



**Research Article**

**RESEARCH PROGRESS ON ALLOMETRIC MODELS AND ITS APPLICATION**

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**ARTICLE INFO**

**Article History:**

Received 12<sup>th</sup> April, 2020

Received in revised form 23<sup>rd</sup>

May, 2020

Accepted 7<sup>th</sup> June, 2020

Published online 28<sup>th</sup> July, 2020

**Key words:**

allometric model, metabolic rate, scaling exponent, body size

**ABSTRACT**

The problem of biological allometric growth relationship has always been a hot issue in ecology. The allometric equation is usually expressed in the form of a power function of metabolic rate and body size. This paper reviews some theoretical models of allometry, including self-similar fractal-like distribution network model, metabolic theory of ecology model and energy consumption model. The metabolic rate of an individual affects the ecological processes at different levels of ecology, and can be applied to individuals, populations, communities, and ecosystems. The application of the allometric models on three different scales of individual, population, community and ecosystem are introduced.

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**INTRODUCTION**

For a long time, the study of individual structural characteristics and physiological properties and their allometric growth relationship has been one of the hot issues in ecological research (Kleiber,1947,West *et al.*, 1997, Darveau *et al.*,2002).Metabolism is the basis of biological growth, development, reproduction, heredity, and evolution, as well as the process of conversion of biological materials and energy. It determines all the material and energy resources that organisms absorb from the environment and controls the distribution of material and energy in the organism. The body size of an individual is one of the important traits of an organism, which determines almost all physiological characteristics and physiological processes of an individual organism. As early as the 19th century, biologists discovered that the basic metabolic rate of an animal is proportional to the 2/3 power of biomass. Based on a large number of experiments, Kleiber (1932) measured more than 100 mammals and birds and found that the scaling exponent of metabolic rate and body size was closer to 3/4, and pointed out that because both animals and plants are adapting to the environment and evolving, this law may also apply to plants, which is called Kleiber's law. By the end of the 20th century, biologists had observed a large number of allometric relationships with multiples of 1/4 as the index (Calder, 1984; Lindstedt *et al.*, 1986).However, for a long time, there has not been a general model that can give a satisfactory theoretical explanation for the universality of allometry (Han W. X., Fang J. Y., 2008).

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This article introduces some allometric models and its application on different scales in ecology.

**Allometric scaling model**

**Models before the mid-1990s**

Rubner (1883) analyzed and explained the relationship between the metabolic rate of animals and the 2/3 power of individual mass according to the Euclidean geometric model. The body length of an animal is proportional to the 1/3 power of its volume. And the body surface area of an animal is proportional to the 2/3 power of the volume. When the body temperature is constant, the heat dissipation rate from the animal body surface to the environment is proportional to the body surface area, and the heat production rateof the animal metabolism must be balanced with the heat dissipation rate, then the metabolic rate is proportional to the 2/3 power of the biomass. However, this analysis method couldn't explain many allometric growth relationships with power exponent of 1/4.Blum (1977) put forward the theory of four-dimensional biology. He believed that organisms live in four-dimensional super volume space rather than three-dimensional. Based on the classical Euclidean geometry, the 3/4 law was deduced, but it was questioned because of the unclear biological significance.

**WBE models**

**WBE-1997 model**

West, Brown and Enquist proposed a series of models to explain the allometric growth relationship, which are denoted henceforth as the WBE models. West *et al.* (1997) proposed

the self-similar fractal network model of organism, and thought that organism supply materials needed by life to each part of it through a fractal network in the body. Based on this, a kind of material exchange and transportation network model with fractal structure was established. The basic assumptions of the model are: (1) To enable the transport network to provide nutrition to the entire organism, the network must be a space-filled network structure with self-similar characteristics. (2) The most terminal branch of the network (such as the capillaries in the circulatory system), is a unit independent of the body size of the organism. In other words, the terminal branch is constant. (3) The energy consumed when resources are transported through the network is minimized. Therefore, West *et al.* proved Kleiber's law. However, for those single-celled algae and protoplasmic organisms that do not have obvious branching structures, this model cannot explain why the metabolic rate and body size also follow Kleiber's law. Makarieva *et al.* (2005a, 2005b), Kozłowski and Konarzewski (2004) conducted a detailed analysis of the WBE-1997 model and pointed out there were three problems in the model. There were contradictions in the derivation process. When the model is applied to the ontogeny, it violates the law of conservation of energy. The 3/4 index was obtained by statistical analysis with non-comparable sample data.

#### **WBE-1999 model**

West *et al.* (1999) developed the viewpoint of the fourth dimension of life. They believed that the natural selection of life evolution makes organisms tend to take in the limited natural resources to the maximum and use them most efficiently. That is, the total surface area of network system tends to be maximized, while minimizing the transport length and energy consumption of the network system. The surface area mentioned here is not the external apparent area in the usual sense, but the functional effective area (such as the total leaf area of the plant, the absorption area of the digestive tract, and the total area of the inner mitochondrial membrane in the cell). In the environment of limited resources, the network transportation system selected by evolution process has higher metabolic capacity than the three-dimensional geometry architecture. For some special organisms, such as roundworms and nematodes, which have only one-dimensional or two-dimensional structure, their allometric relationship index can be adjusted appropriately. Similarly, some biological organs (such as leaves) often change their allometric growth relationship because of their own structural particularity.

#### **Metabolism theory of ecology model**

According to metabolism theory of ecology (Brown *et al.*, 2004), metabolism is the basic attribute of life. The metabolic processes such as the absorption of resources from the environment, the conversion of material and energy, the distribution of products and the discharge of wastes still comply with the physical and chemical principles. That is, the conservation of material and energy and the laws of thermodynamics. The metabolism theory of ecology model is based on the self-similar fractal network model, and several variables such as reaction temperature, reaction activation energy and Boltzmann constant are introduced. In this way, after the temperature variable is included, the model of

distribution network can be well supplemented to explain most of the differences in metabolic rates that cannot be explained by body size.

#### **Energy consumption model**

The energy consumption model (Makarieva *et al.*, 2003) is based on the main process of the organism absorbing energy from the environment, rather than the energy transfer process in the body after the energy has been obtained. The model has two basic assumptions, including the constant energy flux per unit body surface area of the organism and a minimum the metabolic rate per unit mass to maintain the basic life activities of the individual. For plants, a constant energy flux is equivalent to a constant solar flux captured by plant leaves per unit ground projection area. According to the theory of energy consumption, energy consumption is one of the most basic characteristics of life phenomena. In the process of biological evolution, there are only a limited number of effective strategies to grab energy from the environment. The common feature is that energy is exchanged with the environment through the body surface area, and is consumed in the entire three-dimensional volume. The model pointed out that the scale index of the allometric growth model is not a fixed value, but a region, that is, the metabolic rate has no obvious dependence on individual size (Luo and Li, 2011).

#### **Application of Allometric Models in Ecology**

##### **Individual scale**

According to the self-similar fractal network model, Enquist *et al.* (Enquist *et al.*, 2002a, 2002b, Niklas, 2003) put forward three hypotheses for plant transportation structure. During plant ontogeny, the density of stem and root tissue is roughly constant. The effective water pressure of the stem and root has the same cross-sectional area to ensure the conservation of water flowing through the plant. The length of the stem is approximately proportional to the length of the root of the same size. There is a certain allometric growth relationship in the distribution among the three major tissues of root ( $R$ ), stem ( $S$ ), and leaf ( $L$ ) (Enquist *et al.*, 2002c, Enquist, 2003),  $M_L \propto M_S^{3/4}$ ;  $M_L \propto M_R^{3/4}$ ;  $M_S \propto M_R$ . There is the following relationship between biomass production ( $G$ ) and individual biomass and temperature ( $T$ ),  $G \propto M^{3/4} \exp(-E/kT)$ . The application of the allometric growth model in the distribution of biomass has made our research on plant anatomical, physiological and ecological characteristics more systematic (Enquist *et al.*, 1999, Li Y. *et al.*, 2007). Li X. *et al.* (2019) studied the biomass allocation and allometric growth of *Pinus yunnanensis* seedlings from different geographical provenances, and pointed out that the difference of allometric growth index among organs of *Pinus yunnanensis* from different provenances can provide the possibility for early selection of excellent provenances of *Pinus yunnanensis*.

##### **Population and community scale**

According to the metabolism theory of ecology model, Brown *et al.* (2004) obtained the relationship between maximal population growth rates and individual biomass,

$$r_{\max} \propto M^{-1/4} \exp(-E/kT). \quad \text{Savage } et \text{ al. (2004)}$$

conducted a detailed analysis of the data of various species such as single-celled eukaryotes, vertebrates and mammals, and the results showed no significant difference from the predicted values. According to the theory of ecological metabolism (Brown *et al.*, 2004), after the population is stable, its density is basically constant, which has nothing to do with time or other interference factors. The population density at equilibrium has a - 3/4 exponential relationship with individual biomass, but the population density in high temperature environment is smaller. The process of generating and maintaining species diversity is similar to other biological characteristic variables related to biomass and temperature. Temperature is an important ecological factor in the marine environment. After the introduction of temperature as a parameter in ecological metabolism theory, most of the problems that cannot be explained by an individual biomass parameter alone are solved (Kremer *et al.*, 2017, Li *et al.*, 2018).

### Ecosystem scale

For the stable ecosystem, the total biomass per unit area is proportional to the 1/4 power of individual biomass predicted by WBE model. However, ecological metabolism theory believes that temperature is also one of the non-negligible factors affecting the total fixed biomass of the ecosystem. The total biomass per unit area of the ecosystem is proportional to the 1/4 power of the individual biomass, and it decreases with the temperature rises. Brown *et al.* (2004) pointed out that the activation energy of net primary production of global terrestrial communities is about 0.33 eV, which is about half of the activation energy of respiration or secondary production (0.63 eV). This conclusion is extremely important for the study of carbon cycle and organic matter storage.

### CONCLUSIONS

The study of the allometric model of metabolic rate and body size is the basis and focus of metabolic theory. Ecologists gave their own explanations for the power exponential allometric relationship between biological metabolic rate and body size from different theoretical perspectives such as fluid mechanics, bioenergetics, statistical thermodynamics, and physiology. And through the metabolic rate bridge, an organic connection is established between animals and plants, individuals and populations, communities, and ecosystem ecology.

### Acknowledgements

The authors would like to acknowledge with great appreciation for the support provided by the Chinese National Major Science and Technology Program for Water Pollution Control and Treatment (No. 2017ZX07101-002) and the Chinese Fundamental Research Funds for the Central Universities (No. 2017MS065).

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**How to cite this article:**

Yixin Xu, Xiaoling Hu, ZhaoLiu and Huayong Zhang *et al* (2020) 'Research Progress on Allometric Models and its Application', *International Journal of Current Advanced Research*, 09(07), pp. 22811-22814.  
DOI: <http://dx.doi.org/10.24327/ijcar.2020.22814.4509>

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