

ALLOMETRIC SCALING AS AN INDICATOR OF ECOSYSTEM STATE: A NEW APPROACH

BAI-LIAN LI*

*Ecological Complexity and Modeling Laboratory, Department
of Botany and Plant Sciences, University of California, Riverside,
CA 92521-0124, USA*

VICTOR G. GORSHKOV AND ANASTASSIA M.
MAKARIEVA

*Theoretical Physics Division, Petersburg Nuclear Physics
Institute, Russian Academy of Sciences, 188300, Gatchina,
St. Petersburg, Russia*

Abstract. It is argued that the problem of regional environmental security cannot in principle be solved without involving the regulatory environmental potential of the natural biota. Ecological allometry, i.e. the analysis of ecological and environmental phenomena based on body size and spatial scale regularities, is shown to provide clues to understanding the principles of environmental homeostasis in natural ecosystems.

Keywords: Allometric scaling; biotic regulation; energy consumption; forest; leaf area index; primary productivity; transpiration; water cycle

1. Introduction

Environmental security can be considered as a bifocal problem. On the one hand, it is important to protect the environment from being poisoned by the industrial pollution. On the other hand, irrespective of the presence/absence of direct pollution, it is vital to ensure sustainable maintenance of those

*Corresponding Author: Professor Bai-Lian Li, Ecological Complexity and Modeling Laboratory, University of California, Riverside, CA 92521-0124, USA; e-mail: bai-lian.li@ucr.edu

environmental characteristics on which humans, as a biological species, are critically dependent: favorable climate conditions, high biological productivity, and availability of freshwater.

At present, according to satellite data, the civilization actively uses over 60% of the continental areas. Struggle with industrial pollution presents no conceptual difficulties and, given sufficient investments, invariably yields visible environmental improvements. In contrast, despite huge economic investments into the maintenance of exploited lands, their global degradation continues. Soils erode, biological productivity and river runoff decline.

Here we outline a new conceptual approach to the problem of environmental security. It is based on the study of the self-sustainable, self-organizing properties of the natural biota, its apparent ability to maintain all environmental characteristics in a state optimal for life in general and human life in particular for practically infinite periods of time.

Living world is characterized by a unique diversity of forms. This would preclude a quantitative scientific analysis of the biological and ecological phenomena unless one succeeded to find some common variables that could be relevant for all living organisms. Spatial scale and body size belong to the few universal biological variables of this kind. Allometric scaling represents a particular type of functional dependence between any biological, ecological, or environmental parameter x and size or spatial scale L . It can be written as $(x/x_0) = (L/L_0)^\beta$, where x_0 is the value of x at a characteristic size scale $L = L_0$.

Allometric scaling has been actively studied, although predominantly at the organismal level (Peters, 1983), and currently represents one of the hot spots of theoretical research in biology. Here we show that the bases of environmental stability in natural ecological systems can also be analyzed on these grounds. To illustrate the potential of the new approach, two examples are considered: (1) It is shown that the allometric distribution of energy consumption over different-sized species in the ecosystem dictates the magnitude of the fluctuations of biological productivity; and (2) It is shown that the dependence of precipitation on the distance from the ocean is coupled to the degree of disturbance of the natural vegetation cover. Both examples illustrate that allometric scaling of landscape-level ecosystem characteristics can be developed into an informative indicator of the ecosystem's state and of the degree of security of the life-support services that the ecosystem provides.

2. Theoretical platform: biotic regulation of the environment

All living organisms produce certain impact on their environment, consuming some substances from it and returning different ones. Synthesis and decomposition of organic matter in the biosphere occur at such high rates that if all the

organisms in the biosphere had performed these processes chaotically and independently of each other, then the concentrations of all biogenic elements could have changed by a 100% over a time period of the order of 10 years, thus rendering the environment unsuitable for human existence.

The fact that the environment has remained suitable for macroscopic life, which has persisted during at least the last 600 million years, as testified by the available paleodata, indicates that functioning of the ecological communities of the biota does not occur chaotically. Traditionally, this nonrandom character of the biotic processes of organic synthesis and decomposition has been linked to the concept of closed biogeochemical cycles (Commoner, 1971; Schwartzman, 1999). According to this concept, the mean rates of synthesis and decomposition of organic matter coincide with each other with a practically infinite precision, so that functioning of the biota does produce any net impact ("pollution") on the state of the environment.

Indeed, if the environmental impact of the biota were nullified, the environment could only change under the impact of abiotic physicochemical processes. These processes include the emission of inorganic matter from the Earth's interior and the reverse processes of deposition of various substances in sediments. These fluxes are about 10,000 times less powerful than the fluxes of chemical elements during biological synthesis and decomposition. Since the abiotic fluxes of emission and deposition are independent physicochemical processes having different causes, they cannot compensate each other. Their net rate is of the same order of magnitude as the gross rate. This means that under the impact of abiotic processes the environment would be changing by 10^4 times more slowly than in the case of chaotic life functioning, i.e. it would change by a 100% over a time period of a 100,000 years, i.e. on a timescale 10,000 times shorter than the documented age of life.

Moreover, it is in principle impossible to equate the fluxes of synthesis and decomposition precisely. Synthesis and decomposition of organic matter represent independent biochemical processes that are generally performed by different species under different environmental conditions (temperature, humidity, etc.). While primary productivity is limited by the incoming solar radiation, there are no physical limitations on the rate of decomposition, since the latter rate is ultimately dictated by the population numbers of heterotrophic organisms. Characteristic ecosystem values of P^+ and P^- are determined by the individual design of every species, population abundance and overall numbers of autotrophic and heterotrophic species inhabiting Earth. The values of P^+ and P^- cannot coincide with an infinite precision a priori.

Indeed, the global amount of atmospheric CO_2 is of the order of $M^- \sim 10^3$ Gt C (1 Gt = 10^9 t). The mean global rates of biochemical synthesis P^+ and decomposition P^- are of the order of $P^- \sim P^+ \sim 10^2$ Gt C year⁻¹. If the rates of

synthesis and decomposition were not correlated, i.e. if they coincided by the order of magnitude only, their relative difference would be of the order of unity, $|P^+ - P^-| / P^+ \sim 1$. In such a case, if synthesis exceeded decomposition, $P^+ > P^-$, the global biota would use up the entire store of atmospheric carbon on a timescale of $M^- / P^- \sim 10$ years. This would render further photosynthesis and existence of life impossible. The amount of organic carbon in the biosphere (living biomass, humus, and oceanic dissolved organic carbon) is of the same order of magnitude, $M^+ \sim 10^3$ Gt C. If the rate of decomposition exceeded the rate of synthesis, the global biota would be able to destroy itself completely in equally short periods of time. To extend the biotic life span to the documented billion years of life existence, $T \sim 10^9$ years, one has to demand that the living organisms and their ecological communities are designed such that the mean rates of synthesis and decomposition performed by them coincide to the accuracy of $M^\pm / |P^\pm T| \sim 10^{-8}$, one millionths of a percent, which is absolutely improbable.

This unambiguously suggests that the biota should use a conceptually different principle to achieve the environmental homeostasis. Correlation of the ecological fluxes of synthesis and decomposition of the organic matter is achieved indirectly, via continuous sensing of information about the current state of the environment that is performed by the living organisms. The biota reacts to any environmental change as soon as its relative magnitude reaches some critical value, biotic sensitivity ε_b , a fundamental parameter of life organization. As long as the relative magnitude of the environmental change remains lower than biotic sensitivity, synthesis, and decomposition of organic matter by the biota may proceed in a noncorrelated manner at different rates. As soon as some environmental parameter changes by ε_b , the biota initiates compensating negative feedback processes and keeps them going until the disturbance is diminished to a level below ε_b , when the biota no longer notices it. The optimal state to which the ecosystem ultimately returns is thus defined to an accuracy of ε_b .

Environmental control based on biotic sensitivity is performed on a local scale by every individual organism of the biota. The particular forms of this control are dictated by the genetic programs of biological species. Individual organisms acting to compensate the environmental disturbances improve their local environment and enhance their competitive capacity. Local ecological communities with an overly high number of individuals with impaired genetic programs incapable of environmental regulation suffer from environmental degradation, lose competitiveness, and are replaced by normal communities free from such defective individuals. In the result, all ecological communities in the

natural biota act in the same direction supporting the optimal state of the environment already on a global scale. This principle of environmental stabilization forms the basis of the biotic regulation concept (Gorshkov, 1995; Gorshkov et al., 2000, 2004; Makarieva et al., 2006).

3. Allometric scaling of energy consumption in stable ecosystems

In this section we shall see how the biotic regulation principle is implemented in the organization of energy fluxes within natural terrestrial ecosystems; how it allows to minimize fluctuations of plant biomass and to stabilize the flux of primary productivity.

3.1. STABILIZATION OF PHOTOSYNTHESIS

Plants form the basis of ecosystem's energetics. They are responsible for the synthesis of organic matter, which further fuels all life processes in the community. To make this flux stable, the photosynthesizing parts of plants dominating natural terrestrial ecosystems represent a large number of weakly correlated objects of relatively small size (e.g. leaves, needles). The fluctuations of phytomass of individual plant are thus minimized in accordance with the statistical law of large numbers (Li et al., 2004; Makarieva et al., 2004). For example, an adult fir tree has several million needles, $N \sim 10^6$, that fall off and regrows every year. Thus, the yearly relative fluctuation of individual plant's phytomass (when detrended against nonrandom processes like tree growth) does not exceed $\varepsilon \sim 1/(N)^{1/2} \sim 10^{-3}$, i.e. 0.1%. The same figure approximately characterizes the yearly fluctuation of primary productivity.

Clearly, low values of relative fluctuations ε of phytomass and primary productivity could have only evolved and been further maintained in the course of competitive interaction of individual plants with different ε values – plants demonstrating the inability to stabilize their phytomass and productivity at a needed value were losing to those that did so. It would not be advantageous for a plant to keep the process of photosynthesis stable and fluctuations ε of the phytomass minimized, unless the fluctuations of plant biomass introduced by the process of decomposition are equally low. In other words, a plant providing food to heterotrophs that consume it in an erratic fashion would be the same suffering from biomass fluctuations as a plant with unstable photosynthesis. Hence, it is justified to expect that fluctuations of plant biomass introduced by its consumption by heterotrophs do not normally exceed the fluctuations ε introduced by the process of photosynthesis.

3.2. ENERGETICS OF HETEROTROPHS

Whilst photosynthesis is performed by objects of similar size (e.g. leaves), decomposition of the organic matter is performed by organisms with linear size varying from several micrometers (bacteria) to meters (large mammals). Due to the biochemical universality of life organization energy consumption by unit live mass or volume should be the same in organisms of all sizes. This theoretical prediction agrees well with observations: within most taxa, from bacteria to mammals, most species have their mass-specific metabolic rate q in the interval of 1–10 W kg⁻¹ (Makarieva et al., 2005). Energy enters the organism via its body surface, while it is spent within the body volume. The volume/area ratio is constant and size-independent in flat (“two-dimensional”) organisms that can therefore occupy an arbitrary area on the ground surface having a fixed thickness L determined by the energetic demand q (W kg⁻¹) of the organism and by the incoming flux of external energy f (W m⁻²): $L = f/q$.

Plants, fungi, and bacteria feature this type of metabolic organization. Plants absorb solar radiation which is uniformly distributed over the ground surface, so plants can form a continuous cover. The upper limit to the flux of energy that can be consumed by heterotrophs is set by the primary productivity, $f = P^+$. Thus, small organisms with linear body size $L \leq P^+/q \sim 10^{-4}$ m can afford being immobile like plants. Such organisms (bacteria, fungi) can form a continuous cover under the plant canopy and consume primary productivity P^+ without exempting the standing stock of plant biomass. In other words, the smallest heterotrophs can satisfy their energetic needs with the flux of organic matter produced on the area of the projection of their tiny bodies on the ground surface.

A very different situation is realized for large animals with linear body size $L \gg P^+/q$. These organisms cannot afford being immobile and live on plant production; they have to move exempting plant biomass. Their home range must greatly exceed their projection area. This energetic property of animals has fundamental implications for ecosystem stability.

3.3. ECOLOGICAL ALLOMETRY AND STABILITY

While moving over their large home territories and feeding, animals introduce local disturbances of plant biomass, which, in their turn, destabilize the flux of photosynthesis and primary productivity. The larger the animal, the greater fluctuations that it introduces. The overall magnitude of the fluctuations introduced per unit surface area by a population of large plant-feeding heterotrophs depends on their body size, population density N (ind km⁻²) and individual

metabolic rate Q (W ind^{-1}). The value of $\beta \equiv NR/P^+$ characterizes the share of primary productivity allocated to heterotrophs of a given body size.

Theoretical analysis has shown that if all organisms, irrespective of their body size, consumed equal shares of ecosystem primary productivity, the relative fluctuation ε of plant biomass introduced by organisms of a given body size would increase proportionally to linear body size L . In such a case, in the course of evolutionary increase of body size the fluctuations of biomass would increase by approximately 10^4 (Makarieva et al., 2004).

To suppress the growth of plant biomass fluctuations with growing body size of heterotrophs it is necessary to decrease the share of primary productivity allocated to large heterotrophs at the expense of diminishing their population density. Then, although the per capita fluctuations remain large, as dictated by large body size, the absolute magnitude of ecosystem disturbance introduced by large heterotrophs can be kept at a low level not threatening the ecosystem's functioning. It was estimated that in stable ecosystems the share of primary productivity allocated to plant-feeding heterotrophs should scale inversely proportionally to the linear body size, Figure 1. As indicated by the analysis of empirical evidence, this pattern is indeed realized in the natural forest ecosystems of the boreal zone in Eurasia and North America, Figure 1.

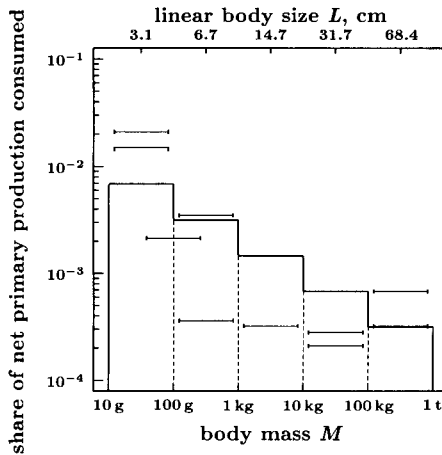


Figure 1. Relative share $\beta(L)$ of net primary production consumed by plant-feeding organisms from different logarithmic body size classes in natural forest ecosystems of the boreal zone. The histogram (thick lines) shows the theoretical distribution $\beta(L) \propto 1/L$; height of each bar is equal to the cumulative energy consumption by all community's organisms with body size falling within the respective logarithmic interval. Thin lines denote the observed $\beta(L)$ values: data from boreal ecosystems in Eurasia and North America (Makarieva et al., 2004).

3.4. IMPLICATIONS FOR ENVIRONMENTAL SECURITY

It is clear from Figure 1 that in stable ecosystems the largest heterotrophs are allowed to consume no more than several tenths of percent of ecosystem's primary productivity. As predicted by the developed approach, in unstable ecosystems, where environment is shaped by abiotic processes uncontrollable by the local biota, no ecological restrictions can be imposed on biotic environmental fluctuations. Consequently, in unstable ecosystems the community's energy flow can be distributed chaotically over differently sized animals, showing on average no dependence on body size.

Conversely, ecosystems where large animals consume large portions of primary productivity cannot be stable. The derived $\beta(L)$ distribution of energy consumption over body size is therefore important for long-term conservation practices. It allows estimating the optimum population densities of the threatened species that can be sustained on a given territory without undermining the long-term stability of the ecosystem.

At present man directly consumes about 10% of the global net primary productivity of the biosphere. (This includes food of man and cattle and consumption of wood (Gorshkov et al., 2000). As is clear from Figure 1, this figure exceeds the energy consumption quota allocated to similarly sized animals in environmentally stable ecosystems by two orders of magnitude. Expectedly, the terrestrial part of the biosphere is undergoing rapid environmental degradation. Further studies of the natural $\beta(L)$ distribution can be useful for elaborating strategies of optimization of the man-biosphere interaction.

4. Allometric scaling and terrestrial water cycle

The central idea behind the biotic regulation concept is that the natural biota creates and maintains its own favorable environment, both internal and external. While achieving this goal life had to repeatedly face the fundamental allometric problem of meeting the demand of matter or energy in an n -dimensional area by a flux of matter or energy via an $(n - 1)$ -dimensional area. For example, living organisms consume energy via the two-dimensional (2D) body surface and spend it within the 3D body volume. To ensure that energy is delivered to living tissues at a size-independent optimum rate, large organisms had to invent active pumps (e.g. lungs, heart), which pump matter and energy into the organism and distribute them within it. Passive diffusion fluxes of organic matter could only satisfy the needs of the smallest unicellular organisms with their linear body size L much less than the characteristic distance to the source of food.

On the ecological scale, one of the most important environmental parameters is moisture. In terrestrial ecosystems, atmospheric moisture enters a

river basin via the linear coastline, while it is spent within the 2D area of the river basin. Passive geophysical fluxes of moisture can ensure sufficient soil moistening at small distances $L \sim 10^2$ km from the ocean only. To keep large territories with $L > 10^3$ km biologically productive, an active biotic pump of atmospheric moisture is necessary. That such a biotic pump does exist is confirmed by the observation that natural forests in South and North America and Eurasia are able to ensure high precipitation fluxes at any distance from the oceanic coast over several thousand kilometers inland. In contrast, in non-forested scarcely vegetated world's regions precipitation drops exponentially with distance from the ocean over a few hundred kilometers (Gorshkov and Makarieva, 2006; Makarieva et al., submitted).

The high leaf area index, a conspicuous feature of the organization of natural forests, is associated with a high rate of transpiration which can exceed evaporation from the open water surface of the ocean. The difference between the forest and ocean evaporation fluxes creates an upwelling flux of air above the forest canopy. This flux is compensated by the horizontal influx of moist air from the ocean. This regular and continuous functioning of the forest pump of atmospheric moisture prevents formation of extreme weather phenomena like hurricanes in the regions with substantial natural forest cover, which thus acts as the main guarantor of environmental security on the regional and global scale. A novel physical mechanism involving the nonequilibrium distribution of atmospheric water vapor was proposed to explain how the high transpiration fluxes developed by forests enable them to pump atmospheric moisture from the ocean to any distance inland to compensate for the runoff losses from the optimally moistened forest soil. Our results suggested that extensive forest cover plays a significantly larger role in the atmospheric circulation than previously assumed (Makarieva et al., submitted). However, more precise physical laws governing the action of the forest moisture pump demand a detailed exploration.

5. Perspectives

It is becoming progressively more evident that the problem of keeping the environment stable and secure is extremely demanding in terms of information resources. At present people attempt to meet this demand by continuously enhancing the computing facilities of the civilization in order to process the avalanche of data collected by the numerous programs of environmental and societal monitoring. No question is posed as to whether it is at all possible to collect an amount of information sufficient for environmental stabilization.

In the meantime, robust estimates indicate that in the natural biota the environmental homeostasis is maintained on the basis of huge information

fluxes of the order of 10^{20} bits $m^{-2} s^{-1}$ on a global average (Gorshkov, 1995; Gorshkov et al., 2000; Makarieva et al., 2006). In the biosphere each square micron is inhabited by several living cells whose per capita information processing capacity is comparable to that of a modern personal computer. Living cells continuously sense the environment and react to its changes in a nonrandom manner dictated by their genetic programs. Since the efficiency of this biotic regulation mechanism has been perfected during the several billion years of biological evolution, it is impossible to replicate this mechanism in technology using a smaller information flux. However, the information processing capacity of the modern civilization amounts to only 10 bits $m^{-2} s^{-1}$; the 19 orders of magnitude's gap dismisses all hopes for a global technology-based environmental control.

This means that the problem of environmental security on a global or regional scale cannot in principle be solved without involving the already existing regulatory potential of natural ecological systems. For this purpose, natural ecosystems will have to be conserved and restored on sufficiently large areas of continental scale. Current demographic trends in the developed countries, where the population numbers gradually decrease, create a favorable opportunity for this scenario. In this perspective the study of the bases of environmental homeostasis in the extant natural ecosystems becomes very important. Here we outlined one of possible approaches to this problem, where ecosystem's properties were analyzed within the allometric framework, i.e. based on regularities dictated by spatial scale and organismal body size. The first results are promising and clearly justifying further efforts in this direction.

Acknowledgments

This work was partially supported by the US National Science Foundation Biocomplexity Program, the University of California Agricultural Experiment Station, the Russian Science Support Foundation, and Russian Fund for Basic Research.

References

- Commoner, B. (Editor), 1971. *The Closing Circle. Nature, Man, Technology*. Knopf, New York.
- Gorshkov, V.G., 1995. *Physical and Biological Bases of Life Stability. Man, Biota, Environment*. Springer, Berlin.
- Gorshkov, V.G., Gorshkov, V.V., and Makarieva, A.M., 2000. *Biotic Regulation of the Environment: Key Issue of Global Change*. Springer, London.

- Gorshkov, V.G., Makarieva, A.M., and Gorshkov, V.V., 2004. Revising the fundamentals of ecological knowledge: the biota-environment interaction. *Ecological Complexity* 1, 17–36.
- Gorshkov, V.G. and Makarieva, A.M., 2006. Biotic Pump of Atmospheric Moisture, Its Links to Global Atmospheric Circulation and Implications for Conservation of the Terrestrial Water Cycle. Preprint No. 2655, Petersburg Nuclear Physics Institute, Gatchina, Russia.
- Li, B.-L., Gorshkov, V.G., and Makarieva, A.M., 2004. Energy partitioning between different-sized organisms and ecosystem stability. *Ecology* 85, 1811–1813.
- Makarieva, A.M., Gorshkov, V.G., and Li, B.-L., 2004. Body size, energy consumption and allometric scaling: a new dimension in the diversity-stability debate. *Ecological Complexity* 1, 139–175.
- Makarieva, A.M., Gorshkov, V.G., and Li, B.-L., 2005. Energetics of the smallest: do bacteria breathe at the same rate as whales? *Proceedings of the Royal Society of London B* 272, 2219–2224.
- Makarieva, A.M., Gorshkov, V.G., and Li, B.-L., 2006. Conservation of water cycle on land via restoration of natural closed-canopy forests: implications for regional landscape planning. *Ecological Research* 21, 897–906.
- Makarieva, A.M., Gorshkov, V.G., and Li, B.-L., submitted. Precipitation on land versus distance from the ocean: Evidence for a forest pump of atmospheric moisture.
- Peters, R.H. (Editor), 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Schwartzman, D. (Editor), 1999. *Life, Temperature, and the Earth: The Self-Organizing Biosphere*. Columbia University Press, New York.