Short Report

Relationship between the Spatial Heterogeneity of Plant Biomass and Biomass Available to Grazing Animals in a Grassland: A simulation

Michio Tsutsumi, Masae Shiyomi*, Shusuke Satoh** and Kazuo Sugawara

Land Ecology, Graduate School of Agricultural Science, Tohoku University, Kawatabi, Naruko, Miyagi 989-6711, Japan
* Faculty of Science, Ibaraki University, 2-1-1, Bunkyo, Mito 310-8512, Japan
** Present address: National Institute of Livestock and Grassland Science, NARO (National Agricultural Research Organization) 768 Senbonmatsu, Nishinasuno, Tochigi 329-2793, Japan

Received: October 17, 2001/Accepted: April 4, 2002

Key words: Available plant biomass, Gamma distribution, Spatial heterogeneity.

Introduction

In grasslands, the spatial distribution of plant biomass is heterogeneous1,10,13,15. It has been suggested that small-scale spatial heterogeneity in grassland vegetation is generated and maintained by the activities of grazing animals, herbage plants, soil-microbes and their interactions3,5,8,9. Grazing animals select their diet10, which accelerates the patchiness of grassland vegetation8. The plants around dung patches are not consumed because of their offensive smell2,4, and the heterogeneity in nutrient distribution by dung patches results in a spatially heterogeneous plant growth7. The result is a patchy grassland consisting of heavily and lightly utilized areas5.

The herbage biomass available for grazing animals per unit area is generally quantified using the mean herbage biomass that is located above several centimeters from the soil surface. However this estimation is not always precise. Grassland vegetation is heterogeneous, and herbage in areas with a large plant biomass is not preferred by grazing animals13,15, while herbage in areas with very short plants cannot be utilized. In order to overcome these problems in determining available biomass, Shiyomi et al.20 theoretically and empirically demonstrated that the spatial pattern of plant biomass in grazed pasture could be approximated using the gamma distribution. The gamma distribution is given by the following equation for \( x \geq 0 \) and \( \mu, \rho > 0 \):

\[
f(x) = \frac{x^{\rho-1} \mu^\rho}{\Gamma(\mu)} \exp\left(-\frac{\rho x}{\mu}\right),
\]

where \( x \) denotes the plant biomass per unit area (quadrat), \( \mu \) is the mean plant biomass per quadrat, \( \rho \) biomass from the mean and heterogeneity of biomass per unit area. This model is based on the gamma distribution, a statistical model, and indicates that the spatial heterogeneity of biomass affects the biomass available to grazing animals.

It is important to investigate how the spatial heterogeneity of grassland vegetation influences animal production. While experimental studies5,10,13,14 have suggested that the spatial heterogeneity of grassland vegetation influences grazing behavior, the influences have never been quantified or discussed theoretically. Therefore, applying the model proposed by Shiyomi et al.20, we simulate and discuss the relationship between plant biomass, its spatial heterogeneity and the biomass available to grazing animals.

Methods

Shiyomi et al.20 theoretically and empirically demonstrated that the spatial pattern of plant biomass in grazed pasture could be approximated using the gamma distribution. The gamma distribution is given by the following equation for \( x \geq 0 \) and \( \mu, \rho > 0 \):

\[
f(x) = \frac{x^{\rho-1} \mu^\rho}{\Gamma(\mu)} \exp\left(-\frac{\rho x}{\mu}\right),
\]

where \( x \) denotes the plant biomass per unit area (quadrat), \( \mu \) is the mean plant biomass per quadrat,
is an index representing the spatial heterogeneity of the plant biomass over the grassland, and $\Gamma(p)$ is a gamma function of $p$ (see details in Shiyomi et al.\(^{22}\)). Here, letting $\sigma^2$ be the variance among quadrats, $p$ is given by $\mu^2/\sigma^2$. The spatial pattern of biomass can be determined as follows:

1. If $p = 1$, the frequency distribution of biomass follows the exponential distribution; that is, the spatial pattern is random\(^{1,18}\).
2. If $0 < p < 1$, the spatial pattern is more heterogeneous than by random expectation, and as $p$ approaches 0, the heterogeneity increases; and
3. If $p > 1$, the spatial pattern is less heterogeneous than by random expectation, and as the $p$-value increases, the heterogeneity decreases\(^{20}\).

It has been suggested that sites with little aboveground biomass do not allow grazing, while sites with abundant biomass are not preferred by grazing animals, and as a result, these sites are not grazed\(^{1,19,30}\). Shiyomi et al.\(^{22}\) assumed that these boundaries were 3.75 (15/4) and 100 g DM 0.25 m\(^{-2}\); that is, they defined sites with a biomass from 3.75 g DM 0.25 m\(^{-2}\) to 100 g DM 0.25 m\(^{-2}\) as "available area". We followed this assumption. Shiyomi et al.\(^{22}\) proposed a model for estimating "available biomass" in a grassland using the gamma distribution. The model is expressed by:

$$A = \int_{3.75}^{100} x^{p-1} \frac{\Gamma(p)}{\Gamma(p)} \exp\left(-\frac{b}{\mu}\right)(x-3.75) dx$$

(2)

where $A$ denotes the available biomass per 0.25 m\(^2\). In this equation, $x = 3.75$ indicates the biomass that allows grazing in a site where $x \geq 3.75$. Therefore, the relative value of available biomass to total biomass (relative available biomass hereafter) in the grassland ($A_r$) is given by:

$$A_r = \int_{3.75}^{100} x^{p-1} \frac{\Gamma(p)}{\Gamma(p)} \exp\left(-\frac{b}{\mu}\right)(x-3.75) dx$$

(3)

Using Equations 2 and 3, we simulated the relationship between spatial heterogeneity of biomass and available biomass.

Shiyomi et al.\(^{22}\) obtained the following equation at their study site empirically:

$$p = 0.0314 + 0.2661, \quad 30 < \mu < 100.$$  

(4)

By applying this Equation 4 to $p$ in Equations 2 and 3, we can obtain the relationship between plant biomass and available biomass.

These analyses were conducted using Mathematica ver. 4.1\(^{10}\).

**Results and Discussion**

Figure 1a shows the results of simulation with Equation 2. The maximum values of available biomass differed markedly depending on the $p$-value. The maximum value of available biomass increased with decreasing heterogeneity of biomass. The lower the $p$-value, the lower the $\mu$-value for the maximum value of available biomass. The available biomass was high over a wide middle-range of $\mu$-values with decreasing heterogeneity, whereas with a $\mu$-value exceeding 100 (g DM 0.25 m\(^{-2}\)), the relationship was reversed. Fig. 1b shows the results of simulation with Equation 2. For very low $\mu$-values, the relative available biomass increased slightly with increasing heterogeneity, although this is not clear in Fig. 1a. For other $\mu$-values, similar results to Fig. 1a were obtained. A high relative available biomass over a wider range appeared with decreasing heterogeneity of biomass. These results suggest that a lower heterogeneity of biomass is desirable for achieving effective utilization of biomass in a managed grassland. If there is a negative correlation between mean biomass and heterogeneity, such as in Equation 4, a condition with high mean biomass and high heterogeneity is not practicable in actual communities.

Figure 2a shows the results of simulations apply-
Fig. 2. Results of simulation applying Equation 4 to Equations 2 and 3 (see text). 
(a) Simulated relationship between available biomass and \( \mu \) (mean biomass per 0.25 m\(^2\)).
(b) Simulated relationship between relative available biomass and \( \mu \).

Applying Equation 4 to Equation 2. The change in available biomass was small, particularly for \( \mu \)-values between 50 and 100. The maximum available biomass was 38.0 g DM 0.25 m\(^{-2}\) (at \( \mu =73.6 \)). When the \( \mu \)-value exceeded 73.6, the available biomass decreased with increasing \( \mu \)-value. In other words, a high biomass may inhibit livestock production in this case. Fig. 2b shows the results of simulations applying Equation 4 to Equation 3. The relative available biomass decreased almost linearly with increasing \( \mu \)-value. This suggests that utilization of grassland with a large biomass for grazing is less effective. Shiromi et al.\(^{21}\) empirically obtained a linear relationship between \( p \) and \( \mu \), as shown in Equation 4, while Shiromi\(^{19}\) suggested that the parameter may differ with spatial scale and grassland. Indeed, the data of Tsutsui et al.\(^{30}\) obtained in a different pasture, but same scale, could not be applied to Equation 4. Therefore, the results in Fig. 2 cannot be considered general results, but only an example. We can consider the trend of the results in Fig. 2 as general, however, if the mean and heterogeneity of biomass are negatively correlated.

In our simulation, the availability of herbage was determined using biomass per area only, although many other factors (e.g., species composition\(^{1}\), plant height\(^{22}\) and developmental stage\(^{22,22}\)) affect the availability of grazing in actual communities. It is important to know how the interaction of spatial heterogeneity of biomass and other factors influences available biomass.

Acknowledgements

The authors would like to thank all the members of the Laboratory of Land Ecology, Tohoku University, for their valuable advice.

References

26) Tsutsui, M., M. Shiromi, S. Sato and K. Sugawara
27) WAllis De Vries, M.F. and C. DaleboutD (1994)
    Oecologia 100, 98-106.

* In Japanese with English summary.