



## LETTER TO THE EDITOR

### A Note on Metabolic Rate Dependence on Body Size in Plants and Animals

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The nature of scaling between the organismal basal metabolic rate  $B$  and its body mass  $M$ ,  $B \propto M^\alpha$ , is currently an important focus of debates in theoretical biology (Whitfield, 2001). For decades, it has been widely accepted that  $\alpha = 3/4$  for virtually all groups of organisms (Hemmingsen, 1960; Kleiber, 1961). A novel approach developed by West, Brown & Enquist (1997) (WBE) explains the value of  $\alpha = 3/4$  (instead of  $2/3$  that is to be expected from basic dimensional considerations) by noting the fractal-like space-filling structure of networks that transport materials within living bodies.

However, the agreement about the ubiquity of  $\alpha = 3/4$  in the living world has recently been seriously challenged by extensive analyses of data unavailable at the time of adopting the “ $3/4$  rule”. Dodds *et al.* (2001) showed that  $\alpha = 0.67$  for 357 mammalian species with mass less than 10 kg and  $\alpha = 0.71$  for the total of 391 species studied by Heusner (1991), while for birds  $\alpha = 0.66$  for the 398 species studied by Bennett & Harvey (1987). For unicellular organisms, a re-analysis of Hemmingsen’s (1960) data for 17 species by Prothero (1986) showed that  $\alpha$  varies from 0.60 to 0.75 depending on which taxonomic groups are considered. Similarly, based on 554 observations for 108 species of *Protozoa*, Vladimirova & Zotin (1985) reported values of  $\alpha$  from

0.66 to 0.86 for different taxonomic groups, with no obvious clustering around any common value. The evidence from plants consistently in favor of the “ $3/4$  rule” was also reported by WBE and their collaborator (Enquist *et al.*, 1998, 1999; West *et al.*, 1999a; Enquist & Niklas, 2001, 2002).

In this letter, we show that the major dependencies of plant energetics on body size can be accounted for by simple biological and physical regularities that characterize the primary process of *energy consumption* by an organism from its external environment, rather than the *transport of materials* on the fractal-like networks within a living body, which is the heart of the WBE approach. Using the same regularities, we explain the observed growth of  $\alpha$  in large mammals and the absence of similar deviations from  $\alpha = 2/3$  in birds.

The crucial feature of organismal energetics is that the energy is consumed from the environment via some part of body *surface*  $S$ , while it is spent within body *volume*  $V$ . If the flux of energy through unit body surface area,  $f$ , is constant, then the metabolic rate per unit volume,  $b \equiv fS/V$ , decreases with growing linear body size  $l$  as  $b \propto l^{\varepsilon_s - \varepsilon_v}$ , where  $\varepsilon_s \leq \varepsilon_v$  are the scaling exponents for body surface and volume,  $S \propto l^{\varepsilon_s}$  and  $V \propto l^{\varepsilon_v}$ , respectively. In the case of geometric similarity  $\varepsilon_s = 2$ ,  $\varepsilon_v = 3$ , and  $b \propto l^{-1}$ .

It is natural to expect that there exists a certain minimum value  $b_{min}$ , which is needed to keep the living matter alive, i.e. to support biochemical

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processes that at least counteract the spontaneous degradation of the highly organized state of life. At fixed  $f$ , the value of  $b_{min}$  determines the maximum size that the organism can attain. There is evidence that the value of  $b_{min}$  is universal for various taxonomic groups of organisms with different  $f$  values (Gorshkov, 1981).

Plants exist due to consumption of solar energy, the mean annual flux of which,  $I(\text{W m}^{-2})$ , is determined by latitude. At a fixed value of efficiency  $\eta$  of assimilation of solar energy by the plant, the flux of energy  $f_p$  assimilated by the plant per unit ground area is constant

$$f_p = \eta I. \quad (1)$$

We now introduce the effective vertical size  $l_e$  equal to the thickness of the layer which forms if all the metabolically active mass of the plant is flattened on the area of projection of the plant on the ground surface. Woody plants are predominantly composed of dead, metabolically inactive mechanical tissues. This property of trees is widely used in dendrochronology and climatic studies [e.g. the discovery of Suess-effect (Suess, 1955)]. Metabolically active parts of trees (leaves mostly) account for no more than 1–5% of the total plant mass (Larcher, 1980). Thus, the characteristic values of  $l_e$  for plants never exceed several millimeters. Effective size  $l_e$  corresponds to the commonly used value of leaf area index,  $d$  (dimensionless) and can be estimated as  $l_e = dh$ , where  $h$  is the leaf's metabolic thickness (Charles-Edwards, 1981).

As the effective size  $l_e$  grows, the metabolic rate per unit metabolically active volume,  $b$ , decreases inversely and proportionally to  $l_e$ . This is because the amount of solar energy available per unit ground area does not change, while it is spent within a larger metabolically active volume. As soon as the minimum possible value  $b_{min}$  is reached, the vertical growth is stopped at

$$l_{emax} = f_p / b_{min} = \eta I / b_{min}. \quad (2)$$

Plants convert the energy of solar photons into the energy of organic molecules that are synthesized from inorganic ones. Inorganic and organic molecules must move to and from the

locality where photosynthesis takes place. Such a highly organized molecular transport is maintained by a complex network of biochemical reactions within the plant. Thus, the efficiency  $\eta$  of assimilation of solar energy by the plant should exponentially depend on ambient temperature,  $\eta \propto e^{-E/kT}$ , where  $E$  (energy dimension) is an energy activation constant characterizing on average these reactions. For relative small changes of temperature,  $T = T_0 + t$ ,  $t \ll T_0$ , we have  $e^{-E/kT} = C_1 e^{C_2 t}$ , where  $C_1 \equiv e^{-E/kT_0}$  and  $C_2 \equiv E/kT_0^2$ .

On average, the air temperature in the troposphere drops with elevation at a constant rate,  $T(H) = T_0 - GH$ , where  $G \sim 6.6 \times 10^{-3} \text{ K m}^{-1}$ . It follows therefore from eqn (2) that at  $I = \text{const}$  (i.e. at the same latitude) the leaf area index  $d$ , proportional to  $l_{e \max}$ , should drop exponentially with elevation  $H$ :

$$d \propto C_1 e^{-C_2 t} = C_1 e^{-C_2 GH}$$

or

$$\ln d = C - \frac{E}{kT_0^2} GH, \quad (3)$$

where  $C$  is a constant. Not making any claims for completeness of this analysis, we plotted the log-transformed  $d$  values for five types of the Alpine mountains ecosystems located at different elevations from 1500 to 3000 m (Vareschi, 1951; Larcher, 1980). As is clear from Fig. 1, the data are very well approximated by a linear semi-log curve  $\ln d = 6.5 - 2.5 \times 10^{-3} \text{ m}^{-1} H$  ( $r^2 = 0.958, P < 0.005$ ), which corresponds to the predicted exponential relationship between  $d$  and  $H$  in eqn (3).

Combining this result and eqn (3) and taking the average temperature of the growing season at  $H = 1600$  m in the Alpine mountains to be about  $T_0 \sim 288 \text{ K}$  ( $15^\circ\text{C}$ ), we obtain that  $E/k \sim [2.5 \times 10^{-3} \text{ m}^{-1} \times (288 \text{ K})^2] / 6.6 \times 10^{-3} \text{ K m}^{-1} = 3 \times 10^4 \text{ K}$ . The obtained value is twice the upper limit of characteristic energy activation constants ( $E_m \sim 1.2 \text{ eV}$ ,  $E_m/k \sim 1.5 \times 10^4 \text{ K}$ ) reported for metabolic reactions in various plants and animals (Gillooly *et al.*, 2001). Although it is possibly caused by the limited number of data, the difference between  $E_m$  and  $E$  is not surprising. The value of  $E/k \sim 3 \times 10^4 \text{ K}$  characterizes

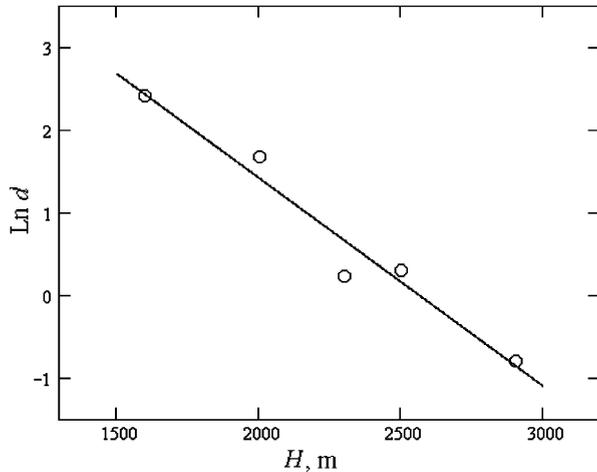


FIG. 1. Leaf area index  $d$  vs. elevation  $H$  (m) for Alpine ecosystems above 1500 m. Note that in the lower troposphere the air temperature in mountainous regions is substantially homogenized by vertical convective heat fluxes. Accordingly, there is no significant change in the leaf area index in ecosystems below 1500 m, where  $d \sim d_{max} \sim 10$ , irrespective of ecosystem woodiness (i.e. same for forests and meadows) (Larcher, 1980).

biochemical reactions responsible for conversion of solar energy into biochemical energy, i.e., a process of organic synthesis unique to green plants. By contrast,  $E_m$  describes metabolic spending of the accumulated biochemical energy in the course of the organism's functioning, i.e. decomposition of the organic matter occurring in all living organisms.

It is to be expected that the total biomass of trees, mostly consisting of dead tissues and having therefore nothing directly to do with solar energy conversion, will be independent of mean ambient temperature and, consequently, elevation. Instead, it is likely to be determined by mechanical conditions (e.g. absence of strong winds, etc.). If these conditions are satisfied, the woody metabolically inactive biomass may remain constant up to very high elevations, which is indeed observed (Enquist & Niklas, 2001).

As soon as the maximum effective vertical size  $l_{e \max}$  [see eqn (2)] is attained, any further increase of the metabolically active mass  $M_a$  of the individual plant may only proceed in the horizontal direction. The growth thus becomes essentially two dimensional (Li *et al.*, 2000),  $M_a \propto l_h^2$ , where  $l_h$  is a characteristic size of the

metabolically active parts of the plant in the horizontal direction. For example,  $l$  may be the round length of the thin cambium layer, which is equal to  $\pi D$ , where  $D$  is the stem diameter, so that  $l_h \propto D$ . A good approximation of  $M_a$  for woody plants is the leaf mass,  $M_l \sim M_a$ . We have therefore  $M_l \propto D^2$  in full agreement with observations (Enquist & Niklas, 2002). The two dimensionality of the growth of  $M_a$  should be observed for sufficiently adult plants that have attained or approached the maximum effective size  $l_{e \max}$  (note again that  $l_{e \max}$  can be many orders of magnitude smaller than the visible height of the plant). At the very early stages of ontogeny, when  $l_e \ll l_{e \max}$ , nothing prevents the growth of  $M_a$  from being fully three dimensional,  $M_a \propto l^3$ . In accordance with this prediction, the data of Enquist & Niklas (2002), that verify  $M_l \propto D^2$ , are obtained for well-grown plants, for which stem diameter could be measured at breast height. This prediction also indicates that the youngest plants should not fit the predictions of the WBE approach, which the authors themselves admitted as well.

There are other important patterns that are interpreted as unique predictions of the WBE approach, e.g. that the plant productivity per unit area does not depend on plant size (Enquist *et al.*, 1998). This pattern is immediately retrieved from eqn (1). The flux of solar radiation  $I$  being determined by latitude and the efficiency  $\eta$  of solar energy assimilation being determined by temperature and biochemical properties of the plant tissues directly interacting with light, the energy uptake  $f_p$  by the plants per unit ground area is constant, which ensures constant, size-independent productivity. Individual plant size  $l$  never enters the derivation of this statement, instead of being cancelled at the final stage of rather extensive  $l$ -dependent derivations, as suggested by Enquist *et al.* (1998). Moreover, this statement is in no way a consequence of  $B \propto M^\alpha$  for any values of  $\alpha$ .

Another statement claimed by the WBE approach is that the growth rate of plants,  $dM/dt$ , is proportional to the second power of stem diameter  $D$  and is independent of wood density (Enquist *et al.*, 1999). Taking into account that, as shown above, the energy uptake  $f_p$  of plants

per unit ground area is constant, we immediately note that the total metabolic rate of individual plant,  $B$ , is proportional to the plant projection area on the ground surface. This, in its turn, is proportional to the second power of the characteristic linear plant size in the horizontal direction, e.g. stem diameter, as discussed above. We thus have  $B \propto D^2$  and  $dM/dt \propto B \propto D^2$ .

Again, we have obtained these results without involving the knowledge about transport of materials within the plant. By definition, the dead, metabolically inactive part of plant mass,  $M_i$ , which in woody plants approximates total mass  $M$ , does not participate in energy consumption. In this sense, consideration of plant metabolism  $B$  per total plant mass  $M \sim M_i$  is the same biologically meaningless as would be a consideration of mammalian metabolism per metabolically inactive body parts (hair, claws, antlers, etc.) or calculation of the metabolic rate in birds per mass of their nests.

It seems justified to expect that a successful approach to description of bioenergetics should be based on, and start from, the consideration of the primary process of energy assimilation by an organism, rather than from the secondary process of material transport, which occurs if only the energy is already available. In the case of plants, the priority of energy consumption over transport of biogens is especially vivid from the fact that while plant communities are able to sequester the needed biogens themselves, they are absolutely unable to change the incoming flux of solar energy, to which they have therefore to fit all their other characteristics, including material transport.

So far we have predicted the exponential decrease of leaf area index with elevation and explained  $M_l \propto D^2$  for adult plants,  $dM/dt \propto D^2$  and the independence of plant productivity from plant size using the two basic principles: constancy of (solar) energy flux per unit (ground) surface area and the existence of a minimum value of the volume-specific metabolic rate  $b_{min}$  ensuring the living state of life. Using the same two principles it is possible to explain the observed patterns of the metabolic rate dependence on body size in mammals and birds.

Homeothermic organisms maintain constant body temperature, approximately equal for all

species. Therefore, homeothermic animals, same as plants, but for a different reason, can be on average characterized by a constant flux of energy  $f_h$  through unit body surface area. In the case of geometric similarity, the volume-specific metabolic rate  $b \propto l^\mu$ , where  $\mu = -1$ . Assuming  $V \propto M$  (in this sense  $V$  and  $M$  are interchangeable in the allometric analysis), this corresponds to  $B \propto M^{2/3}$ , as far as

$$\begin{aligned} b &\equiv f_h S / V \propto l^\mu, V \propto l^3, \\ B &\equiv bV \propto M^\alpha, \alpha = (\mu + 3)/3. \end{aligned} \quad (4)$$

With increasing body size,  $b$  approaches the minimum possible value  $b_{min}$ , which determines the critical body size  $l_{cr} = f_h / b_{min}$ . Without changing the body geometry, it is impossible to design homeothermic organisms with body size  $l > l_{cr}$  to cope with the overheating problem. The amount of energy produced by the organism is  $b_{min} V \propto l^3$ , while the amount of lost energy is  $f_h S \propto l^2$ , i.e. it grows more slowly. Thus, in the limiting case of  $b = b_{min} = const$ , in order to avoid overheating, the organisms larger than  $l_{cr}$  must have the maximum possible scaling  $S \propto V$  (Dodds *et al.*, 2001), which corresponds to  $\mu_{max} = 0$  and  $\alpha_{max} = 1$  from eqn (4).

In reality, the change of scaling between  $S$  and  $V$  may occur more smoothly. As body size approaches the critical value  $l_{cr}$ , the decrease of  $b$  slows down, while the ratio  $S/V$  in units of  $l$  starts to grow. This corresponds to the increase of  $\mu$  from  $-1$  towards  $0$  and  $\alpha$  from  $2/3$  towards  $1$  in large animals. Biologically, this is manifested as the appearance of "surface-rich" parts of body in large animals (e.g. ears of elephants, neck of giraffes, etc.). Economos (1982) found that, indeed, the relationship between body mass and body size in mammals is different for the larger as compared to the smaller ones. He identified 20 kg as the breakpoint of scaling.

We enlarged the dataset of Heusner (1991) by adding several data points for the largest mammals. In Fig. 2 we plotted the relationship between  $y \equiv \log_{10} b$  and  $x \equiv \log_{10} l$ . For 362 mammalian species with mass less than 20 kg ( $x \leq 1.43$ ) we have the following regression line:  $10 y_1(x) = -1.58 - 1.01x$ ,  $r^2 = 0.77$ ,  $p < 10^{-5}$ . That is,  $\mu_1 = -1.01 \pm 0.03$  (S.D.) and  $\alpha_1 = 0.66$ , see eqn (4). Assuming that the curve  $b(l)$  in

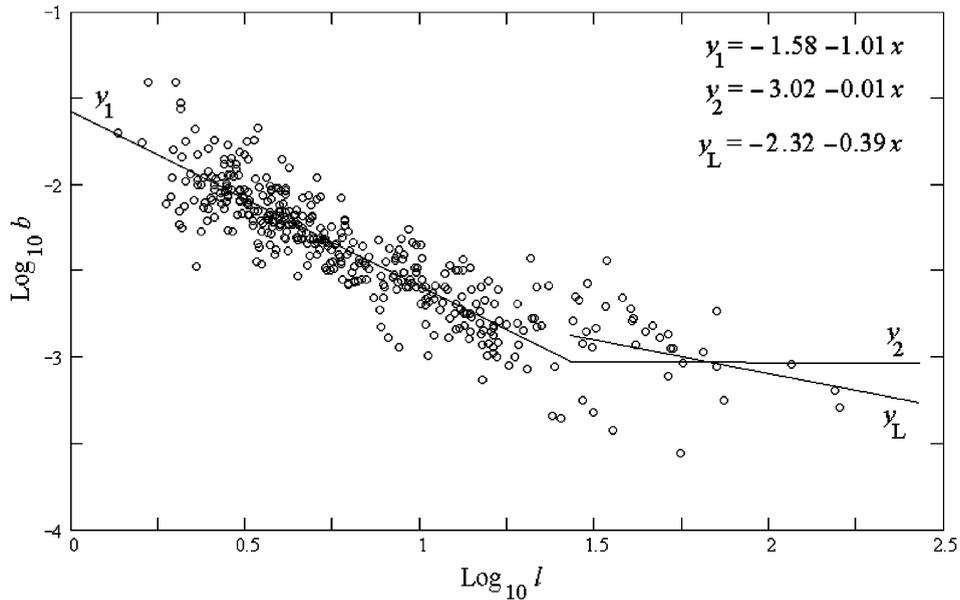


FIG. 2. Mass-specific metabolic rate  $b$  of mammals (original units in  $\text{Wg}^{-1}$ ) vs. body size  $l$ , defined here as the 1/3 power of body mass (original units in g),  $\log_{10} l \equiv 1/3 \log_{10} M$ . Most data for basal metabolic rate are taken from Heusner (1991). Additional data ( $M > 20 \text{ kg}$ ): *Loxodonta africana* (Langman *et al.*, 1995) *Alces alces* (Renecker & Hudson, 1985); *Halichoerus grypus*, *Zalophus californianus*, *Balaenoptera acutorostrata* (Hind & Gurney, 1997).

mammals is continuous, we then find the linear approximation of the 34 data points for the largest mammalian species in the following form:  $y_2(x) = y_1(1.43) + \mu_2(x - 1.43)$ . That is, we demand that  $y_2(x)$  coincides with  $y_1(x)$  at the breakpoint  $x = 1.43$ . Such a regression (with only one free parameter  $\mu_2$ ) yields  $\mu_2 = -0.01 \pm 0.15$ , which corresponds to  $\alpha_2 = 1.00$  from eqn (4), in full agreement with the limiting values of  $\mu$  and  $\alpha$  predicted above. Additionally, based on analysis of basal metabolic rates of 16 phocid seals with  $M > 30 \text{ kg}$  (specific data points are not available, but, judging by  $M$  values, they are unlikely to overlap with the data of Heusner, 1991, Lavigne *et al.* (1987) also reported a significantly elevated value of  $\alpha = 0.87$  ( $r^2 = 0.81$ ), which corresponds to  $\mu = -0.39$  and  $y_L = -2.32 - 0.39x$  (see Fig. 2). In studying large marine mammals, Lavigne *et al.* (1987) did not have to account for the continuity of  $b(l)$  in the whole class of mammals, which quite expectedly resulted in a departure of their  $\alpha$  and  $\mu$  values from  $\alpha_{max}$  and  $\mu_{max}$ .

The maximum body masses attained in birds are at least two orders of magnitude lower than those of the largest mammals. Thus, birds never go significantly beyond the critical body size for homeothermic animals  $l_{cr}$ , after which the

scaling exponents  $\alpha$  and  $\mu$  start to grow conspicuously. That is why the basic rule  $\alpha = 2/3$  ( $\mu = -1$ ) is fully applicable to birds throughout the whole range of their body sizes (Bennett & Harvey, 1987; Dodds *et al.*, 2001).

The obtained high uncertainty range of  $\mu_2 = -0.01 \pm 0.15$  in the above analyses is not surprising. One source of uncertainty is that in Fig. 2 we pool together the data for large animals living in environments with different heat conductivity (i.e. water vs. air) [cf. the high correlation coefficient  $r^2 = 81$  found by Lavigne *et al.* (1987) for phocid seals—aquatic animals only]. Second, despite expecting that  $\mu$  increases as the size of large mammals grows beyond  $l_{cr}$ , we approximated the dependence between  $b$  and  $l$  by a log-log linear curve, thus presuming the constancy of  $\mu_2$ .

Moreover, it is likely that at  $l > l_{cr}$  the relationship between  $b$  and  $l$  is no longer described by the allometric power law. Deviations from the power law are to be expected any time when there appears a fixed dimensional constant, in our case— $b_{min}$  and  $l_{cr}$ . Power law becomes the single possible one only for the problems lacking a characteristic scale. Indeed, in such a case the only way to establish a

dependence between any two variables,  $a$  and  $l$ , is to study the relation between their relative increments  $da/a$  and  $dl/l$ , which corresponds to a functional dependence between logarithms of  $a$  and  $l$  (Gorshkov, 1995, p. 38). The simplest case of direct proportionality between the logarithms results in the power law,  $a \propto l^p$ . By contrast, if there is a fixed characteristic scale  $l_0$ , the relation between  $a$  and  $l$  can be arbitrary, for example,  $a \propto \exp(l/l_0)$ ,  $a \propto \sin(l/l_0)$ , etc., with no preference for the power law. In this light, the 3/4 power dependence cannot be a mathematical consequence of the basic WBE assumption that there exists a characteristic linear scale  $l_0$  common to the design of all organisms (West *et al.*, 1999b).

To sum up, we used two fundamental biological and physical principles (constancy of energy flux per unit surface area and the existence of minimal levels of the volume-specific metabolic rate for supporting life) to derive or explain most, if not all, of results on metabolic rate dependence on body sizes of animals and plants, which were originally claimed by the WBE approach. In addition, we also predicted and explained the exponential decrease of leaf area index with elevation, the change of animal body geometry and the breakpoint of the allometric scaling. Since the process of *energy consumption* by an organism from the external environment is much more fundamental than the *transport of matter* in a living body, our approach should be more general and robust. We agree completely with Heusner (1991), who stressed that it is not the scaling exponent ( $\alpha$  or  $\mu$ ) that is of primary theoretical interest, but the “location of the metabolic regression line in the mass/power plane”. This location is determined by the characteristic values of the energy flux  $f$  through body surface. It may well be the case that in the course of evolution life invented but a limited number of ways how to uptake the energy from the environment. By their  $f$  values, immobile organisms will be principally different from those capable of active locomotion, homeothermic from poikilothermic, etc. (Gorshkov, 1995; Gorshkov *et al.*, 2000). Plotting the whole living world in the log–log transformed  $b/l$  plane (such as Fig. 2), investigating the resulting metabolic groupings of organisms and identify-

ing the universal metabolic characteristics of life (optimum, minimum and maximum values of  $b$ ) should be a fascinating scientific endeavor.

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