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信息生态学研究

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内 容 简 介

本书是中国科学院植物研究所植被数量生态学开放研究实验室近年来工作内容的总结。主要收载了有关信息生态学方面的研究论文、综述与专论。内容包括沙地草地、农林系统植被与环境的动态仿真模拟，植被与环境信息系统的建立，中国全球变化与陆地生态系统研究，全球变化的中国东北陆地样带的研究，毛乌素沙地草地的生理生态研究，以及中国各植被类型的有关植被数量分析和建模工作，如内蒙古草原、东北红花尔基沙地、山东植被、中亚热带及南亚热带常绿阔叶林、青藏高原高寒植被地区等。

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目　　录

MAGE, A DYNAMIC MODEL OF ALKALINE GRASSLAND ECOSYSTEMS WITH VARIABLE SOIL CHARACTERISTICS[①]

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Abstract

An area-based process model for alkaline grassland ecosystem, MAGE, was developed to address the problems associated with the soil alkalization/de-alkalization processes coupled with surface vegetation on Songnen Plain, northeast China. The model gave special consideration to the variation of soil characteristics such as water retentivity and hydraulic conductivity as functions of surface vegetation. Soil within one meter depth was divided into two layers, a surface layer on top of a core layer at bottom. The amount of non-capillary pores and hence the hydraulic conductivity and water retentivity characteristics of the surface layer were considered to be dependent on surface vegetation status. The model is able to handle multiple plant species succession, with competition between species reflected as soil water sharing and species niche overlapping along soil water and alkali axes. The model was parameterized using published data and field observations on soil water content, soluble sodium

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and calcium cation concentrations, and aboveground and belowground biomass.

The model was used to evaluate the effects of variable soil characteristics, the harvesting intensity and the core layer soil alkaline status on surface soil alkalization/de-alkalization processes. Surface vegetation dynamics and optimal harvesting control in light of maximum harvest subject to system stability were also simulated. The results showed that surface soil alkalization process was primarily determined by the chemical status of the core soil. Increasing vegetation and the non-capillary soil water capacity can reduce the rate and extent of soil alkalization or increase the rate and extent of soil de-alkalization. Hence for given chemical conditions in deep soil, surface vegetation and soil non-capillary porosity are indeed crucial factors for soil alkalization/de-alkalization. The results also indicated that there existed an optimal harvest intensity which renders the total harvest a maximum while maintaining system stability, and that the maximum total harvest and the associated optimal harvest control level decreased with core soil alkali but increased with the maximum non-capillary water capacity in surface soil.

Key words: Ecosystem dynamics, Grassland, Harvest control, Soil alkalization.

A List of Symbols

Symbol	Unit	Definition
a	m	Coefficient in soil retentivity expression
b		Exponent in soil retentivity expression
C_{ab}	mol L^{-1}	Calcium cation concentration in core soil layer
C_{abT}	mmol cm^{-2}	Area concentration of total calcium cation in core soil
C_{as}	mol L^{-1}	Calcium cation concentration in surface soil water
C_{asT}	mmol cm^{-2}	Area concentration of total calcium cation in surface soil
C_{bb}	m cm^{-1}	Boundary water capacitance
C_{ec}	mme $(100\ g)^{-1}$	Cation exchange capacity, molar equivalent per 100 g soil
d		Exponent in soil water conductivity expression
d_{ai}		Death coefficient of aboveground biomass of species i
D_{ai}	g m^{-2} yr^{-1}	Death rate of aboveground biomass of species i
d_{bi}	yr^{-1}	Death coefficient of belowground biomass of species i
D_b	cm	Core soil thickness
D_{bi}	g m^{-2} yr^{-1}	Death rate of belowground biomass of species i

D_s	cm	Surface soil thickness
E_{ab}	(100 g) cm^{-2}	Number of 100 g core soil per square centimeter area
E_{as}	(100 g) cm^{-2}	Number of 100 g surface soil per square centimeter area
E_T	cm	Evapotranspiration
g_b	cm m^{-1} yr^{-1}	Core soil water conductive coefficient
G_{bb}	cm m^{-1} yr^{-1}	Conductive coefficient at the bottom of the core soil
g_{fi}	yr^{-1}	Germination coefficient of species i
G_{gi}	g m^{-2} yr^{-1}	Germination of species i
G_{ri}	yr^{-1} m^2 KJ^{-1}	Assimilation coefficient of plant species i
g_s	cm m^{-1} yr^{-1}	Surface soil water conductive coefficient
G_{sb}	cm m^{-1} yr^{-1}	Conductive coefficient between surface and core soil
HCL	g m^{-2}	Harvest control level
H_i	g m^{-2} yr^{-1}	Harvesting rate to species i
K		Cation exchange coefficient
K_0	cm yr^{-1}	Saturated soil hydraulic conductivity
m_{ai}	g m^{-2}	Aboveground biomass of species i
m_{bi}	g m^{-2}	Belowground biomass of species i
m_{bT}	g m^{-2}	Total belowground biomass
M_{bT}	g m^{-2}	Saturation constant of non-capillary pore expression
M_{Pi}	g m^{-2}	Saturation coefficient of assimilation for plant species i
N_{ab}	mol L^{-1}	Sodium cation concentration in core soil layer
N_{abT}	mmol cm^{-2}	Area concentration of total sodium cation in core soil
N_{as}	mol L^{-1}	Sodium cation concentration in surface soil water
N_{asT}	mmol cm^{-2}	Area concentration of total sodium cation in surface soil
P	cm	Precipitation as a function of time
p_{ai}		Partition coefficient for aboveground biomass of species i
p_{bi}		Partition coefficient for belowground biomass of species i
P_{erc}	cm yr^{-1}	Bottom boundary percolation
Ph_i	g m^{-2} yr^{-1}	Assimilation rate of plant species i

Q_{gi}		Germination function of species i
Q_{pi}		Unimodal function used to describe species niche
Q_{xi}		Alkali niche function of plant species i
Q_{wi}		Water niche function of plant species i
r_{ai}	yr^{-1}	Maintenance respiration coefficients of aboveground biomass of species i
R_{ai}	$g\ m^{-2}\ yr^{-2}$	Respiration of aboveground biomass of species i
r_{bi}	yr^{-1}	Maintenance respiration coefficients of aboveground biomass of species i
R_{bi}	$g\ m^{-2}\ yr^{-1}$	Respiration of belowground biomass of species i
r_{dai}		Growth respiration coefficients of aboveground biomass of species i
r_{dbi}		Growth respiration coefficient of belowground biomass of species i
R_f	$cm\ yr^{-1}$	Surface runoff
RH		Relative humidity as a function of time
R_s	$kJ\ m^{-2}$	Net radiation as a function of time
S_b		Switch variable of core soil layer
$\bar{S}_b$		Conjugated switch variable of core soil layer
S_s		Switch variable of surface soil
$\bar{S}_s$		Conjugated switch variable of surface soil layer
t	yr	Time, the independent variable
T	℃	Temperature as a function of time
t_{ei}	yr^{-1}	End of the growing season of species i
t_{si}	yr^{-1}	Start of the growing season of species i
u		General niche variable
u_i		($i = 1,2,3,4$) parameters used in unimodal function
V_w	$m\ s^{-1}$	Wind velocity as a function of time

W_b	cm	Core soil water content (volumetric water content multiplied by thickness of core soil layer)
W_{BP}	cm	Core soil water capacity by capillary pores
W_s	cm	Surface soil water content (volumetric water content multiplied by thickness of the surface soil)
W_{SN}	cm	Surface soil water capacity by non-capillary pores
W_{SNM}	cm	Maximum surface soil water by non-capillary pores
W_{SP}	cm	Surface soil water capacity by capillary pores
W_{ST}	cm	Total surface soil water capacity
X_{Cab}	mme $(100\ g)^{-1}$	Molar equivalent of calcium cation in 100 g core soil
X_{Cas}	mme $(100\ g)^{-1}$	Molar equivalent of calcium cation in 100 g surface soil
X_{Nab}	mme $(100\ g)^{-1}$	Molar equivalent of sodium cation in 100 g core soil
X_{Nas}	mme $(100\ g)^{-1}$	Molar equivalent of sodium cation in 100 g surface soil
a_i		Exponent of death rate expression for species i
δ		Impulse function
t_{ij}	yr	Time of harvesting operation
ψ_b	m	Core soil water potential
ψ_{bb}	m	Water potential at lower boundary
ψ_s	m	Surface soil water potential

1. INTRODUCTION

Measuring approximately 300 km from east to west, 500 km from north to south, and centered approximately at 44.3 °N and 124.3 °E, Songnen Plain in northeast China is one of the major areas of animal husbandry of the country. The climate there is warm and humid in summer but cold and dry in winter, with mean temperature around 23℃ in July and −20℃ in January. The annual precipitation is around 500 mm, most of which is concentrated between July and August. According to the climatic conditions there, the area has been classified as meadow steppe in terms of vegetation zonation (Hou, 1988). Major plant species include *Aneurolepidium chinense*, *Puccinellia tenuiflora*, *Chloris virgata*, *Calamagrostis epigeios* and *Suaeda glauca*.

Songnen Plain is largely a basin surrounded by mountains and thus has very poor drainage. Runoff from surrounding mountains carries a large amount of solutes down to plain, resulting in an annual net solute input of 150 metric tons (Zheng and Li, 1990).

The accumulation of the solute causes a primary soil alkalization process with Na_2CO_3 and $NaHCO_3$ as major sources of soil alkali. In addition to the soil alkalization resulting from the topographical condition, the grassland is also facing degradation caused by overgrazing and hay cutting due to the population pressure and mismanagement. The degradation of vegetation in turn induces a secondary soil alkalization process, resulting in further deterioration of the soil conditions for plant growth.

While the slow primary soil alkalization due to the topographical condition is still not feasible to control today, the secondary soil alkalization induced by over utilization can be controlled by better management. Indeed, the optimal utilization control of the Songnen alkaline grassland resources subject to the constraint of ecosystem stability has long been a concern of ecological scientists in China. For example, Chang and Zhu (1989) quantified experimentally the evapotranspiration of *Aneurolepidium chinense* grassland, based on which the annual water balance of the grassland was estimated. Guo and Zhu (1988) studied the nitrogen budget of the grassland and concluded that the soil has enough nitrogen deposit and thus nitrogen is not a limiting factor for plant growth in the grassland. Field measurements of photosynthesis were also conducted for major plant species in the grassland (Feng, 1986). From the mid-eighties, different strategies has been employed to classify the grassland vegetation according to the ecological characteristics of the major grassland plant species (Zheng and Li, 1986; Li and Zheng, 1988; and Zheng and Li, 1990). The result showed that soil alkali is the major ecological gradient and also the main limiting factor for vegetation development in the area. Subsequent studies on the soil hydraulic parameters (Gao and Zhang, 1993; Zhang and Gao, 1994), salinity distribution, tolerance and resistance of major plant species to soil alkali were also conducted recently (Yin and Zhu, 1988; Wang, 1992). On the other hand, Ge and Li (1990) and Yin and Zhang (1994) evaluated the importance of vegetation in the process of soil de-alkalization, and found a significant correlation between soil de-alkalization and the amount of soil non-capillary pores, which is strongly related to surface vegetation.

A very important and well accepted hypothesis generated based on these studies is that better surface vegetation helps to improve the soil physical characteristics by increasing the amount of non-capillary pores in surface soil where plant roots reside. The more the non-capillary pores, the larger the downward water flux, and hence the greater the downward flux of the alkaline elements such as Na^+. The process leads to surface soil de-alkalization which further improves the plant growth conditions. In contrast, excessive grazing and hay cutting cause surface vegetation to deteriorate, resulting in less amount of non-capillary pores in the surface soil. Consequently, upward water flux induced by evapotranspiration may outbalance the downward water flux and bring alkaline solutes up to the surface soil from the deep soil layer. The alkalization of the surface soil results in even worse conditions for plant growth. Thus the above described process of alkalization/de-alkalization is a positive feedback loop, although the system nonlinearity prevents the process from blowing-up in either of the two directions.

The studies on the alkaline grassland ecosystem so far have all concentrated in specific aspects of the ecosystem. However, the optimal utilization of grassland resources is a problem at system level in nature. Therefore, a dynamic ecosystem model is highly desirable to link the above described individual experimental studies for addressing the system response including soil alkalization/de-alkalization to various environmental and managerial parameters, and their interactions.

Numerous ecosystem simulation models have been developed for various ecosystem processes and structure dynamics. Shugart et al. (1991) provided a very good review about these models. FORET, CENTURY, MAGIC and STEPPE are only a few well known examples. Some of these ecosystem models, such as FORET and STEPPE, which concentrated on system structure, simplified the ecosystem processes. On the other hand, some models, such as MAGIC and CENTURY, emphasized the dynamic processes of soil chemicals and nutrients at expenses of system structure. There have been no model available that directly addresses the problems of alkaline grassland vegetation dynamics coupled with soil alkalization in light of variable soil characteristics.

The objective of this study was to develop a general-purpose model, named MAGE, for the alkaline grassland ecosystem with variable soil characteristics. The model was designed flexible enough so that it is capable of ① testing the above described hypothesis of positive feedback by evaluating the importance of vegetation, non-capillary soil water capacity and the associated variability of soil water characteristics in the process of soil alkalization; ② analyzing the effects of soil alkali on plant growth and vegetation development; ③ handling the ecosystem structure dynamics by including multiple species succession along the soil alkali gradient; ④ deriving the optimal utilization intensity under different environment conditions with constraint of system stability; and ⑤ allowing adjustment of input parameters such as climatic variables, soil physical and chemical characteristics, and plant physiological parameters, so that problems such as effects of climate change and soil heterogeneity can be effectively queried.

While large-scale experiment are being designed and conducted for a full parameterization and validation, this paper reports the general structure, preliminary parameterization with available experimental data and general simulation capacity of the model.

2. MODEL DESCRIPTION

2.1 Assumptions and Simplifications

MAGE was developed with the following assumptions and simplifications:

(1) Soil within the depth of 1 m was divided into two layers, a top or surface layer

and a bottom or core soil layer. The surface soil layer is where most plant root system resides. Hence the physical characteristics of the surface soil layer depends on both the original soil matrix and surface vegetation. In contrast, the bottom soil characteristics are determined by the surface properties and size distribution of the soil particles.

(2) The effect of vegetation on surface soil characteristics was described by the dependence of soil non-capillary porosity on belowground biomass.

(3) Vertical water flow was regarded as the only carrying medium for solute transport. Thermal effects on solute movement were neglected.

(4) Soil alkalization was described as the process of replacement of calcium cation Ca^{+2} by sodium cation Na^+ on the surface of soil particles. Since Na_2CO_3 and $NaHCO_3$ are the major sources of soil alkali in Songnen grassland, only the movement and exchange of these two cation species were considered.

(5) The effects of soil water and surface soil alkali on carbon assimilation of plants were described by unimodal functions of surface soil water and soil alkali. It was assumed that there exist an optimal soil water content and an optimal soil alkali content for each plant species to achieve a maximum assimilation rate. Deviations of soil water and soil alkali from the optima will reduce the assimilation rate. These unimodal functions of soil water and alkali define the niche of each species, which determines partially the competition among plant species.

(6) Plant state was characterized by two quantities: the belowground biomass and aboveground biomass. The assimilated materials were partitioned based on a strategy for most perennial plants that allows most material to go to aboveground biomass at the early stage of plant growth. But at late growing season, the assimilation is mostly distributed to root in order to store energy for the germination or rejuvenation for the next year.

(7) Plant respiration was treated proportional to biomass (maintenance respiration), and net growth rate (growth respiration).

(8) The death of plant tissue was assumed to be induced primarily by out-balance of respiration to assimilation. The excessive biomass was assumed to die in order to maintain the assimilation-respiration balance. Damages caused by plant disease and insects were not included at the moment.

2.2 State variables, and input and output variables of MAGE

To address the interaction between vegetation dynamics and soil alkali, MAGE included the following state variables (with subscript 's' for surface soil and 'b' for core soil respectively): soil water contents (W_s, W_b), concentrations of soluble sodium cations (N_{as}, N_{ab}) and calcium cations (C_{as}, C_{ab}), concentrations of exchangeable sodium cations (X_{Nas}, X_{Nab}) and calcium cations (X_{Cas}, X_{Cab}), bottom boundary water potential (ψ_{bb}), and aboveground biomass (m_{ai}) and belowground biomass (m_{bi}) of each plant species. Climatic variables such as precipitation P, temperature T, relative humidity RH, net radiation R_s and wind velocity V_w, and harvest control level HCL (the amount of aboveground biomass to be kept from harvest) were major input variables to drive the model. The output variables of MAGE include all the state variables plus evapotranspiration E_T, bottom boundary percolation P_{erc} and runoff R_f. Details of the definition and units of the variables are provided in the list of symbols.

2.3 Governing equations

(1) Soil water movement

Water contents of surface soil (W_s) and core soil (W_b) were defined as the products of respective volumetric water contents multiplied by soil layer thickness. The differential equations for W_s, W_b and the boundary water potential (ψ_{bb}) were expressed as

$$\frac{dW_s}{dt}=P-G_{sb}(\psi_s-\psi_b)-E_T \tag{1}$$

$$\frac{dW_b}{dt}=G_{sb}(\psi_s-\psi_b)-G_{bb}(\psi_b-\psi_{bb}) \tag{2}$$

$$\frac{d\psi_{bb}}{dt}=\frac{G_{bb}}{C_{bb}}(\psi_b-\psi_{bb}) \tag{3}$$

where P and E_T are the precipitation and evapotranspiration rates as functions of time t; ψ_s and ψ_b are the water potentials of the surface and core soil layers; G_{sb} and G_{bb} are the conductivity coefficients between the surface and core soil and at the bottom boundary; C_{bb} is a capacitive parameter describing the drainage conditions at the bottom boundary. Surface runoff will be produced if surface soil is saturated and the right hand side of Equation (1) is greater than zero.

The precipitation rate P was statistically derived from the monthly average precipitation records from 1989 to 1993 so that an integration of P over t in a one-year interval should yield the mean annual precipitation. The evapotranspiration rate was obtained by multiplying the relative water content (ratio of actual water content to saturation capacity) of the surface soil by the potential evapotranspiration rate. The potential evapotranspiration rate was calculated using the well-known Penman's formula from net radiation R_s, wind velocity V_w, relative humidity RH and temperature T. All the climatic variables were derived in the similar way to precipitation.

While G_{bb} and C_{bb} were constant parameters used to describe the boundary conditions, G_{sb} was determined by the hydraulic conductivities of the two soil layers, in analogy to two conductances connected in series:

$$G_{sb}=\frac{g_s g_b}{g_s+g_b} \tag{4}$$

where g_s and g_b are respectively the hydraulic conductivities of the surface and core soil layers.

(2) Soil water potentials and hydraulic conductivities

Following Koorevear et al. (1983), the surface soil water potential (retentivity) was calculated by

$$\psi_s=\begin{cases} 0, & W_{SP}<W_s\leqslant W_{ST} \\ a\left[\left(\frac{W_{SP}}{W_s}\right)^b-1\right], & W_s\leqslant W_{SP} \end{cases} \tag{5}$$

where W_{SP} is the maximum surface soil water capacity attributed to capillary pores, defined as the volumetric fraction of surface soil occupied by capillary pores multiplied by the thickness of the surface soil; W_{ST} is the total saturation capacity of the surface soil; and a and b are constant parameters determining together with W_{SP} the shape of the suction curve.

The difference between W_{ST} and W_{SP}, termed as W_{SN}, i.e., $W_{SN}=W_{ST}-W_{SP}$, is the saturation capacity due to non-capillary pores in surface soil, and was considered to be a product of the volumetric fraction of non-capillary pores in the surface soil and the thickness of the surface soil. W_{SN} was treated as a function of total belowground biomass, m_{bT}:

$$W_{SN}=W_{SNM}\left[1-\exp\left(-\frac{m_{bT}}{M_{bT}}\right)\right] \tag{6}$$

where W_{SNM} is the maximum possible surface soil non-capillary water capacity, a parameter depending on the texture, density and particle size distribution of the original soil matrix; and M_{bT} is the total belowground biomass at which the non-capillary water capacity in surface soil is approximately 63% of W_{SNM}. W_{SNM} sets up an upper limit for W_{SN}, hence preventing the non-capillary water capacity of the surface soil from belowing out when belowground biomass grows to very large values.

The water potential of the core soil layer was described by

$$\psi_b= a\left[\left(\frac{W_{BP}}{W_b}\right)^b-1\right]-\frac{D_s+D_b}{200} \tag{7}$$

where W_{BP} is the maximum water capacity of the core soil layer; D_s and D_b are respectively the thickness of the surface and core soil layers. Similar to W_{SP}, W_{BP} is defined as the volumetric fraction of capillary pores in the core soil multiplied by the thickness of the core soil layer. The last term in (7) defines the gravity potential.

The hydraulic conductivities of the surface and core soil layers were calculated by,

$$g_s=\begin{cases} \frac{K_0}{D_s}\left(\frac{W_s}{W_{SP}}\right)^d, & \text{if } \psi_s\geqslant\psi_b \text{ or } W_s\leqslant W_{SP} \\ K_0/D_s, & \text{Otherwise} \end{cases} \tag{8}$$

$$g_b = \frac{K_0}{D_b}\left(\frac{W_b}{W_{BP}}\right)^d \qquad (9)$$

where K_0 is the saturated volumetric hydraulic conductivity coefficient due to capillary porosity; and d is a shape parameter. Notice that g_s can be greater than K_0/D_s for downward flow due to the non-capillary pores in the surface soil, while g_b cannot exceed K_0/D_b because there were no non-capillary pores assumed for the core soil layer. The surface soil conductivity coefficient g_s is bounded by K_0/D_s if upward water flux is detected.

(3) Cation movement and exchange

The total area concentrations of sodium and calcium cations were expressed as

$$N_{asT} = W_S N_{as} + E_{as} X_{Nas} \qquad (10)$$

$$C_{asT} = W_S C_{as} + \frac{1}{2} E_{as} X_{Cas} \qquad (11)$$

$$N_{abT} = W_b N_{ab} + E_{ab} X_{Nab} \qquad (12)$$

$$C_{abT} = W_b C_{ab} + \frac{1}{2} E_{ab} X_{Cab} \qquad (13)$$

where N_{asT}, C_{asT}, N_{abT} and C_{abT} are the total area concentrations (volumetric concentration multiplied by soil layer thickness) of sodium for surface soil, calcium for surface soil, sodium for core soil and calcium for core soil respectively; N_{as}, C_{as}, N_{ab} and C_{ab} are the corresponding volumetric concentrations of soluble sodium and calcium cations in the two soil layers; X_{Nas}, X_{Cas}, X_{Nab}, and X_{Cab} are the respective exchangeable cations of sodium and calcium for the two soil layers; and E_{as} and E_{ab} are two constants signifying the number of 100 g dry soil mass per square centimeter for the two soil layers.

The differential equations describing the dynamics of the total cation concentrations were

$$\frac{dN_{asT}}{dt} = -G_{sb}(\psi_s - \psi_b)(N_{as}S_s + \bar{S}_s N_{ab}) \qquad (14)$$

$$\frac{dC_{asT}}{dt} = -G_{sb}(\psi_s - \psi_b)(C_{as}S_s + \bar{S}_s C_{ab}) \qquad (15)$$

$$\frac{dN_{abT}}{dt} = G_{sb}(\psi_s - \psi_b)(N_{as}S_s + \bar{S}_s N_{ab}) - G_{bb}(\psi_b - \psi_{bb})(N_{ab}S_b + N_{abb}\bar{S}_b) \qquad (16)$$

$$\frac{dC_{abT}}{dt} = G_{sb}(\psi_s - \psi_b)(C_{as}S_s + \bar{S}_s C_{ab}) - G_{bb}(\psi_b - \psi_{bb})(C_{ab}S_b + C_{abb}\bar{S}_b) \qquad (17)$$

where S_s and S_b are two switch variables for the surface and core soil layers; and $\bar{S}_s$ and $\bar{S}_b$ are the conjugated variables of S_s and S_b. If $\psi_s > \psi_b$, $S_s = 1$ and $\bar{S}_s = 0$; otherwise $S_s = 0$ and $\bar{S}_s = 1$. Similarly if $\psi_b > \psi_{bb}$, $S_b = 1$ and $\bar{S}_b = 0$; otherwise $S_b = 0$ and $\bar{S}_b = 1$. Parameters N_{abb} and C_{abb} describe the boundary concentrations of soluble sodium and calcium cation, respectively.

Cation exchange were formulated after Bohn et al. (1985)

$$X_{Cas}+X_{Nas}=C_{ec} \tag{18}$$

$$X_{Cab}+X_{Nab}=C_{ec} \tag{19}$$

$$N_{as}+X_{Cas}=K\sqrt{C_{as}}X_{Nas} \tag{20}$$

$$N_{ab}+X_{Cab}=K\sqrt{C_{ab}}X_{Nab} \tag{21}$$

where C_{ec} is the soil cation exchange capacity and K is a constant.

(4) Vegetation dynamics

The carbon assimilation rate for plant species i was formulated in the following form

$$Ph_i=G_{ri}R_sQ_{xi}(X_{Nas}/C_{ec})Q_{wi}(W_s)m_{ai}\left[1-\frac{\sum_i m_{ai}}{M_{Pi}}\right] \tag{22}$$

where Ph_i is the assimilation rate for species i, $R_s(t)$ is the net radiation in; m_{ai} is the aboveground biomass of species i; Q_{xi} and Q_{wi} are unimodal functions of X_{Nas}/C_{ec} and W_s (described in full later); and G_{ri} and M_{Pi} are constant parameters. Equation (22) implies that the assimilation rate is positively proportional to net radiation but inhibited by the stress of soil water and soil alkali. Competition between different plant species was partially reflected in the brackets indicating the effects of aboveground biomass of other species on species i.

The assimilation was partitioned into above- and belowground biomass (Brouwer, 1962) by,

$$p_{ai}=\frac{t_{ei}-t}{t_{ei}-t_{si}} \tag{23}$$

$$p_{bi}=1-p_{ai} \tag{24}$$

where p_{ai} and p_{bi} are fractions of assimilated materials partitioned to aboveground and belowground biomass; t_{si} and t_{ei} are respectively the start and end time of growing season of species i, respectively. While all assimilated material goes to aboveground biomass at the very beginning of the growing season, the portion to aboveground biomass decreases until the end of the growing season when all material goes to belowground biomass.

Plant respiration in MAGE included two parts, the maintenance respiration proportional to biomass and the growth respiration proportional to growth rate (Thornley, 1972).

$$R_{ai}=r_{ai}m_{ai}+r_{dai}\dot{m}_{ai} \tag{25}$$

$$R_{bi}=r_{bi}m_{bi}+r_{dbi}\dot{m}_{bi} \tag{26}$$

where R_{ai} and R_{bi} are total respiration rates of aboveground biomass and belowground biomass respectively; r_{ai}, r_{bi}, r_{dai} and r_{dbi} are constant coefficients; $\dot{m}_{ai}=dm_{ai}/dt$; and $\dot{m}_{bi}=dm_{bi}/dt$.

Germination or rejuvenation of a plant species are controlled by its phenomenological characteristics and the external environment, and was described by

$$G_{gi}=g_{fi}m_{bi}Q_{gi}(t)Q_{xi}(X_{Nas}/C_{ec})Q_{wi}(W_s) \tag{27}$$

where G_{gi} is the germination/rejuvenation rate of species i, Q_{gi} is a unimodal function of time t describing the phenomenological characteristics of germination/rejuvenation; and g_{fi} is a constant parameter.

While the death of aboveground organs was considered to maintain the balance between respiration and assimilation, plant root was assumed to die at a specific rate as a function of time t. Thus,

$$D_{ai}=\begin{cases} 0, & \text{if } Ph_i+G_{gi}-R_{ai}>0 \\ d_{ai}(R_{ai}-Ph_i-G_{gi}), & \text{otherwise} \end{cases} \tag{28}$$

$$D_{bi}=d_{bi}m_{bi}t^{\alpha_i} \tag{29}$$

where D_{ai} and D_{bi} are respectively the death rates of aboveground and belowground biomass of the i'th species; d_{ai} and d_{bi} are the death coefficients for the two biomass variables; and α_i is a constant parameter.

With the above treatments of plant physiology, the equations for vegetation dynamics of the model were expressed as,

$$\frac{dm_{ai}}{dt}=Ph_ip_{ai}+G_{gi}-R_{ai}-D_{ai}-H_i \tag{30}$$

$$\frac{dm_{bi}}{dt}=Ph_ip_{bi}-G_{gi}-R_{bi}-D_{bi} \tag{31}$$

where H_i is the harvesting intensity defined as follows:

$$H_i=\begin{cases} \sum_{j=1}^{N_h}\delta(t-\tau_{ij})\ (m_{ai}-\mathrm{HCL}), & \text{if } m_{ai}>\mathrm{HCL}_j \\ 0, & \text{otherwise} \end{cases} \tag{32}$$

in which $\delta(t-\tau_{ij})$ is the Kronecker impulse function at time $t=\tau_{ij}$; HCL is a prescribed harvest control level; and N_h is the number of times of harvests. Equation (32) states that if the aboveground biomass is greater than prescribed HCL when the harvest time is due, cut the excessive amount and keep the HCL. Otherwise simply skip the harvesting operation.

(5) The unimodal functions used in this model