A model for Seasonal Changes in Productivity and Solar Energy Utilization of Grazing Pasture

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The efficiency of solar energy utilization in pasture plant production is often observed to be higher in the cutting use than in the grazing use in most of the measurements done from the agricultural viewpoint. The annual mean efficiency in the cutting use on fertile fields is generally found to be in the range from 0.6% (temperate grasses and legumes) to 1.4% (rotational cultivation of temperate and tropical grasses, e.g. Italian ryegrass—Guineagrass), while the efficiency in the grazing use is estimated to be at most 0.2–0.3% in temperate grass (clover pasture) in this country. When the conversion efficiency from solar radiant energy to cattle body weight gain was calculated, very low efficiency values are obtained as shown in Table 1. It is shown that there is a big difference in the efficiency between the actual field value and the laboratory value, though both of the calculations are only rough estimation. The difference would be mostly due to the unbalance between herbage production and intake by animals under grazing in hilly grasslands. It would be important, therefore, to study the mutual actions among environment, pasture plants and animals, especially in grazing grassland. It must be important also that the efficiency of pasture production should be evaluated from the viewpoint of the long term stability in case of grazing use.

Modeling and simulation would be an effective approach to evaluate stable productivity in such a complex system and to clarify the interaction among the components of the system. A mathematical model concerning biomass dynamics in grazing grassland was already formulated as a preliminary trial in the previous paper (Ōkubo et al. 1975[4]). The main purpose of the model was to describe the seasonal changes of plant growth under grazing conditions different in solar radiation and temperature.

In the present paper, concepts and equations of the model are described in a digested form but are expressed in terms of the energy flow dynamics and efficiency. Emphasis is placed on the response of photosynthesis to radiation, response of respiration to temperature, and the response of reserve substances in reserve organs of plants such as rhizome or stolon to the defoliation caused by grazing to various extent.

Elements of the flow system considered are plant, litter, animal and feces. The plant element is divided into five compartments; leaf, stem, rhizome, root and standing dead. The leaf is considered not only as photosynthetic organ but also as main food for animals. The rhizome or stolon in prostrate type grasses as well as the stubble or shoot base in bunch type grasses are expressed similarly in a compartment as the reserve organ. Effect of grazing severity and frequency on both the photosynthetic organ and the reserve organ is also important, so that attention was paid to express the changes in these two compartments. A compartment for the herbage intake by cattle is taken as an additional dummy compartment. The basic idea for the formulation

Table 1. Examples of the energy conversion efficiency in production of pasture plants and cattle under grazing condition in hilly grasslands of Japan, compared with those of cultivation field

Name of farm	Districts	Year	Area of pasture[1]	Number of cattle	Pasture production	Cattle gain or lactation
			ha	head	kg DM/ha/year	kg/head/day
Kamishihoro	(Hokkaidō)	1968	388	604	1, 330	0. 70
		1970	569	1, 169	1, 410	0. 68
Sotoyama	(Tōhoku)	1969	{ 33 294 (native)	186	5, 400	0. 43
		1971	{ 57 583 (native)	229	6, 400	0. 38
Owzasa	(Kantō)	1968	242	574	4, 640	0. 48
		1970	257	538	6, 720	0. 48
Sankyo	(Kyūshu)	1967	60	45 (milking) 85 (others)	6, 450	milk 7. 4
Average		—	—	—	4, 600	0. 53
Coversion efficiency						
from solar radiant energy to harbage available					0. 204%	
from herbage available to body weight gain (Body weight of cattle=300 kg, net energy per D. G.=500 Mcal/kg)						1. 44%
from solar radiation to body weight gain						0. 0029%
Rotational cultivation field of Italian ryegrass·Guineagrass[2]			—	—	kg DM/ha 34, 000	
Conversion efficiency in cutting yield from solar radiant energy					1. 36%/year	
Sown-pasture mixed of orchardgrass and ladinoclover[3]			—	—	kg DM/ha 13, 000	
Conversion efficiency in cutting yield from solar radiant energy					0. 58%/year	
Conversion efficiency from herbage intake to body weight gain in laboratory work (Digestibility=60%, Efficiency in body weight gain from digestible harbage intake=18%[4])						10. 80%
Conversion efficiency from solar radiant energy to body weight gain in laboratory work						0. 062%

Note 1) The main species of vegetation are orchardgrass and white clover.
2) The highest yield record determined in Shikoku Agr. Exp. Sta.
3) Determined in Nat'l Grassl. Res. Inst. located in Kanto.
4) Determined in Nat'l Inst. Animal Industry.

of this kind of compartment model is similar to those by Van Dyne[5].

The model

The compartment model for the dynamics of the grazing grassland ecosystem considered in this paper is given in Fig. 1 as a flow diagram. A series of 9 differential equations shown in Fig. 1 describes the energy flow rates in 9 compartments, V_i, where i=1 to 9. The coefficients f_{ij} indicate the transfer coefficients of energy flow V_i to V_j, and most of them are functions of time t in number of days from the beginning of shoot growth, 1st of May in the present case of the experimental pasture. Most of these functions f_{ij} were the same as those in the previous paper[4], but several functions such as f_{70}, f_{78}, f_{80}, f_{88} and D were revised for the expression in terms of energy flow basis

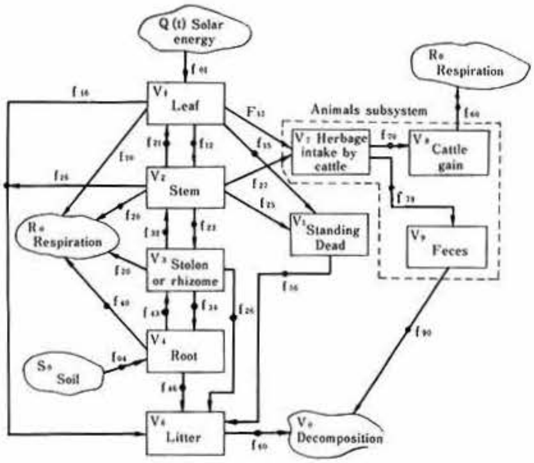

Fig. 1. Flow diagram for plant and cattle growth in grazing grassland

Note 1. Differential equations showing flow rate of organic matter in 9 compartments are:

(1) $dV_1/dt = f_{01}Q(t) + f_{21}V_2 - (f_{10}+f_{12}+f_{15}+f_{16})V_1 - F_{17}$

(2) $dV_2/dt = f_{12}V_1 + f_{32}V_3 - (f_{20}+f_{21}+f_{23}+f_{25}+f_{26})V_2 - F_{27}$

(3) $dV_3/dt = f_{23}V_2 + f_{43}V_4 - (f_{30}+f_{32}+f_{34}+f_{36})V_3$

(4) $dV_4/dt = f_{04}V_4 + f_{34}V_3 - (f_{40}+f_{43}+f_{46})V_4$

(5) $dV_5/dt = f_{15}V_1 + f_{25}V_2 - f_{56}V_5$

(6) $dV_6/dt = f_{16}V_1 + f_{26}V_2 + f_{36}V_3 + f_{46}V_4 + f_{56}V_5 - f_{60}V_6$

(7) $dV_7/dt = F_{17} + F_{27} - (f_{78}+f_{79})V_7$

(8) $dV_8/dt = f_{88} \cdot f_{78}V_7 - f_{80}V_8$

(9) $dV_9/dt = f_{79}V_7 - f_{90}V_9$

Note 2. In the previous report[4], f_{01} of the equation (1) was misprinted as f_{10}, and $f_{26}V_2 + f_{36}V_3$ of the equation (6) as $f_{26}V_2 - f_{36}V_3$

(Table 2).

The detailed explanation for the important functions is given as follows:

1) Solar radiation: The solar radiant flux density (Q, K cal/m^2/day) was represented by equation 1 as a function of time t and which includes parameters both of the annual mean value (a_1) and the maximal deviation from the mean (a_2). The parameters a_1 and a_2 were 3100 and 1100 K cal/m^2/day respectively in the experimental field with *Zoysia*-type vegetation studied here. In case when solar radiation data are available, it will be better to use the actual values.

2) Photosynthesis: The energy yield or total dry matter production of a grass sward is the balance of the input of total photosynthesis (gross photosynthesis) and the output of total respiration. The rate of photosynthesis of the sward depends on solar radiation as well as on leaf area index (L). The value of the maximum photosynthesis (a_9) can be determined by measuring "the maximum crop growth rate" at the optimum L on energy basis at various light intensity and then by adding total respiration estimates (equation 3). L is calculated by the equation 2 from the leaf dry matter (V_1/h_1, where h_1=heat of combustion per gram of dry matter) by using specific leaf area (leaf area per unit leaf dry weight), of which seasonal change is expressed as a function of mean temperature T.

3) Translocation of photosynthate: The growth of leaves started at the beginning of May in the field studied. The initial growth is made by utilizing reserve substance in rhizome with high rate of transfer. Thus, the transfer coefficients, f_{21} and f_{32}, are rather high in spring and early summer but decreases exponentially after mid-summer, which are expressed by equation 4 and 17. On the other hand, the coefficient of transfer rate from leaf to stem (f_{12}) increases from the start on May 1 till the heading stage of the grass (heading stage; $t=1/4$. (a_{18}–a_{17})) and then decreases towards autumn, as expressed by a sine curve of time t in the equation 5. The coefficient from stem to rhizome (f_{23}) is expressed by a logistic curve in the equation 16, which increases slowly in spring and rapidly in autumn.

4) Dead plant materials: The coefficients f_{15} and f_{25} are also expressed by a logistic curve, which shows that the senescence and death of leaves and stalks occur gradually from summer and become remarkable in autumn towards frosty days. Otherwise, a part of leaves and stalks sustains damage from treading by cattle, covering by their feces and biting off by other small animals, which leads to litter (equation 11, 19).

Table 2. Expression of transfer coefficients of energy

No.	Expression of transfer coefficients	Notes
1	$Q=a_1+a_2[\sin(2\pi(t+a_3)/a_4)]$	Q: Solar radiant flux density (kcal/m²/day This equation is used in case when the actual solar radiation data are not available.
2	$L=a_5(a_6+a_7T+a_8T^2)V_1/h_1$	L: Leaf area index. T: Average temperature for every ten days (°C). h_1: Heat of combustion (kcal/g D. M.).
3	$f_{01}=a_9\{1-1/(a_{10}L+1)\}\{a_{11}/(a_{11}Q+1)\}$	$f_{01}\cdot Q$: Photosynthesis of sward on ground area basis (kcal/m²/day). f_{01}: Efficiency of solar energy conversion. f_9: Maximum photosynthesis (kcal/m²/day).
4	$f_{21}=a_{12}\exp(-a_{13}t)+a_{14}F_{17}$	F_{17}: Amount of grazing from leaves per ground area (kcal/m²), which accelerates f_{21}.
5	$f_{12}=a_{15}+a_{16}[\sin(2\pi(t+a_{17})/a_{18}]$	f_{12}: This coefficient attains to the maximum during the heading stage of the grasses.
6	$f_{10}=a_{19}+a_{20}T$	$f_{10}, f_{20}, f_{30}, f_{40}$: Rates of energy consumption by respiration, relating linearly to temperature.
7	$f_{20}=a_{21}+a_{22}T$	
8	$f_{30}=a_{23}+a_{24}T$	
9	$f_{40}=a_{25}+a_{26}T$	
10	$f_{15}=a_{27}/\{1+\exp[-a_{28}(t-a_{29})]\}$	a_{27}: Final rate of leaf death of the year
11	$f_{16}=a_{30}V_W+a_{31}V_9$	V_W: Live weight of cattle per ground area (g/m²)
12	$W=V_W\cdot 10^4/AN$	W: Live body weight of cattle per head (kg/head). AN: Number of cattle per 1000 ha.
12-2	$W_{CAL}=V_8\cdot 10^7/AN$	W_{CAL}: Quantity per head of cattle on energy basis (kcal/head).
13	$D=\{V_W[(a_{33}+a_{34})W^{0.75}+a_{35}\cdot W^{0.75}+a_{36}]/W\cdot 10^3\}/(a_{38}\cdot a_{39})$	D: Energy requirement for cattle per ground area (kcal/m²) $W^{0.75}$: Metabolic body size. a_{33}: Parameter for net energy for maintenance. a_{34}: Parameter for net energy for activity. a_{35}, a_{36}: Parameter for net energy for gain. a_{38}: Digestibility. a_{39}: Net energy content of digestible energy of food.
14	$HA=a_{40}\cdot V_1+a_{41}\cdot V_2$	HA: Available herbage amount for grazing per ground area (kcal/m²). a_{40}: Rate of the available part for grazing to the standing crop leaves. a_{41}: Ratio of the available part for grazing to the standing crop stalks.
15	$F_{17}=a_{40}V_1\ (HA\leqq D)$ $F_{17}=D(a_{40}V_1/HA)(HA>D)$	When HA is not enough to D, cattle graze all the available herbage, while cattle can graze herbage enough to D during the time when HA is supplied over D.
16	$f_{23}=a_{42}/[1+\exp\{-a_{43}(t-a_{44})\}]$	
17	$f_{32}=a_{45}\exp(-a_{46}t)+a_{47}\cdot F_{27}$	F_{27}: Amount of grazing from stalks per ground area (kcal/m²).
18	$f_{25}=a_{48}/[1+\exp\{-a_{49}(t-a_{50})\}]$	a_{48}: Final rate of stalks' death of the year.
19	$f_{26}=a_{51}V_W+a_{52}\cdot V_9$	
20	$F_{27}=a_{41}V_2\ \ (HA\leqq D)$ $F_{27}=D(a_{41}V_2/HA)\ \ (HA>D)$	
21	$f_{34}=a_{53}$	
22	$f_{36}=a_{54}$	
23	$f_{43}=a_{55}$	
24	$f_{46}=a_{56}$	
25	$f_{56}=a_{57}\cdot\exp(a_{58}\cdot t)$	
26	$f_{60}=a_{59}+a_{60}T$	f_{60}: Rate of decomposition of litter.
27	$f^{88}=FWNE=a_{61}\cdot \ln W^{0.75}+a_{62}$	FWNE: Conversion factor from net energy into live body weight.
28	$f_{78}=a_{38}\cdot a_{39}$	a_{38}: Digestibility a_{39}: Net energy content of digestible energy of food.
29	$f_{70}=a_{38}(1-a_{39})$	f_{70}: Rate of energy loss through the excreted urine and aspirated gas by cattle.
30	$f_{80}=a_{63}\cdot W^{0.75}/W_{CAL}\ (a_{63}=a_{33}+a_{34})$	f_{80}: Rate of the comsumption of net energy by respiration for maintenance and activity.
31	$f_{79}=1-a_{38}$	f_{79}: Rate of feces excretion.
32	$f_{90}=a_{64}+a_{65}T$	f_{90}: Rate of decomposition of feces.
33	$f_{04}=a_{66}$	f_{04}: Absorption rate of organic matter from soil.

Note Revised equations from the previous report are 11, 12, 12-2, 13, 19, 27, 28, 29 and 30.
The equation 15 of F_{17} was misprinted as $F_{17}=D(a_{40}/HA)$ in the previous report.

5) Grazing by animals (F_{17}, F_{27}): The mean rate of grazing per day per unit area by cattle can be a function of the amount of available herbage when the amount is less than that needed by the animals. The rate on the other hand, depends on the animal's requirements when the available herbage is sufficient. This consideration is introduced in equation 15 and 20. The demand of dry matter by the animals (D) is estimated empirically by using the Japanese feeding standard of beef cattle, as a function of the metabolic body size of the grazing animals, based on the net energy requirement for maintenance, activity and body weight gain (equation 13). The data of the net energy for activity were not available so that an appropriate value was chosen by taking into account the approximate compatibility with the energy for maintenance.

Grazing by animals accelerates the transfer rate f_{21} and f_{23} to some extent and the regrowth of new leaves are affected by reserves in the rhizome.

6) Growth of animals: The animal growth can be determined by the energy gain by food intake with the substraction of the energy loss due to excretion and heat. The excretion (gases, urine and feces) in terms of the proportion of food intake and the heat loss expressed in the metabolic body size are assumed to be constant at this step (f_{70}, f_{78}, f_{79}, f_{80}). Thus, the growth of animals becomes a function mainly of the amount of daily food intake and its efficiency of utilization, the latter being assumed to be a function of the metabolic body size (equation 27, 29). Since most of information about animal energy metabolism are obtained on the basis of metabolic body size and live body weight per head, the conversion factor from net energy intake into live body weight gain (FWNE) is determined by the equation 27 and the daily gain in live body weight per land area (V_W) is also calculated by the differential equation 9 in Table 2, while body weight per head (W) by the equation 12.

Results

The parameters (a_1–a_{70}) of the equations are estimated from the results of field survey in a representative grassland. For the *Zoysia*-type grassland, the parameters were determined from the measurements of Tashirotai pasture of Mt. Nanashigure located near to Morioka city, northern part of Honshu, conducted for two years. Those for the temperate-grass sown pasture are not yet available because of the determination is still in progress.

The changes in dry matter weight and calorific content of each plant organ and dead materials of the *Zoysia*-type pasture were measured monthly for both grazing and non-grazing plots. The maximum rate of photosynthesis per unit ground area of the *Zoysia* sward was estimated by growth analysis method. Herbage intake was measured with "Cage method". Decomposition of litter was measured with "Litter bag method".

The computed results of seasonal growth of *Zoysia* grass are given in Fig. 2 on dry matter basis for the both cases. In comparison of the simulated results with actual observations, there still remained a little discrepancy in the seasonal changes of standing dead and litter especially in autumn, but the growing pattern and the level of the other compartments of plant organs showed a better agreement to the observation.

Little information was available with regards to the rate of energy loss by activity of animals in relation to environmental factors for the case of grazing animals, and the animal growth was only an estimation in present studies. An agreement between simulated results and actual observations was clearly shown also with rhizome in both grazing and non-grazing cases, indicating that the rhizome was most remarkably affected by cattle grazing in all the compartments.

The factor of precipitation or soil moisture

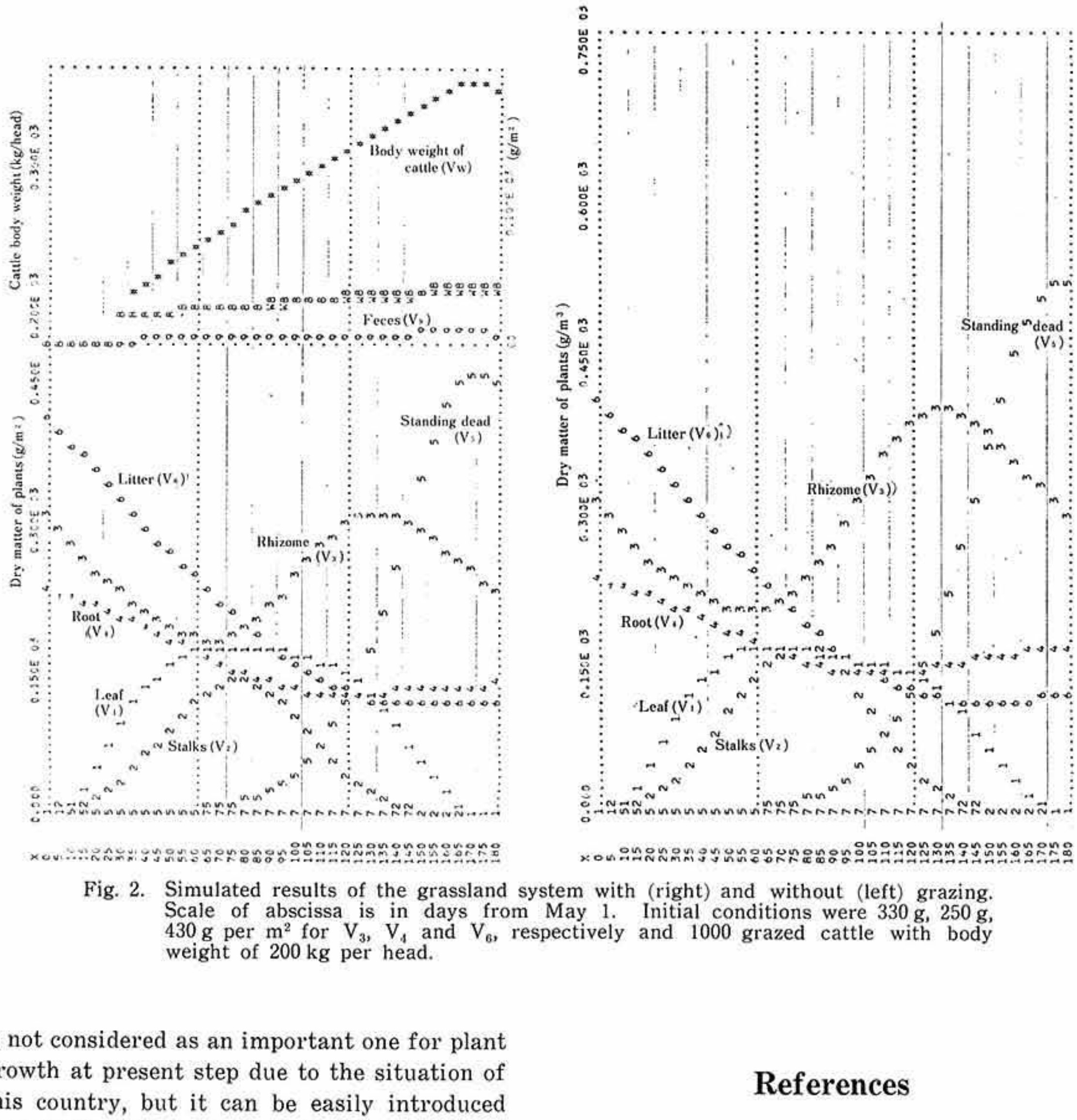

Fig. 2. Simulated results of the grassland system with (right) and without (left) grazing. Scale of abscissa is in days from May 1. Initial conditions were 330 g, 250 g, 430 g per m² for V_3, V_4 and V_6, respectively and 1000 grazed cattle with body weight of 200 kg per head.

is not considered as an important one for plant growth at present step due to the situation of this country, but it can be easily introduced by reflecting the moisture effect on L, a_9 and a_{11}. For the future step, precipitation factor must be included into the model by using equations expressing the responses of photosynthesis and leaf growth to precipitation, because there is a possibility of growth retardation of grasses due to lack of precipitation for a period of 3 weeks in midsummer. The effect of precipitation must also be taken into equations for the rate of decomposition of litter and feces and the treading pressure to plants in future step.

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