Spatial heterogeneity of soil fertility, plant biomass, and productivity in grasslands

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Key words: Mitscherlich's growth equation, plant biomass, plant production, soil fertility, spatial heterogeneity

Introduction Grassland vegetation under livestock grazing is spatially heterogeneous, because animal grazing and excretion disturb the vegetation. We clarified the relationship between spatial heterogeneity and plant production. The following assumption is plausible: plant biomass y at a site with soil fertility x varies according to Mitscherlich's (1930) growth equation among plots. That is, if soil fertility is low, then there will be little biomass, and biomass will increase with an increase in fertility; however, if soil fertility is high, then the increase in biomass with increases in fertility is low (Figure 1). Mitscherlich's equation is expressed as: $y_1 = K\{1\text{-}\exp(\text{-}ax)\}$, where a is the increasing coefficient, and K is the maximum limit of biomass as $x \to \infty$.

Biomass If fertility is evenly distributed and $x = \mu$, then the relationship between x and y is expressed as $y = K[1 - \exp(-a\mu)]$, which indicates that fertility is the same throughout the grassland. In a grassland where fertility is not even, as is generally the case, x follows the gamma distribution $f(x)$ with a mean of μ and shape parameter p:

$$f(x) = \frac{x^{p-1} p^p}{\Gamma(p)\mu^p} \exp\left(-\frac{p}{\mu} x\right).$$

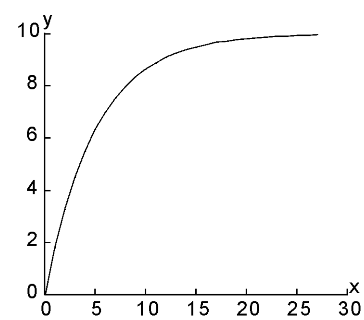

Figure 1 *An example of Mitschelrich's growth equation for fertility x, where a = 0.2 and K = 10.*

Total biomass in the grassland is then expressed as

$$y_2 = \int_0^\infty K\{1 - \exp(-ax)\} \times \frac{x^{p-1} p^p}{\Gamma(p)\mu^p} \exp\left(-\frac{p}{\mu} x\right) dx = k\left\{1 - \left(\frac{p}{a\mu + p}\right)^p\right\}.$$

The difference between y_1 and y_2, Δy, for any μ is as follows:

$$\Delta y = K\{1 - \exp(-a\mu)\} - K\left\{1 - \left(\frac{p}{a\mu + p}\right)^p\right\}.$$

Δy is 0 for $p \to \infty$, otherwise $\Delta y > 0$. This equation indicates that biomass is lower when fertility is spatially heterogeneous than when it is evenly distributed.

Plant productivity When fertility is evenly distributed throughout the grassland, if fertility is improved by δ throughout the grassland, then biomass is expressed as $y = K[1 - \exp\{a(\mu + \delta)\}]$. Then the increase of biomass, Δy_1, is $K\exp(-a\mu) - K\exp\{\text{-}a(\mu + \delta)\}$ for any μ. Now assume that fertility is spatially heterogeneous. Here we use the gamma distribution to express fertility heterogeneity. The increase in biomass, Δy_2, based on a fertility increase is expressed as:

$$\Delta y_2 = \int_0^\infty K[\exp(-ax)\} - \exp\{-a(x + \delta)\}] \times \frac{x^{p-1} p^p}{\Gamma(p)\mu^p} \exp\left(-\frac{p}{\mu} x\right) dx = K\left\{\frac{p}{a\mu + p}\right\}^p \{1 - \exp(-a\delta)\}.$$

When we compare Δy_2 to Δy_1, $\Delta y_2 - \Delta y_1 = K\left[\left\{\frac{p}{a\mu + p}\right\}^p - \exp(-a\mu)\right]\{1 - \exp(-a\delta)\}] > 0$.

This result indicates that the increase in biomass with improved fertility is larger in a heterogeneous fertility environment than in an even environment, excluding the case of $p \to \infty$.

Reference

Mitschelrich E. A., (1930). Die Bestimmung des Düngerbedürfnisses des Bodens. Paul Parey, Berlin.