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The Upper and Lower Ecological Limits of Specific Metabolic Power of Different Organisms

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Abstract—It has been demonstrated that bioenergetic properties of plants (independence of productivity from size, proportionality between radial growth of woody plants and plant mass, etc.) and animals are not related to the presumed universal linear relationship between metabolic power and body mass to the power of 3/4. This relationship is not true for plants and endothermic animals. The observed bioenergetic characteristics of these organisms are explained by simple biological and physical laws, including the existence of the lower and upper limits of the specific metabolic power of living matter.

Key words: metabolic power, body size, leaf area index, temperature, allometry, mammals.

1. INTRODUCTION

Recently, interest in the problem of the dependence of organisms' metabolic power (B) on body mass (M) has been revived. This dependence is traditionally described as the allometric relationship: $B = B_0M^{\alpha}$. There have been many attempts to substantiate theoretically the value of $\alpha = 3/4$, which was considered, for a long time, to hold true for most organisms (Hemmingsen, 1960; Kleiber, 1961). One explanation of $\alpha = 3/4$ is based on the assumption on a nontraditional scaling (a fractal nature) of the surface through which organisms exchange energy with their environment (West *et al.*, 1997).

However, recent large-scale studies (Dodds *et al.*, 2001) demonstrated that birds and mammals (about 800 species in total) did not conform to the "3/4 law." The exponent in the equation describing the dependence of the metabolic power of these organisms on body mass is close to $\alpha = 2/3$, which corresponds to the surface-to-volume ratio traditionally assumed for living organisms. Available data on other organisms, e.g., unicellular organisms and fishes, are contradictory (see, e.g., Brett and Groves, 1979; Vladimirova and Zotin, 1985; Prothero, 1986). Therefore, most researchers began to use data on plants for substantiating the "3/4 law." For example, the following predictions were made for plants: (1) productivity is independent of plant size, (2) radial growth of woody plants is proportional to the plant mass to the power of 3/8, and (3) the growth of the total plant metabolism is proportional to the plant mass to the power of 3/4 (Enquist *et al.*, 1998, 1999; West *et al.*, 1999; Enquist and Niklas, 2001, 2002).

Here, we further develop and generalize the assumptions made earlier (Makarieva *et al.*, 2003) and demonstrate that most of the aforementioned predictions are not related to the presence or absence of the "3/4 law" in plants. They are explained by simple biological and physical laws characterizing the organization of plants and animals, e.g., the existence of the lower and upper limits of the specific metabolic power of living matter. We use these laws to predict the exponential relationship between leaf area index and the elevation (above sea level) at which the ecosystem is located. We use the same simple laws to explain the relationship with $\alpha = 2/3$ observed in mammals and birds, as well as deviations from $\alpha = 2/3$ in large and small mammals and the absence of such deviations in birds.

2. THE LOWER AND UPPER LIMITS OF SPECIFIC METABOLIC RATE

All organisms receive energy from the environment through part of their body surface and expend it in the entire body volume (V). Hereinafter, the power of energy expenditure by the body, i.e., the power of metabolism, is called metabolism. If we assume that the energy flux (f) across a unit area (S) is constant, then specific metabolism (metabolism per unit volume or mass) is $b = fS/V \propto l^{\sigma - \upsilon} \equiv l^{\mu}$, where l is the characteristic linear body size, and $\mu \equiv \sigma - \upsilon$, σ and υ being the exponents in the equation for the dependence of body surface (S) and volume (V) on linear size (l). In the case of geometric similarity, $\sigma = 2$, $\upsilon = 3$, and $b \propto l^{-1}$, $\mu = -1$, which corresponds to $\alpha = 2/3$ for the dependence of the total body metabolism (B) on body mass or volume, $B \equiv bV \propto l^{-1}l^3 \propto V^{2/3}$.

Thus, metabolism per unit mass or volume (b) decreases with an increase in body size. It would be reasonable to suppose that there is the minimum value of specific metabolism (b_{min}) characterizing the minimum energy that is necessary to maintain the biochemical processes that constitute the essence of life. This value determines the minimum energy flux necessary for maintaining the highly organized animate living matter and preventing its spontaneous decay.

At a given energy flux across a unit body surface (f), b_{min} determines the maximum body size that the organism can reach. It has been established (Gorshkov, 1981) that taxonomic groups characterized by different values of f have the same b_{min} values. This is a natural expression of the universal biochemical organization of life.

Similarly, there must be the maximum energy consumption per unit mass of living matter (b_{max}) determining the minimum body size in a given taxonomic group. Direct measurements have demonstrated that the biochemical limit (b_{maxBCH}) is also the same for various organisms. For example, the energy expenditure per unit of living mass during the most rapid known division of bacteria (Gorshkov, 1981) and the energy expenditure per unit of muscle weight during maximum jump performance in insects (Katz and Gosline, 1993) and mammals (Alexander, 1975) have the same order of magnitude. Obviously, the maximum metabolism of existence (b_{max}) must be lower than b_{maxBCH}, which is only reached in certain tissues under special conditions.

3. ENERGETICS OF ENDOTHERMIC ORGANISMS

Let us consider what conclusions about the dependence of total metabolism (B) on body mass (M) in endothermic animals can be made proceeding from the assumption that there are upper and lower limits of metabolism per unit body mass (b_{max} and b_{min}).

Endothermic organisms (mammals and birds) maintain a constant body temperature, which is roughly the same for all species. Therefore, they may be characterized by the same average energy flux across a unit surface: $f_{end} = \text{const}$. Thus, we obtain $B = f_{end}S \propto V^{2/3} \propto M^{2/3}$, where S is the body surface area, and V is the body volume.

The results of the largest scale study on the $B \propto M^\alpha$ dependence in 391 mammalian species (Heusner, 1991) performed to date demonstrated that, for the total class, $\alpha = 0.678 \approx 2/3$. It was also shown that α was higher for the largest mammals. Dodds *et al.* (2001) analyzed the data reported by Heusner (1991) and found that the mean α was also substantially higher than the average value of 0.68 ($\alpha = 0.79$) for 81 species of the smallest mammals (with body masses no larger than 32 g).

In the case of geometric similarity, i.e., if $S \propto l^2$, $V \propto l^3$, and $\alpha = 2/3$, where l is the characteristic linear body size, specific metabolism (b) is inversely proportional to l. This is evident from the condition of the conservation of thermal balance. As body size increases, b approximates the minimum (b_{min}) corresponding to the maximum body size (l_1). When the body size has reached its maximum, further decrease in b is impossible.

The formation of organisms with body sizes larger than l_1 with α remaining equal to 2/3 is impossible, because the body may become overheated. Indeed, the amount of energy produced by the body becomes equal to $b_{min}V$, which is proportional to l^3, whereas the rate of heat release increases with an increase in body size only as $f_{end}S$, which is proportional to l^2. Therefore, the existence of large mammals is possible only if their surface-to-volume ratio has changed. In the extreme case, when $b = b_{min} = \text{const}$ for $l > l_1$, large mammals must have the largest possible effective surface, which must increase proportionally to volume: $S \propto V$ (Dodds *et al.*, 2001) corresponding to $\alpha_{max} = 1$ and $\mu_{max} = \alpha_{max} \times 3 - 3 = 0$. This is the case, e.g., with cetaceans (Kasting *et al.*, 2001).

Actually, the surface-to-volume ratio (S/V) changes more smoothly. As l approximates l_1, the decrease in specific metabolism (b) with an increase in body size becomes slower, and the ratio S/V expressed in units of l begins to grow, which corresponds to the increase in α within the interval $2/3 < \alpha < 1$. In practice, this means the appearance of body parts with a small volume but a large surface (e.g., the elephant's ears, the giraffe's neck, and the giant dorsal fin of the killer whale). Thus, large and medium-sized mammals should substantially differ in the surface-to volume ratio, i.e., the geometry of the body surface. This difference is actually observed (Economos, 1982).

As was noted above, $B \propto M^\alpha$ corresponds to $b \propto l^\mu$, $\mu = 3\alpha - 3$, where l is the characteristic linear body size of the animal. In double logarithmic coordinates, this relationship is expressed as $\log_{10}b = c + \mu\log_{10}l$. Thus, the increase in $\alpha = (\mu + 3)/3$ to 1 at large and small l corresponds to a decrease in the slope of the $\log_{10}b$ curve to zero in these intervals (Fig. 1).

Figure 1 shows the dependence of the specific basal (Brody, 1945) metabolism (b) on linear body size (l). The interval of body size values is divided into two ranges: less and more than 20 kg. Economos (1982) has determined that 20 kg is the critical body mass for mammals: if the body mass increases above this value, the aforementioned increase in body surface-to-volume ratio begins. To draw the plot shown in Fig. 1, we used data analyzed earlier (Makarieva *et al.*, 2003) and extended it by adding several values from other sources to increase the amount of data on large mammals.

For mammals with body masses less than 20 kg, estimation of the linear regression of $y \equiv \log_{10}b$ on

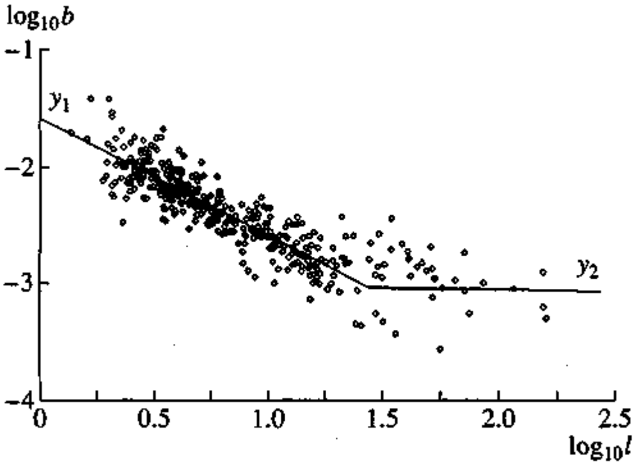

Fig. 1. Dependence of specific basal metabolism (b, W g^{-1}) on linear body size, which is here taken to be proportional to the power of 1/3 of body weight (m, g): $\log_{10}l \equiv 1/3\log_{10}m$. Most data are from the study by Makarieva *et al.* (2003); some data on large mammals ($m \geq 20$ kg) are from other studies (Kasting *et al.*, 1989; Lovegrove, 2000; Hurley and Costa, 2001). The parameters of linear approximations y_1 and y_2 are indicated in the text. Note that addition of new data improved the correlation for regression y_2 compared to the one estimated previously (Makarieva *et al.*, 2003).

$x \equiv \log_{10}l$ yielded the following results: $y_1(x) = -1.58 - 1.01x$, $r^2 = 0.77$, $P < 10^{-5}$. This corresponds to the exponent $\mu_1 = -1.01$ in the dependence $b \propto l^{\mu}$ and the exponent $\alpha_1 = (\mu_1 + 3)/3 = 0.67 \approx 2/3$ in the dependence $B \propto M^{\alpha}$. It is reasonable to assume that the $b(l)$ curve is continuous in the class Mammalia. According to this assumption, we attempted to approximate the logarithmic dependence of $y \equiv \log_{10}b$ on $x \equiv \log_{10}l$ by the straight line $y_2(x) = y_1(1.43) + \mu_2(x - 1.43)$ with the only parameter being μ_2. Here, $x = 1.43$ corresponds to a body mass of 20 kg. This approximation yielded $\mu_2 = 0.04 \pm 0.02$ for large animals, which corresponds to $\alpha_2 = 1.01$ and agrees with the aforementioned theoretical predictions: $\alpha_{max} = 1$ and $\mu_{max} = 0$.

The maximum sizes of birds are smaller than the maximum sizes of mammals by more than an order of magnitude. This is related to the limitations posed by the energetics of flight (Gorshkov, 1983). In other words, birds, on average, do not reach the range of maximum sizes. Therefore, in contrast to mammals, there is no flattening of the logarithmic curve $y(x)$ ($y \equiv \log_{10}b$, $x \equiv \log_{10}l$) with an increase in size (Fig. 1) in the case of birds. For 398 bird species, $\alpha = 0.66 \approx 2/3$ (Dodds *et al.*, 2001). This is additional evidence for the universal metabolic limit, b_{min}.

4. ENDOTHERMIC ORGANISMS WITH SMALL BODY SIZES

The metabolism per unit volume increases with a decrease in body size, approximating the highest possible value, b_{max}. In the extreme case, i.e., if the size has reached the minimum (l_2) corresponding to b_{max}, further increase in b is impossible. The formation of organisms with sizes smaller than l_2 with α remaining equal to 2/3 is impossible, because the body may become overcooled. In other words, the rate of heat release decreases more slowly (proportionally to l^2) than the amount of energy produced by the body (which is proportional to l^3). Therefore, the formation of the smallest mammals is also possible only if the body surface-to-volume ratio has changed. Small mammals must minimize heat emission, i.e., the surface-to-volume ratio. An almost spherical body lacking any parts with large surface-to-volume ratios meets this requirement. This change in the body geometry also corresponds to an increase in α compared to the value of 2/3 characteristic of an unchanged geometry. In other words, with a decrease in body size relative to the average body size of mammals, body surface decreases more rapidly than l^2. This explains the high α value ($0.79 > 2/3$) found in 81 species of small mammals with body masses no larger than 32 g (Dodds *et al.*, 2001).

5. MINIMUM SPECIFIC METABOLISM OF PLANTS

Solar energy, whose flux per unit area is determined by the geographic latitude and the albedo (reflection factor) of the Earth's surface, is the energy basis of plant life. At a given energy assimilation coefficient (η), determined by the biochemical properties of living matter and temperature, the flux of energy (f_{plant}) assimilated by the plant per unit area is constant. In other words, plants, as well as endothermic animals, although for a different reason, may be characterized by a constant energy flux across the unit area. Therefore, primary plant production per unit area, which is proportional to the energy assimilated, does not depend on plant size (Gorshkov, 1995). Contrary to the notion of Enquist *et al.* (1998), this fact may be explained without assuming fractal organization of the transport of substances in plants.

To characterize plant metabolism, let us introduce effective linear size (l_{eff}), which is equal to the thickness of the layer that would be formed if the entire metabolically active mass of the plant were distributed, at even density, over the area occupied by the entire plant. Most of the mass of woody plants is metabolically inactive; therefore, the characteristic l_{eff} values of trees are no larger than 2 mm (Gorshkov, 1995). As the metabolically active mass of the plant per unit area and, hence, l_{eff} increase, metabolism per unit volume of the plant (b_{plant}) decreases. b_{plant} is inversely proportional to l_{eff} because, other conditions being the same, the energy flux per unit area (f_{plant}) remains constant. When metabolism has reached the minimum value ($b_{min} = f_{plant}/l_{eff\,max}$), further increase in the thickness of the vertical layer of the metabolically active biomass becomes impossible. Further increase in the metabolically active mass of an individual plant is only possible through its radial growth (in a horizontal direction), i.e., a growth in width rather than in height.

Metabolically active organs and tissues of plants (the foliage, cambium, and root surface) encompass the entire surface of the plant. Therefore, the height (H) of the plant cover and the effective thickness of metabolically active parts (l_{eff}) closely correlate with each other. For example, in forests, $H = kl_{eff}$, where $k \sim 10^3–10^4$ (Gorshkov, 1995). Since b_{min} is common to all plants, the characteristic height (H) of the vegetation cover decreases in the direction from the equator to the poles (Larcher, 1978). In other words, $H > l_{eff} = f_{plant}/b_{min} \propto f_{plant}$, where f_{plant} is determined by the annual average radiation flux and mean temperature of the growing period, which decrease in the direction from the equator to the poles. In a given area, b_{min} determines the vertical size of forest ecosystems.

Obviously, if the maximum l_{eff} is fixed, the metabolically active plant mass may further increase only in the horizontal direction; hence, this increase is effectively two-dimensional. In other words, $m \propto l^2$, where l is the characteristic horizontal linear size of the plant, e.g., the diameter of the trunk ($l \equiv D$). The mass of leaves (m_{leaf}) is a good approximation of the metabolically active mass. For this parameter, the relationship that we predict ($m_{leaf} \propto D^2$) fits available experimental data (Enquist and Niklas, 2002).

However, the two-dimensional growth of the metabolically active mass may occur only in mature plants that have reached, or almost reached, the maximum l_{eff}. The dependence $m_{leaf} \propto D^2$ estimated by Enquist and Niklas (2002) in mature trees (whose breast-height diameter could be measured) confirms this prediction. At initial stages of plant growth, i.e., at low l_{eff} and at rates of metabolism per metabolically active unit mass considerably higher than b_{min} ($b > b_{min}$), there is no obstacle to the three-dimensional growth of the metabolically active biomass, which corresponds to $m_{leaf} \propto D^3$. Therefore, data on young plants contradict the prediction that follows from the assumption (West *et al.*, 1997) that $m_{leaf} \propto D^2$ holds true during the entire period of plant growth (Enquist and Niklas, 2002).

For the metabolically inactive part of the plant (trunk wood), limitations on the spatial dimensionality of the growth are absent, because the increase in metabolically inactive mass is not directly related to changes in specific metabolism (b). In other words, the metabolically inactive mass of the plant may grow both two- and three-dimensionally. Therefore, the exponent of the equation $D \propto M^{\varepsilon}$, where M is the total mass of the plant, and D is the diameter, should fall within $1/3 < \varepsilon < 1/2$. The value 3/8 reported by West *et al.* (1997) is within this interval.

Note again that the relationship $m_{leaf} \propto D^2$ was derived on the basis of the only assumption that there exists a lower limit of metabolic power per metabolically active unit plant mass. Therefore, this dependence may be observed at any relationship $B \propto M^{\alpha}$ (where B is the total metabolism of an individual plant, and M is the total plant mass); it does not follow from the relationship $\alpha = 3/4$, contrary to the notion of Enquist and Niklas (2002). This is accounted for by the fact that, by definition, the metabolically inactive plant mass, which constitutes the major part of the biomass of woody plants, is not directly involved in energy consumption. Only metabolically active parts of the plant are responsible for the latter. The main functions of metabolically inactive parts of the trunk and wood (support in the gravitation field and transport of dissolved biogenic substances) may have been performed by inorganic vascular constructions, such as artificial substitutes of bone tissue and artificial blood vessels that are used in modern surgery. From this viewpoint, the calculation of metabolism for the total mass of the plant is as senseless as the calculation of the metabolism of mammals and birds taking into account the mass of metabolically inactive parts of their bodies (down, feathers, hair, claws, etc.) and birds' nests.

Similarly, the statement that plant growth rate is proportional to the diameter of the trunk and is independent of wood density (Enquist *et al.*, 1999) is not a unique prediction of the "3/4 law." If $m_{leaf} \propto D^2$ and $B \propto D^2$, this result follows from the natural assumption that the growth rate (R) is proportional to plant metabolism: $R \propto B \propto D^2$.

6. CHANGE IN LEAF AREA INDEX WITH AN INCREASE IN ALTITUDE

The existence of the lower limit of specific metabolic power of the plant also allows us to predict the change in leaf area index with an increase in altitude. The dimensionless leaf area index (d) is the ratio of the total area of leaves of the entire plant cover to the area of soil. Assuming that leaves constitute the main part of metabolically active tissues of the plant, we may assume that, roughly, $l_{eff} = dh$, where h is the mean leaf thickness.

The flux of energy assimilated by the plant per unit area (f_{plant}) may be written as $f_{plant} = \eta I$ where I is the solar radiation flux per unit of earth surface, and η is the solar energy assimilation coefficient. In this case, the value l_{eff} determined by b_{min} is $l_{eff} = \eta I/b_{min}$, and, since the leaf area index is $d = l_{eff}/h$, we obtain

$$d = \eta I/b_{min}h. \quad (1)$$

The absorption of solar energy by the plant is connected with the transformation of the energy of massless light photons into the energy of organic molecules

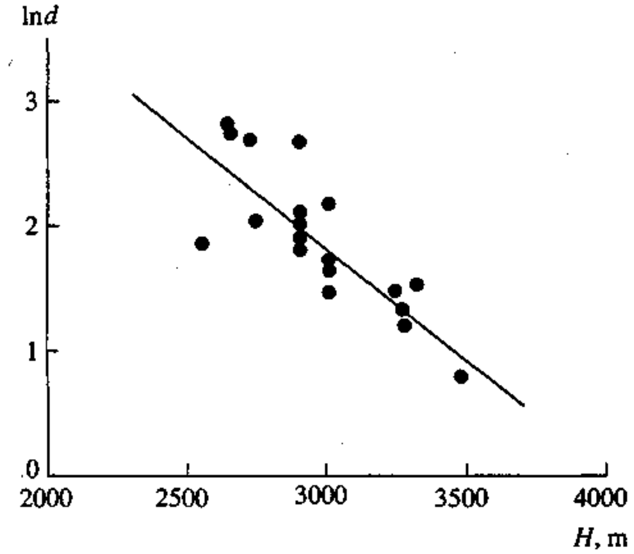

Fig. 2. Dependence of leaf area index (d) on elevation above sea level (H) for 27 biomes located between 31 and 40° N in China and the United States (not all points are discernible, because some data overlap). See the text for the parameters of linear regression.

synthesized from inorganic compounds. This is accompanied by the highly organized transport of inorganic and organic molecules within the plant determined by a complex system of biochemical reactions within the plant. Therefore, the solar energy assimilation coefficient (η) should exponentially depend on the ambient temperature: T: $\eta \propto e^{E/k_BT}$, where E is the mean activation energy for the plant biochemical reactions, T is absolute temperature expressed in degrees Kelvin, and k_B is the Boltzmann constant. For relatively small changes in temperature, $T = T_0 + t$, $t \ll T_0$, we obtain $\eta \propto e^{At}$, where $A \equiv -E/(k_BT_0^2)$. On average, the temperature of lower atmospheric layers decreases with height (H) with a constant gradient $G = 6.6°\mathrm{C\ km^{-1}}$, $T(H) = T_0 - GH$; therefore, it follows from Eq. (1) that, at a fixed I value (i.e., at a given latitude), leaf area index should exponentially decrease with height:

$$d \propto \eta \propto e^{-AGH} \text{ or } \ln d = C - \frac{E}{kT_0^2}GH, \qquad (2)$$

where C is a constant independent of height (H).

Anthropogenic transformation of natural terrestrial ecosystems often leads to insignificant changes in leaf area index: For example, tropical deforestation leads to artificial desertification and, hence, decrease in leaf index. Therefore, empirical testing of Eq. (2) should be performed for nondeteriorated areas. The anthropogenic transformation of natural ecosystems mainly occurs within the lower altitudinal zone (no more than 1–2 km above sea level); therefore, it is reasonable to test Eq. (2) for ecosystems located at higher elevations.

Excessively high temperatures of the earth's surface, which are unfavorable for the development of plant cover, are another potential source of deviations from Eq. (2) at low altitudes. For example, if a desert with characteristic temperatures of 40 to 50°C is located at the foot of a mountain, it would be natural to assume that the leaf area index increases with height as the earth-surface temperature approaches the values optimal for plants. However, as height further increases and temperature decreases, the leaf area index should begin decreasing again according to Eq. (2).

We used the database (Scurlock *et al.*, 2001) for leaf surface indices of various ecosystems to test Eq. (2) for 27 biomes located at elevations of 2500 to 3500 m in China and the United States, between 31 and 40° N. As seen from Fig. 2, these data are sufficiently well approximated by the semilogarithmic straight line (2). Estimation of the linear regression $\ln d = aH + b$ yielded the following results: $a = -(1.8 \pm 0.3) \times 10^{-3}\ \mathrm{m^{-1}}$, $b = 7.1 \pm 0.8$, $r^2 = 0.64$, $P < 0.00001$. Similar results were obtained for ecosystems located in the Alps at elevations of 1500 to 3000 m above sea level (Makarieva *et al.*, 2003). Using the values $a \equiv -1.8 \times 10^{-3}\ \mathrm{m^{-1}}$, $T_0 \approx 288$ K, and $G = 6.6\ \mathrm{K\ km^{-1}}$, we may estimate the activation energy as $E/k_B = = -a(T_0)^2/G \approx 2.2 \times 10^4$ K. The order of magnitude of this value agrees with independent estimates of the values $E/k_B \sim (1.2\text{–}1.5) \times 10^4$ K for biochemical reactions (Gillooly *et al.*, 2001), which confirms that Eq. (2) is correct.

7. DISCUSSION

Thus, the dependence of energy characteristics on body size observed in plants and endothermic animals can be easily explained on the assumptions of (a) a constant energy flux per body surface (in plants, this is the solar energy flux; in endothermic animals, this is the heat emission flux determined by the constant body temperature) and (b) the existence of the upper and lower limits of specific metabolism (b) per unit body mass. These values should be calculated for the metabolically active unit mass.

We agree with Heusner (1991) that the fluxes (f) across the unit body surface, rather than the exponents α and μ, are most interesting for researchers. The f values determine absolute metabolic rates. We may predict that, body sizes being equal, actively moving and immobile organisms should have substantially different metabolic rates. For example, we may expect that f values are different in unicellular organisms that have special organs for increasing the flow of nutrients and in more passive unicellular organisms of the same size that only use diffusive flows for nutrition. It may be assumed that a finite number of methods for increasing f have been "discovered" in the course of evolution. Earlier, one of us (Gorshkov, 1981) analyzed the grouping of organisms living on the Earth according to their f values.

Apparently, a successful approach to the explanation of the dependence of energy characteristics of organisms on body size should be based on the analysis of energy consumption by organisms (the primary basis of energetics), rather than transport of substances, which is coupled with energy consumption but only occurs when energy has already been consumed. This is especially obvious in the case of plants. In natural ecosystems, plants themselves regulate the concentrations of biogenic substances required (Gorshkov *et al.*, 2000); however, they cannot, in principle, change the external flux of the consumed solar energy. Therefore, all vital processes in plants, including the transport of biogenic substances, are inevitably adjusted to the solar energy flux. The consumption of biogenic substances (inorganic nutrients) from the soil cannot be compared with the nutrition of animals, which receive energy from organic food. Plants assimilate the energy of massless solar photons, whereas inorganic biogenic substances do not contain energy. Therefore, as shown in this study, the analysis of the characteristics of energy consumption (namely, the constant energy flux per unit area) entirely determines the energy properties of plants as dependent on their size.

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