

Ecological dynamic model of grassland and its practical verification

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Abstract Based on the physico-biophysical considerations, mathematical analysis and some approximate formulations generally adopted in meteorology and ecology, an ecological dynamic model of grassland is developed. The model consists of three interactive variables, i.e. the biomass of living grass, the biomass of wilted grass, and the soil wetness. The major biophysical processes are represented in parameterization formulas, and the model parameters can be determined inversely by using the observational climatological and ecological data. Some major parameters are adjusted by this method to fit the data (although incomplete) in the Inner Mongolia grassland, and other secondary parameters are estimated through sensitivity studies. The model results are well agreed with reality, e.g., (i) the maintenance of grassland requires a minimum amount of annual precipitation (approximately 300 mm); (ii) there is a significant relationship between the annual precipitation and the biomass of living grass; and (iii) the overgrazing will eventually result in desertification. A specific emphasis is put on the shading effect of the wilted grass accumulated on the soil surface. It effectively reduces the soil surface temperature and the evaporation, hence benefits the maintenance of grassland and the reduction of water loss in the soil.

Keywords: grassland, ecological dynamic model, evapotranspiration, shading effect, moisture index, desertification.

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Grassland is an open ecological system, interacting with the surrounding environment by the exchange of mass, energy and information. The growth of plant relates to the activities such as photosynthesis, respiration and transpiration. Besides, there are budburst, aging and wilting. The dynamical ecosystem model can be developed if the relevant physical and bio-

physical laws and the influences of environment are all known. This issue is not only of practical interest in the ecological investigation, but also one of the important subjects in the studies of vegetation-climate interactions as well as the globe change problems.

Generally speaking, there are three major approaches in the studies of the ecosystem dynamics,

i.e., field observations and laboratorial experiments^[1], physico-mathematical analyses (i.e. development of theoretical models)^[2-4], and numerical simulations^[5-7]. These methods are often used in combination with each other, e.g., the theoretical models should be calibrated and verified by the observational and experimental data, and the successful numerical simulations can only be based on good dynamical models. It should be pointed out that the processes of photosynthesis and transpiration are very complicated, and the transfer and exchange of mass and energy between vegetation and surrounding environment include macroscopic, mesoscopic and microscopic processes. Up to now relevant formulas are obtained by semi-theoretical and semi-experimental methods as well as semi-macroscopical and semi-microscopical considerations. Even so, these formulas still include many parameters that should be determined by the experiments or observations. Therefore, more or less comprehensive models developed nowadays in such a way can be applied only to the numerical simulations with massive computation, and are difficult in giving clear ecological pictures and conclusions.

The parameterization method is often used to describe the processes involved in a system by some macroscopic variables and a few parameters. Using this method with reliable physico-mathematical consideration, we can develop models that are suitable for making theoretically qualitative and even quantitative analyses and are practical in application. Based on physical laws, mathematical logics and reality constraints, we had developed such a simplified grassland model^[8-10]. There are only two variables in the model, and the essential processes such as photosynthesis and evapotranspiration are parameterized with a few parameters determined by the field observational data and remote sensing data. The two-variable model is further improved and extended into a three-variable one^[11]. In this paper we will first briefly describe this new model, and then emphasize the estimation and determination of the model parameters as well as the practical verification of the model results by using the observational data. Such research is of the same importance as the development of models.

1 Ecological dynamic model of grassland with three variables

Consider that the ecosystem consists of living grass with biomass x ($\text{kg} \cdot \text{m}^{-2}$), soil wetness with available water mass y ($\text{kg} \cdot \text{m}^{-2}$, or mm), and the wilted grass (accumulated on the soil surface) with biomass z ($\text{kg} \cdot \text{m}^{-2}$). According to the mass conservation law, we have

$$dx/dt = F_1 = G(x, y) - D(x, y) - C(x), \quad (1)$$

$$dy/dt = F_2 = P - E(x, y, z) - R(x, y, z), \quad (2)$$

and

$$dz/dt = F_3 = G_z(x, y) - D_z(z) - C_z(z), \quad (3)$$

where terms G , D , and C are the growth (net primary productivity), wilting, and consumption (including grazing) of the living leaves respectively, G_z , D_z , and C_z are the accumulation, decomposition, and consumption of the wilted leaves respectively, P is the water sources of soil (including precipitation, irrigation and so on, but denoted simply as precipitation in this paper), E is the evapotranspiration, and R is the runoff.

In the model, P is prescribed, and the formulations of other processes are derived from physical laws and mathematical analyses. For example, the growth term G can be expressed as $\mathbf{a}^* G_1 G_2$, where G_1 and G_2 are functions depending only on the variables x and y respectively, and the coefficient \mathbf{a}^* is the maximum growth rate depending on the climatic and environment conditions such as sunlit, temperature and soil fertilizer. The similar method can be applied to the formulations of D , E and R . Besides, G_z is proportional to D , and terms C and C_z are assumed as functions of x and z respectively (see ref. [11] for detail). Denote that the fraction of living grass coverage is \mathbf{s}_f ($0 \leq \mathbf{s}_f \leq 1$), and assume that the accumulation of wilted grass on the soil surface is uniform. Then we have

$$G = \mathbf{a}^* (1 - e^{-e_g x/x^*}) (1 - e^{-e'_g y/y^*}), \quad (4)$$

$$D = \mathbf{a}^* \mathbf{b} (e^{e_d x/x^*} - 1)(1 - e^{-e'_d y/y^*})^{-1} \quad (5)$$

$$C = \mathbf{a}^* \mathbf{g} (1 - e^{-e_c x/x^*}), \quad (6)$$

$$G_z = \mathbf{a}_z D = \mathbf{a}^* \mathbf{a}_z \mathbf{b} (e^{e_d x/x^*} - 1)(1 - e^{-e'_d y/y^*})^{-1}, \quad (7)$$

$$D_z = \mathbf{a}^* \mathbf{b}_z (e^{e_{dz} z/z^*} - 1), \quad (8)$$

$$C_z = \mathbf{a}^* \mathbf{g}_z (1 - e^{-e_{cz} z/z^*}), \quad (9)$$

$$E = E_s + E_r, \quad (10)$$

$$E_s = e_s^* e^{-e_3 z/z^*} \left[(1 - \mathbf{s}_f) + \mathbf{s}_f \left(1 - \mathbf{k}_1 \left(1 - e^{-e_1 x/x^*} \right) \right) \right] (1 - e^{-e_2 y/y^*}), \quad (11)$$

$$E_r = e_s^* \mathbf{j}_{rs} \mathbf{s}_f (1 - \mathbf{k}'_1 e^{-e'_1 x/x^*}) (1 - e^{-e'_2 y/y^*}), \quad (12)$$

$$R = \mathbf{I} P e^{-e_3^* z/z^*} \left[(1 - \mathbf{s}_f) + \mathbf{s}_f \left(1 - \mathbf{k}''_1 \left(1 - e^{-e_1^* x/x^*} \right) \right) \right] (e^{e_2^* y/y^*} - 1), \quad (13)$$

and

$$\mathbf{s}_f = 1 - e^{-e_g x/x^*}, \quad (14)$$

where x^* , y^* , and z^* are the characteristic values of the corresponding state variables x , y and z (the characteristic value is only the approximate scale and its introduction makes the order of the magnitude of the corresponding dimensionless variable, e.g. x/x^* , being 1, which is convenient for computation). All the parameters, except for \mathbf{a}^* and e_s^* , are dimensionless; E_s and E_r are the evaporation from the soil surface and the transpiration from the living grass foliage respectively; e_s^* is the potential evaporation and takes place as ($x \rightarrow 0$, $z \rightarrow 0$, $y \rightarrow \infty$), and $e_r^* \equiv \mathbf{j}_{rs} e_s^*$ is the potential transpiration and takes place as ($x \rightarrow \infty$, $y \rightarrow \infty$). The shading of plants reducing the sunshine and the covering of wilted grass both can reduce surface evaporation. The runoff term can be also reduced by the obstacle of the living and wilted grass. It should be pointed out that the formulation of C and C_z in (6) and (9) is arbitrary to some extent, but this does not affect the qualitative analysis.

In principle, all parameters in the model as well as the characteristic values x^* , y^* , and z^* can be determined by theoretical calculations if the relevant properties of the ecosystem and the data of its environment are available. However, such data are very difficult to be obtained. A more convenient way is to infer these parameters by the application of inverse method to the observational data or remote sensing^[12, 13]. Moreover, some parameters are of secondary importance, to which the model is less sensitive (see section 2). In addition, under considering the seasonal variations all coefficients, \mathbf{a}^* and e_s^* and P should depend on time.

2 The determination of the characteristic values and the model parameters

2.1 The characteristic values

Take the temperate semi-arid grassland in Inner Mongolia as an example. The characteristic value x^* can be chosen as the average over a large area of natural grassland. As x is taken as the dried green grass, $x^* = 10^3 \text{ kg} \cdot \text{hm}^{-2} = 0.1 \text{ kg} \cdot \text{m}^{-2}$ according to the observational data from the Inner Mongolian grassland (provided by Gang Zhao and Mingxu Zhao) as well as the data in refs. [1, 14]. These data also show that about half of the grass wilts and accumulates on the soil surface after autumn. This means that z^* and x^* are of the same order of magnitude, so we take $z^* = x^*$.

There are only few stations monitoring the soil wetness. Although both the climatological mean of soil wetness (y^*) and the field capacity (denoted as y^{**}) in each station vary a lot from west to east in the Inner Mongolia grassland, it can be inferred that $y^*/y^{**} \approx 0.5$ ^[1, 16, 17]. Hence we take a local y^* , and let $y^* = 0.5y^{**}$.

2.2 Parameters e_g , e'_g , e_1 , e'_1 , e_2 , e'_2 , \mathbf{k}_1 and \mathbf{j}_{rs}

According to the aforementioned data, the fraction of grass coverage \mathbf{s}_f in Inner Mongolia is around 0.25—0.8; and in the eastern part \mathbf{s}_f can be as high as 0.9, where x/x^* is around 2 and the growth term G should approach its maximum value, i.e. $1 - e^{-e_g x/x^*} \approx 1$. Therefore we can take $e_g = 1$. From eqs. (4)—(14)

it is easy to know that e_1 and e'_1 are approximately equal to e_g .

The general formulation for the evaporation from bare soil can be expressed as

$$E_s = e_s^* (1 - e^{-y/y^{**}}). \quad (15)$$

When the soil water is near saturated, it should have $y/y^{**} \approx 1$ and $E_s \approx e_s^*$, so in this paper, we take $e = 2$. Let $y^*/y^{**} \approx 0.5$. We have $e_2 = e y^*/y^{**} = 1$. Consider that the influence of soil water on transpiration and photosynthesis is similar to that on evaporation, so we take $e'_g = e'_2 = e_2$.

The parameters k_1 and j_{rs} are two essential parameters describing the vegetation-soil interaction in the model. However, so far they can only be inferred indirectly from some incomplete observational data. Obviously, from eq. (11) we have

$$k_1 = \frac{E_s(0, \infty, 0) - E_s(\infty, \infty, 0)}{E_s(0, \infty, 0)}. \quad (16)$$

Substituting the evaporation formula expressed by the vertical gradient of water vapor density and the resistance to (16), we obtain

$$k_1 = \frac{p_{vsat}(T_s^*) - p_{vsat}(T_s^{**})}{p_{vsat}(T_s^*) - RH \cdot p_{vsat}(T_a)}, \quad (17)$$

where p_{vsat} is the saturation vapor pressure, T_s^* and T_s^{**} are the soil surface temperature under the condition of $(x \rightarrow 0, y \rightarrow \infty, z \rightarrow 0)$ and $(x \rightarrow \infty, y \rightarrow \infty, z \rightarrow 0)$ respectively, and T_a and RH are the air temperature and the relative humidity respectively. Thus, k_1 can be determined if T_a, T_s^*, T_s^{**} and RH are all available.

Inner Mongolia Institute of Meteorology has set up several stations to monitor the surface soil temperature in August for several years. In each sta-

tion there are a pair of observational points (A and B) that are separated by about 400—500 meters and have significantly different vegetation distribution (with $S_f \approx 0.2$ in A and $S_f \approx 0.9$ in B). Data show that the surface soil temperatures in A and B differ from 5—6°C in the daytime (the major hours for evapotranspiration). Hence we can assume that $T_s^* - T_s^{**} \approx 5—10^\circ\text{C}$. Taking $RH=0.6$, the average relative humidity in summer in Inner Mongolia, the values of k_1 under different T_s^* , $\Delta_s \equiv T_s^* - T_s^{**}$, and $\Delta_{sa} \equiv T_s^* - T_a$ are calculated and shown in table 1.

Obviously, parameter k_1 is the major index of the shading effect of the living leaves in blocking the sunlight and reducing the soil surface temperature and hence in reducing the evaporation from the soil surface, so it depends only on the climatic conditions and soil properties but not the grass species. From table 1, it is reasonable to choose $k_1=0.3—0.7$ in Inner Mongolia.

Now we determine j_{rs} , i.e. the ratio of potential transpiration to potential evaporation. The transpiration can be treated as the wet surface evaporation under the temperature at the leave T_l^* , which is approximate to the air temperature at the same height and so is below T_s^* , hence we have $j_{rs} < 1$. Because $(x \rightarrow \infty, y \rightarrow \infty)$ is an ideal state, j_{rs} depends only on the climate-soil conditions and plants height excepting some drought-resistant species. Hence, j_{rs} can be expressed as

$$\begin{aligned} j_{rs} &= \frac{e_r^*}{e_s^*} = 1 - \frac{e_s^* - e_r^*}{e_s^*} \\ &= 1 - \frac{p_{vsat}(T_s^*) - p_{vsat}(T_l^*)}{p_{vsat}(T_s^*) - RH \cdot p_{vsat}(T_a)}. \end{aligned} \quad (18)$$

Table 1 The dependence of k_1 on T_s^*, T_s^{**} and T_a

T_s^*	(Δ_{sa})	20°C			15°C			10°C		
	(Δ_s)	5°C	8°C	10°C	5°C	8°C	10°C	5°C	8°C	10°C
40°C		0.30	0.44	0.52	0.32	0.48	0.57	0.35	0.54	0.63
35°C		0.31	0.44	0.52	0.34	0.48	0.58	0.37	0.55	0.67
30°C		0.31	0.45	0.54	0.34	0.49	0.59	0.37	0.56	0.67

Denote that $\Delta_{sl}=T_s^*-T_l^*$, during summer time in Inner Mongolia $\Delta_{sl} \leq 7^\circ\text{C}$. Table 2 shows the value of \mathbf{j}_{rs} under different T_s^* , Δ_{sl} and Δ_{sa} . In general, Δ_{sl} increases and \mathbf{j}_{rs} decreases with the height of the plant.

In this paper we use $(\mathbf{k}_1, \mathbf{j}_{rs})=(0.3, 0.7), (0.4, 0.6), (0.5, 0.5),$ and $(0.7, 0.7)$ for the numerical simulations.

2.3 Parameters such as $\mathbf{a}^*, \mathbf{b}, \mathbf{g}, \mathbf{g}_z, \mathbf{a}_z$

Parameter \mathbf{a}^* can be derived from the observational data by the inverse method. For example, taking

$$x^* = \int_{\Delta t = \text{half year}} \mathbf{a}^* G_1 G_2 dt \approx \bar{\mathbf{a}}^* \bar{G}_1 \bar{G}_2 \Delta t,$$

we have
$$\bar{\mathbf{a}}^* = \frac{x^*}{\Delta t} (\bar{G}_1 \bar{G}_2)^{-1} \equiv \frac{x^*}{\Delta t} \mathbf{a}. \quad (19)$$

If the characteristic time scale is given as $t^* = \Delta t = 0.5$ a, the dimensionless variable $\bar{\mathbf{a}} \left(= \frac{t^*}{x^*} \frac{x^*}{\Delta t \bar{G}_1 \bar{G}_2} \right)$ is approximate to 1. Note that in this paper we investigate the equilibrium state which is independent of t^* , so we take the correspondent dimensionless $\mathbf{a} = 1$. Besides, when the soil is nearly fully covered and canopy water is near to saturation (e.g. $x/x^* \approx 2$ and $y/y^{**} \approx 1$), the growth term G should balance the wilting term D , i.e. $G=D$, therefore, $\mathbf{b} \approx 0.1$. Also, as we have mentioned above, half of the wilted leaves are accumulated on the ground, so we take $\mathbf{a}_z = 0.5$.

Parameters \mathbf{g} and \mathbf{g}_z should be determined by the practices of grazing or other consumptions, and are

adjustable. Here we take $\mathbf{g}=0.1$ and $\mathbf{g}_z=0.0$ for the case of no-heavy grazing.

There are less data for calibrating parameters such as $\mathbf{b}_z, \mathbf{e}_d, \mathbf{e}'_d,$ and \mathbf{e}_{dz} . They are to be determined by doing sensitivity numerical experiments and then fitting the data to the observed ecosystem. Note that these parameters are of less importance, and the solution of the ecosystem is indeed less sensitive to them.

3 Dimensionless equations and parameters

Let $x \equiv x/x^*, y \equiv y/y^*, z \equiv z/z^*$, and $t \equiv t/t^*$ denote the dimensionless variables of the corresponding state variables respectively, and introduce two new dimensionless variables $\mathbf{a} = \mathbf{a}^* t^*/x^*$ (i.e., $\bar{\mathbf{a}}$ presented in section 2), and

$$\mathbf{m} = P/e_s^*, \quad (20)$$

where \mathbf{m} is called the ‘‘moisture index’’ in the following. It is one of the important parameters for describing the climatic conditions.

Substituting the dimensionless variables to eqs. (1)—(3), we can get the dimensionless equations.

Obviously, the characteristic values of dimensionless variables $x, y,$ and z are 1. In the following sections we denote $x, y,$ and z as $x, y,$ and z . Table 3 shows the values of the dimensionless parameters when the seasonal and annual variations are neglected.

4 The stable equilibrium states of the ecosystems

Integrating eqs. (1)—(3) with a prescribed \mathbf{m} the

Table 2 The dependence of \mathbf{j}_{rs} under different T_s^*, T_l^* and T_a

T_s^*	(Δ_{sa})	20°C			15°C			10°C			5°C		
	(Δ_{sl})	3°C	5°C	7°C	3°C	5°C	7°C	3°C	5°C	7°C	3°C	5°C	7°C
40°C		0.81	0.70	0.61	0.80	0.68	0.58	0.78	0.65	0.51	0.72	-	-
35°C		0.81	0.69	0.59	0.80	0.66	0.56	0.77	0.63	0.48	0.72	-	-
30°C		0.81	0.69	0.59	0.79	0.66	0.56	0.77	0.63	0.48	0.71	-	-

Table 3 Values of the dimensionless parameters

x^*, y^*, z^*	\mathbf{a}	\mathbf{a}_z	\mathbf{b}, \mathbf{b}_z	\mathbf{g}	\mathbf{g}_z	$\mathbf{e}_g, \mathbf{e}'_g, \mathbf{e}_{dg}, \mathbf{e}'_{dg}, \mathbf{e}_o, \mathbf{e}_{dz}, \mathbf{e}_{cz}$	
1.0	1.0	0.5	0.1	0.1	0	1.0	
\mathbf{m}	\mathbf{j}_{rs}	\mathbf{l}	\mathbf{k}_1	\mathbf{k}'_1	\mathbf{k}''_1	$\mathbf{e}_1, \mathbf{e}''_1$	$\mathbf{e}'_1, \mathbf{e}_2, \mathbf{e}'_2, \mathbf{e}''_2, \mathbf{e}_3, \mathbf{e}''_3$
Adjustable	(0.3—0.7)	0.015	(0.7—0.3)	1.0	0.5	0.7	1.0

system always approaches the equilibrium states. The stable and unstable equilibrium states under different values of the moisture index m are shown in fig. 1. Note that only the stable equilibrium state associates with the possible ecosystem in nature. Fig. 1 implies that the ecosystem is a desert with no grass ($x = 0$) in the case of $m < m_1$, is a grassland in the case of $m > m_2$, and is a grassland or desert depending on the initial conditions of (x, y, z) in the case of $m_1 < m < m_2$. Hence, a minimum annual precipitation is required to maintain a grassland. Under the chosen (k_1, j_{rs}) , m_1 is around 0.3 and m_2 is larger than 0.3. For comparison, some segmental data of the observed grass productivity in Inner Mongolia (after chapter 15 of ref. [1], see table 4) are also plotted in fig. 1, and the geographical distribution of Inner Mongolia ecological regimes overlapped with the contour of moisture index is shown in fig. 2. It can be seen that the simulation results are well consistent with the observational data.

Note that: (i) some new observational data (although incomplete) obtained by Gang Zhao and Mingxu Zhao as well as cited from ref. [14—16, 18] give almost the same results as in Chapter 15 of ref.

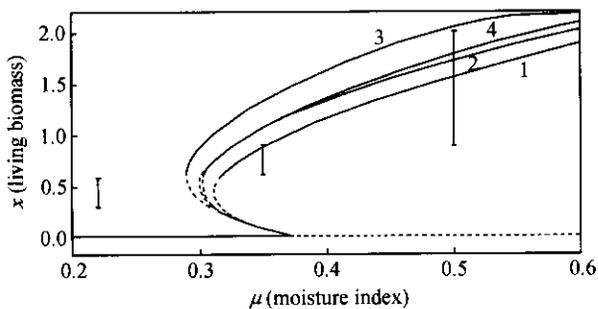


Fig. 1. The dependence of the equilibrium living biomass x on the moisture index m . The solid and dash lines refer to the stable and unstable equilibrium states respectively. The vertical segments show the observed living biomass (after table 4), but the grass in $m < 0.3$ belongs to another species. Curves 1—4 correspond to the cases of $(k_1, j_{rs}) = (0.3, 0.7)$, $(0.4, 0.6)$, $(0.5, 0.5)$, and $(0.7, 0.7)$.

Table 4 Grass productivity in the Inner Mongolian grassland^[15]

$P/\text{mm} \cdot \text{a}^{-1}$	m	$x/\text{kg} \cdot \text{hm}^{-2}$	x/x
≥ 400	≥ 0.4	900—2000	0.9—2.0
300—400	0.3—0.4	600—900	0.6—0.9
150—300	0.15—0.3	300—600	0.3—0.6

[1]; (ii) the horizontal scale of climatic condition (larger than 100 km) is very much larger than that of the soil properties (less than 10 m), so in table 4, m and x can be only averaged over a large enough area and divided into several intervals; (iii) the precipitation in Inner Mongolia is concentrated in summer time, and the annual mean of m is almost the same as the seasonal mean in summer; and (iv) in Inner Mongolia, in the extreme eastern part $m > 0.6$ and there is forest or forest-grass ecosystem, while in the western part $m < 0.3$ and there grows sparse desert grass and shrub, and the species in these two ecosystems are very different from the typical grassland and so are not considered in our model.

5 Conclusions and discussions

An ecological dynamical model of grassland is developed from the physio-mathematical laws and some practical constraints. The model is theoretically solid and suitable to practical application. The model parameters are adjusted to the observational data or remote sensing data by using the inverse method.

Analyses of the model results and their comparison with the observational data in Inner Mongolia lead to the following conclusions: (i) a minimum annual precipitation is required for the existence of grassland; (ii) the transition from grassland to desert is abrupt, and (iii) when the moisture index m is in the region of (m_1, m_2) , two equilibrium states of grassland and desert can coexist, and overgrazing will result in irreversible desertification. Especially, in order to rebuild a grassland from a degraded one, the long enough irrigation would be needed for the grass to grow approaching the equilibrium state of grassland. Besides, in the western parts of China which are mainly arid and semi-arid regions, it is better to plant drought-resistant grass than trees that consume too much of groundwater. Our other conclusions are: (iv) the coverage of wilted vegetation is important to shade the soil surface and block the transport of water-vapor in the soil, which is in agreement with the experiences of farmers, i.e., the planting of dead or wilted leaves can conserve soil water and prevent the soil from being removed.

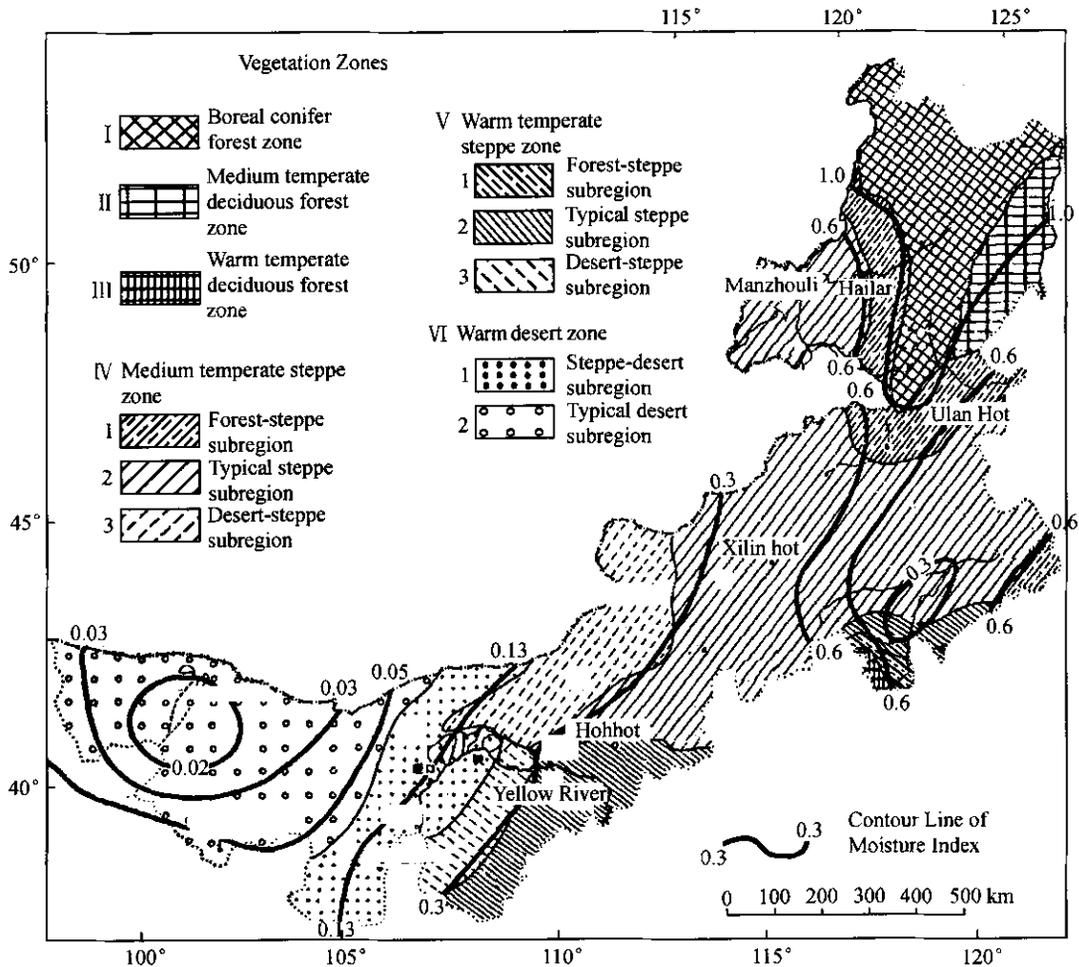


Fig. 2. Distribution of vegetation zone and moisture index in the Inner Mongolia.

However, wilted leaves carry the hazard of fire, so it should be kept at a proper level; (v) the shading of vegetation and wilted biomass effectively reduces evaporation from the soil surface, and also benefits water resources conservation and natural environment improvement.

Our future work will be: (i) making use of the data around the world to further verify the model; (ii) calculating the parameters from the remote sensing data; (iii) taking into account the seasonal variations of the parameters in the model; (iv) considering the interannual variation of moisture index m and then investigating the long-term evolution of grassland.

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