t \cdot B_t^{C^4} + \lambda) - \lambda \cdot \alpha_{sf} \cdot \\
781 & \frac{B_g+k \cdot w_0}{B_g+k} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_1^t \cdot W_1^{C^4} \cdot \alpha_1 - \lambda \cdot \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_2^t \cdot W_2^{C^4} \cdot \\
782 & (\alpha_1 + E_1 + \gamma_1^g \cdot B_g^{C^4} + \gamma_1^t \cdot B_t^{C^4} + \lambda) - \lambda \cdot \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot \gamma_1^t \cdot W_1^{C^4} \cdot c_t \cdot \gamma_1^t \cdot B_t^{C^4} \cdot \\
783 & (E_2 + \gamma_2^t \cdot B_t^{C^4} + \lambda) + c_g \cdot \gamma_1^g \cdot B_g^{C^4} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_2^t \cdot W_2^{C^4} \left(\frac{k \cdot (1-w_0)}{(B_g^{C^4}+k)^2} \cdot \alpha_{sf} \cdot W_{sf}^{C^4} - \right. \\
784 & \left. \gamma_1^g \cdot W_1^{C^4} \right) \lambda - c_g \cdot \gamma_1^g \cdot B_g^{C^4} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_1^g \cdot W_1^{C^4} \gamma_2^t \cdot W_2^{C^4} \alpha_{sf} \cdot \frac{B_g^{C^4}+k \cdot w_0}{B_g^{C^4}+k} = \\
785 & -C_4 \lambda^4 - C_3 \lambda^3 - C_2 \lambda^2 - C_1 \lambda - C_0. \\
786 & C_4 = \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k}, \quad C_3 = \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} (\alpha_1 + E_1 + \gamma_1^g \cdot B_g^{C^4} + \gamma_1^t \cdot B_t^{C^4} + E_2 + \\
787 & \gamma_2^t \cdot B_t^{C^4}), \quad C_2 = \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot (\alpha_1 + E_1 + \gamma_1^g \cdot B_g^{C^4} + \gamma_1^t \cdot B_t^{C^4}) \cdot (E_2 + \gamma_2^t \cdot B_t^{C^4}) + \\
788 & \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_2^t \cdot W_2^{C^4} + \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot \gamma_1^t \cdot W_1^{C^4} \cdot c_t \cdot \gamma_1^t \cdot B_t^{C^4} \quad , \\
789 & C_1 = \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_1^t \cdot W_1^{C^4} \cdot \alpha_1 + \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_2^t \cdot \\
790 & W_2^{C^4} \cdot (\alpha_1 + E_1 + \gamma_1^g \cdot B_g^{C^4} + \gamma_1^t \cdot B_t^{C^4}) + \alpha_{sf} \cdot \frac{B_g+k \cdot w_0}{B_g+k} \cdot \gamma_1^t \cdot W_1^{C^4} \cdot c_t \cdot \gamma_1^t \cdot B_t^{C^4} \cdot \\
791 & (E_2 + \gamma_2^t \cdot B_t^{C^4}) - c_g \cdot \gamma_1^g \cdot B_g^{C^4} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_2^t \cdot W_2^{C^4} \left(\frac{k \cdot (1-w_0)}{(B_g^{C^4}+k)^2} \cdot \alpha_{sf} \cdot W_{sf}^{C^4} - \gamma_1^g \cdot \right. \\
792 & \left. W_1^{C^4} \right), \quad C_0 = c_g \cdot \gamma_1^g \cdot B_g^{C^4} \cdot c_t \cdot \gamma_2^t \cdot B_t^{C^4} \cdot \gamma_1^g \cdot W_1^{C^4} \gamma_2^t \cdot W_2^{C^4} \alpha_{sf} \cdot \frac{B_g^{C^4}+k \cdot w_0}{B_g^{C^4}+k}.
\end{aligned}$$

793 Based on Routh–Hurwitz criterion, all the eigenvalues of $f_{J_C^4(x_C^4)}(\lambda)$ have
794 negative real part if $C_1 > 0$, $C_3 C_2 > C_4 C_1$ and $C_3 C_2 C_1 > C_4 C_1^2 + C_0 C_3^2$.

795 Hence the theorem.

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