GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 16 (2015) 469–479

Basic and Applied Ecology

www.elsevier.com/locate/baae

Testing predictions of the energetic equivalence rule in forest communities

Wei-Ping Zhang[a,*], E. Charles Morris[b], Xin Jia[c], Sha Pan[d], Gen-Xuan Wang[e]

[a]*Beijing Key Laboratory of Biodiversity and Organic Farming, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China*
[b]*School of Science and Health, University of Western Sydney, Richmond 2753, NSW, Australia*
[c]*Key Laboratory of Soil and Water Conservation and Desertification Combating, Ministry of Education, Beijing Forestry University, Beijing 100083, China*
[d]*Department of Environmental Hygiene, School of Public Health, Guiyang Medical University, Guiyang 550004, China*
[e]*Institute of Ecology, College of Life Sciences, Zhejiang University, Hangzhou 310058, China*

Received 13 May 2014; received in revised form 24 March 2015; accepted 6 April 2015
Available online 29 April 2015

Abstract

As growth rate is a reasonable proxy measure of the rate of resource use per plant individual, the 'energetic equivalence rule' predicts that net primary productivity (the rate of biomass production per unit area, *NPP*) will be independent of plant biomass and maximum population density in plant communities. However, only a few studies have tested these relationships in plant communities. In this study, we investigated allometric scaling of net primary productivity (*NPP*) to tree biomass (*M*) and density (*N*) across a range of tree-dominated communities in China. The aim was to test the universality of the 'energetic equivalence rule' (i.e. whether the exponents of these relationships take a universal value of 0) in forest communities. We used both ordinary least square (OLS) and standardized major axis (SMA) regression for selected boundary points, and quantile regression (QR) to estimate the slopes of regression lines. QR, OLS and SMA regression all showed that four *NPP–M* and two *NPP–N* exponents were different from 0 across the 8 forest types. In addition, when we combined all the data to determine a larger pattern that typifies Chinese forests, five out of the six exponents of *NPP–M* and *NPP–N* relationships deviated strongly from 0. Therefore the universality of the 'energetic equivalence rule' does not hold for forest communities at both the regional and the national scale of China. However, the "zero" exponent seems to be a central tendency for *NPP–M* and *NPP–N* relationships in 7 out of 8 forest types. Deviation from the energetic equivalence possibly reflects multiple, unsound assumptions for "an average idealized forest" by metabolic scaling theory, as well as unaccounted-for variations of site factors (e.g. stand age and stand conditions) within forest communities. In addition, our study suggested that statistical methods should be subject to strict scrutiny in testing the 'energetic equivalence rule'.

Zusammenfassung

Da die Wachstumsrate näherungsweise ein gutes Maß für die Rate der Ressourcennutzung pro Pflanze ist, sagt die Regel von der energetischen Äquivalenz voraus, dass die Nettoprimärproduktion (die Rate der Biomasseproduktion je Flächeneinheit: NPP) von der Pflanzenbiomasse und der maximalen Populationsdichte von Pflanzengemeinschaften unabhängig sein

*Corresponding author. Tel.: +86 10 62734684; fax: +86 10 62731016.
E-mail address: zhangwp@cau.edu.cn (W.-P. Zhang).

http://dx.doi.org/10.1016/j.baae.2015.04.005

wird. Indessen haben nur wenige Studien diese Beziehungen in Pflanzengemeinschaften untersucht. Wir untersuchten die allometrische Beziehung zwischen der Nettoprimärproduktion (NPP) und der Baum-Biomasse (M) und -Dichte (N) über eine Reihe von baumdominierten Gemeinschaften in China. Unser Ziel war, die Allgemeingültigkeit der Regel von der energetischen Äquivalenz zu überprüfen, d.h., ob die Exponenten dieser Beziehungen einen universellen Wert von Null annehmen. Wir benutzten die Methode der kleinsten Quadrate (OLS), standardisierte Hauptachsen-Regression (SMA) für ausgewählte Grenzpunkte sowie Quantil-Regression (QR), um die Steigungen von Regressionsgeraden zu bestimmen. QR, OLS und SMA zeigten, dass über die acht untersuchten Waldtypen vier NPP-M- und zwei NPP-N-Exponenten von Null verschieden waren. Als wir alle Daten kombinierten, um das größere, für chinesische Wälder charakteristische Muster zu bestimmen, unterschieden sich fünf der sechs NPP-M- und NPP-N-Beziehungen stark von Null. Damit ist die Regel von der energetischen Äquivalenz für Waldgemeinschaften in China weder auf der regionalen noch auf der nationalen Ebene allgemein gültig. Indessen scheint der Null-Exponent eine zentrale Tendenz für die NPP-M und NPP-N-Beziehungen in sieben von acht Waldtypen zu sein. Die Abweichung von der energetischen Äquivalenz spiegelt möglicherweise mehrere unbegründete Annahmen der Theorie der metabolischen Skalierung hinsichtlich eines durchschnittlichen, idealisierten Waldes wider, sowie die unberücksichtigt gebliebenen Schwankungen von Standortfaktoren in Waldgemeinschaften (z.B.: Bestandsalter, Bestandsbedingungen). Darüberhinaus legt unsere Untersuchung nahe, dass bei der Prüfung der Regel von der energetischen Äquivalenz die statistischen Methoden einer äußerst eingehenden Überprüfung unterzogen werden sollten.

Keywords: Scaling; Net primary productivity; Biomass; Density; Forest communities; Self-thinning; Upper boundary; Quantile regression; Standardized major axis regression; Metabolic scaling theory

Introduction

Metabolic scaling theory (MST) argued that metabolic rate (or resource use rate, Q) per individual would scale approximately as the 3/4 power of body mass (M): (i.e. $Q \propto M^{3/4}$) (West, Brown, & Enquist 1997; Niklas & Enquist 2001). In addition, maximum population density (N_{max}) should scale with body mass $M^{-3/4}$ (i.e. $N_{max} \propto M^{-3/4}$) (Damuth 1981, 1987; Enquist, Brown, & West 1998; Niklas & Enquist 2001; Niklas, Midgley, & Enquist 2003). Since the maximum rate of resource use per unit area $R_{max} = Q \times N_{max} \propto M^{3/4} \times M^{-3/4} \propto M^0 \propto N_{max}^0$, the maximum rate of resource use per unit area will be independent of average plant biomass and density. The relationship is termed as the 'energetic equivalence rule' (Damuth 1981, 1987), and is considered as one of the fundamental laws of nature (Deng et al. 2008). The 'energetic equivalence rule' has been tested using different kinds of organisms and across a range of biological scales, but with mixed results (Enquist et al. 1998; White, Ernest, Kerkhoff, & Enquist 2007; King 2010). In addition, both the 3/4 scaling of metabolic theory (Q–M) and the −4/3 scaling of biomass–density relationship (M–N_{max}) are challenged on theoretical and empirical grounds (Russo, Wiser, & Coomes 2007; Dai et al. 2009; Mori et al. 2010; Bai et al. 2010, 2011). Therefore, controversy continues over the validity and universality of the 'energetic equivalence rule' (White et al. 2007; Deng et al. 2008; King 2010).

It is mathematically difficult to examine the applicability of the 'energetic equivalence rule' directly in plant communities (Enquist et al. 1998; Deng et al. 2008). As growth rate is a reasonable proxy measure of the rate of resource use per plant individual (Q) (Niklas & Enquist 2001), net primary productivity (the rate of biomass production per unit area, NPP) is predicted to scale proportionally to total energy use per unit area in plant communities. It follows from the 'energetic equivalence rule' that $NPP_{max} \propto R_{max} \propto M^0 \propto N_{max}^0$. More importantly, these relationships provide an alternative indicator for 'energetic equivalence'. However, only a few studies have tested these relationships in plant communities (Niklas & Enquist 2001; Niklas et al. 2003).

Recent literature indicates that both scaling of metabolic theory and biomass–density relationship are not a constant, but rather vary with environmental conditions or particular taxonomic groups across a range of forest communities in China (Li, Han, & Wu 2005; Li, Han, & Wu 2006; Zhang, Jia, Bai, & Wang 2011; Zhang, Jia, Morris, Bai, & Wang 2012). Based on the same dataset, we further investigated allometric scaling of net primary productivity (NPP) to tree biomass (M) and maximum density (N_{max}) across a range of tree-dominated communities in China. The aim of was to test the universality of the 'energetic equivalence rule' (i.e. whether the exponents of these relationships take a universal value of 0) in forest communities.

Materials and methods

Data source

We examined the allometric scaling of net primary productivity (NPP) to tree biomass (M) and density (N) by using the compilation of Luo (1996) for standing biomass and production. These data were compiled from the Chinese literature for continuous forest-inventory plots of the forestry departments between 1970 and 1994. The dataset includes