NEGATIVE HYPERGEOMETRIC SERIES AND TAYLOR'S POWER LAW IN OCCURRENCE OF PLANT POPULATIONS IN SEMI-NATURAL GRASSLAND IN JAPAN

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ABSTRACT

Attempts were made to determine whether the spatial distribution of the plant species composing vegetation of a semi-natural grassland is heterogeneous, using negative hypergeometric series (NHG) and Taylor's power law (TPL). The occurrence of each species was observed, in an area of the grasslands, using 100 quadrats with a size of 50 cm x 50 cm, each of which was divided into 4 small quadrats with an area of 25 cm x 25 cm. For all species dominating in the grassland, good fits to the NHG and TPL were obtained. Species which grow stolons, rhizomes and tillers for propagation such as *Potentilla freyniana* and *Hydrocotyle ramiflora*, exhibited a highly heterogeneous spatial pattern.

KEYWORDS

Grassland, heterogeneity, negative hypergeometric distribution, Taylor's power law, vegetation

INTRODUCTION

It appears that the spatial heterogeneity of plant species is caused by the uneven distribution of dung and urea excreted by the grazing animals on the grassland, uneven use of the grassland by the grazing animals, and uneven management, etc.

In this study, "frequency of occurrence" was used to evaluate the spatial heterogeneity of species distribution in a grassland. A discrete probability distribution, i.e., negative hypergeometric series (NHG), was introduced to evaluate the heterogeneity in grassland, and spatial het- erogeneity for each of plant species grown in a semi-natural grassland was determined by using the parameters and Taylor's power law (TPL).

MATERIALS AND METHODS

Model for the spatial heterogeneity of a single species population

First it is assumed that although (1) the vegetation in the grassland is composed of many species of plants, we concentrate on only one species. (2) N large quadrats with a given area (L-quadrat), each of which is composed of n small quadrats with equal area (S-quadrat), are set at random sites in the grassland, and, in each S-quadrat, the occurrence of the species is determined by visual observation.

If the vegetation is not heterogeneous over the grassland, the distribution of individuals of species A composing the vegetation follows a random pattern. "Random pattern" indicates that the number of plants of species A per S-quadrat follows a binomial distribution. Here, let the probability that species A occurs in an S-quadrat be p, which does not change all over the grassland. Then, the probability that species A occurs in i of the n S-quadrats within an L-quadrat, $P(i)$, is expressed by: $P(i)={}_nC_i p^i(1-p)^{n-i}$.

In a grassland that experienced substantial disturbance such as grazing the vegetation may exhibit a heterogeneous distribution. Then, we assume that p changes continuously, from site to site, in the grassland according to a beta distribution. The density of p is expressed by : $p^{-1}(1-p)^{-1}/B(,)$ where $B(.,.)$ indicates beta function, and α and β are parameters of the distribution (α, β 0).

The derived distribution, NHG, is expressed by the following equation (see Shiyomi 1981; Hughes and Madden 1993):

$P(i) = {}_nC_i\ B(+i,+n-i)/B(,)$ or

$P(0)=(+1)...(+n-1)/\{(+)(++1)...(++n-1)\}$,

$P(i)=P(i-1)(n-i+1)(+i-1)/(+n-1)$ for $i=1,2, ..., n$.

Indices for heterogeneity

Two different methods for deter- mining spatial heterogeneity were used as follows: Hughes and Madden (1993) proposed an adjusted power law (Taylor, 1961) in their studies of phytopathology. The function for the power law is expressed by the following simple regression equation:

$$\log [v/n^2]= A + b \log [p(1-p)/n],$$

where v denotes the variance estimated from occurrence data, $p(1-p)/n$ indicates the theoretical variance for the binomial parameter p, which is given by (the observed mean)/n, and A and b are constants to be estimated. If b, A1, we conclude that the overall spatial pattern is heterogeneous, and if b1, the degree of heterogeneity changes with p. If $b=A=1$, the spatial pattern is random.

Another index, the correlation coefficient between n S-quadrats in an L-quadrat, can be used. The correlation coefficient, ρ is expressed by $\rho = (\alpha+\beta+1)^{-1}$ where 0 - ρ - 1. A large -value indicates a high heterogeneity in occurrence between n S-quadrats.

Experiment: A semi-natural grassland at the National Grassland Research Institute, Japan, was used for the experiment. Cattle have been regularly grazed from May to October each year. The area surveyed was ca. 15 a, and 100 L-quadrats with an area of 50 cm x 50 cm were set every ca. 12 m^2 in the grassland. Each L-quadrat was divided into 4 S-quadrats with 25 cm x 25 cm. All the plant species appearing in each S-quadrat were recorded.

RESULTS AND DISCUSSION

Thirty-four species were observed, but only 13 species had high frequencies of occurrence (one of which, *Zoysia japonica*, was excluded because it appeared in all quadrats). Observed and expected frequency distributions for i= 0,1,...,4 for the 13 species and estimated values of p and are shown in Table 1. For the dominating 13 species, except for *H. ramiflora*, the goodness of fit was statistically high. This fact indicates that the frequency distributions for occurrence of these plant species can be expressed by the NHG. *P. freyniana* and *H. ramiflora* exhibited high -values, while *P. japonica and Viola* spp. exhibited rather low values.

Figure 1 depicts the application of adjusted TLP to the 34 plant species. The estimated simple regression equation is given by:

$\log [v/16]= 0.5151 +1.0435 \log [p(1-p)/4]$.

This equation indicates that the overall tendency of the spatial pattern is random because b1. But, results for the 13 species dominating in the grassland are fairly consistent with the previous ones: *H. Ramiflora* (3) and *P. Freyniana* (9) are over the regression line and *P. Japonica* (7) and *Viola* spp. (2) are under the regression line.

Species which grow stolons, rhizomes and tillers for propagation, such as *P. Freyniana* and *H. maniflora*, exhibited a highly heterogeneous spatial pattern. On the other hand, *P. japonica and Viola* spp. which tend to grow in isolation among individuals showed low heterogeneity. Undoubtedly, the propagation type is one of the major factors controlling the heterogeneity.

The concept of NHG was theoretically developed by Skellam (1948) and introduced into the fields of vegetation science (Kemp and Kemp 1956), and plant epidemiology (Shiyomi 1981; Hughes and Madden 1993). The TPL is introduced into entomology by Taylor (1961). The present work is an application of those theoretical works to grassland science. These methods can be widely applied to studies on vegetation with short height, especially in grasslands and pastures.

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Figure 1

Application of the adjusted TPL to the grazing semi-natural grassland data. Real and broken lines indicate the power law estimated from data and that assuming a random spatial pattern for each plant species, respectively; the estimated power law is given in the text; *v* and *p* indicate the observed variance and the proportion of occurrence. Figures denote the species which are indicated in Table 1.