Metabolic principles of river basin organization

Ignacio Rodriguez-Iturbe^{a,1}, Kelly K. Caylor^a, and Andrea Rinaldo^{b,c}

^aDepartment of Civil and Environmental Engineering, Princeton University, Princeton, NJ 08544; ^bLaboratory of Ecohydrology, School of Architecture, Civil and Environmental Engineering, Ecole Polytechnique Fédérale de Lausanne, 1015 Lausanne, Switzerland; and 'Dipartimento IMAGE, Universitá di Padova, Padova, Italy

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The metabolism of a river basin is defined as the set of processes through which the basin maintains its structure and responds to its environment. Green (or biotic) metabolism is measured via transpiration and blue (or abiotic) metabolism through runoff. A principle of equal metabolic rate per unit area throughout the basin structure is developed and tested in a river basin characterized by large heterogeneities in precipitation, vegetation, soil, and geomorphology. This principle is suggested to have profound implications for the spatial organization of river basin hydrologic dynamics, including the minimization of energy expenditure known to control the scale-invariant characteristics of river networks over several orders of magnitude. Empirically derived, remarkably constant rates of average transpiration per unit area through the basin structure lead to a power law for the probability distribution of transpiration from a randomly chosen subbasin. The average runoff per unit area, evaluated for subbasins of a wide range of topological magnitudes, is also shown to be remarkably constant independently of size. A similar result is found for the rainfall after accounting for canopy interception. Allometric scaling of metabolic rates with size, variously addressed in the biological literature and network theory under the label of Kleiber's law, is similarly derived. The empirical evidence suggests that river basin metabolic activity is linked with the spatial organization that takes place around the drainage network and therefore with the mechanisms responsible for the fractal geometry of the network, suggesting a new coevolutionary framework for biological, geomorphological, and hydrologic dynamics.

ecohydrology | self-organization | watershed

River basins are three-dimensional landscapes organized around dendritic structures that constitute the drainage network whose role is to convey water and sediment from every site of the basin to a common outlet. The network dendritic structure exhibits clear statistical self-similarity (1–3) where subbasins of different sizes embedded among themselves and as part of the larger basin show topological and metric organizations independent of scale (2). Any subbasin, independent of its size or location, may be considered a self-contained hydrologic unit operating under the same hydrologic principles that control its organization. We hypothesize that these principles are grounded in the metabolism of the river basin. From a hydrologic perspective we define the metabolism of a river basin as the set of processes that allow the basin to maintain its structure and respond to its environment through the physical and biological processing of the precipitation it receives. Green or biotic metabolism refers to the transformation undergone by precipitation in the process of carbon fixation by photosynthesis carried out by the basin vegetation. A quantitative measure of green metabolism is provided by the transpiration rate (T) at any particular site. Blue or abiotic metabolism refers to the processes involved in the transport of runoff from every site to the outlet.

Blue water metabolism as defined above is different from the classical notion of metabolism as a biochemical (e.g., biotic) process. It is used here to convey the idea of a set of processes related to the functioning of the river basin that are necessary to maintain

the dendritic structure of its drainage network. Also, the green water metabolism as previously defined does not include the role of water on processes like microbial activity, food web dynamics, etc. Rather it focuses on what is by far the largest transformation of energy taking place in the basin through biological mechanisms.

The definitions of green and blue metabolism are based on the concepts of green and blue water used to distinguish between water directly used by vegetation or coming from irrigation (4) in order to address issues related to either rain-fed or irrigation-based agriculture.

The subbasins are parts of a whole where, in analogy with physical principles responsible for their self-similar structure, one expects common metabolic rates operating independently of size. Indeed it has been shown (2, 5, 6) that a principle of equal average energy expenditure per unit area relates to (dynamically accessible) minimization of total energy expenditure at the scale of the whole basin, a feature that rules the landscape evolution through which the network structure is extracted (7). Initially proposed as a principle, it was later shown through reparametrization invariance to be an exact property of the steady states of the general landscape evolution equation in the small-gradient approximation (8, 9). Fig. 1A shows a basin divided in subbasins highlighted by the corresponding topological magnitudes of the different links that make up the drainage network. Magnitude is defined as the number of sources—e.g, links of magnitude one that drain into the link under consideration. The magnitude of a subbasin—i.e., of the link at its outlet—is a precise surrogate variable for the area of the subbasin (2). It is expected that topologically and metrically self-similar structures of river basins will preserve common average metabolic rates within the network structure. Nevertheless, one should also expect fluctuations in those rates even among subbasins of the same magnitude due to their pronounced heterogeneous geographical distribution.

The spatial variability of transpiration has been studied for humid forests of northern Europe, where it is observed that variations in soil water content have negligible effects on transpiration rates (10). In these cases understory provides effective buffers to any tree canopy differences. Stand-level evapotranspiration has also been observed to have minor interannual variability for temperate deciduous forests in relatively flat regions regardless of more pronounced fluctuations in interannual rainfall (11). This observation is not generally applicable to most river basins where, in addition to interannual rainfall fluctuations, there exist strong spatial gradients in rainfall and temperature coupled to changes in elevation throughout the basin and that, as result of this, frequently exhibit a marked spatial variety of functional types of vegetation.

Adjacent ecosystems composed of plants of different characteristics have also been observed to have very similar produc-

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¹To whom correspondence should be addressed. E-mail: irodrigu@princeton.edu.

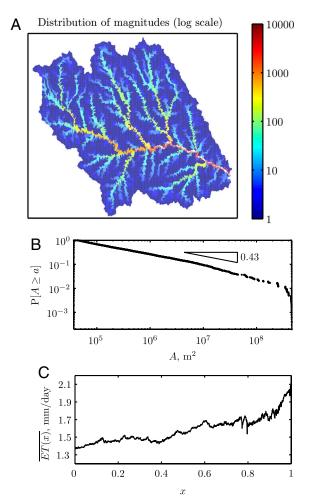


Fig. 1. Hydrological and geomorphological spatial structure of the Upper Rio Salado. Pronounced geographical differences exist in the basin where altitude plays a dominant role in the overall hydrologic dynamics. (A) The drainage network drains an area of 464 km² with elevation ranging from 1,985 to 2,880 m a.s.l. The stream network at 30-m pixel resolution exhibits magnitudes of up to 3,000. (B) Power-law distribution of the upstream contributing area at any randomly chosen point in the basin. The self-similar structure is characterized by the typical scaling exponent -0.43 ± 0.01 . (C) Mean daily evapotranspiration averaged over all pixels located at the same distance x from the basin outlet measured along the network flowpaths (x = 1 is the longest distance from the outlet to the basin divide). A strong topographic gradient is shown to exist in evapotranspiration.

tivity (12, 13) supporting the theoretical finding based in plant allometry (14) that productivity of plants in ecosystems per unit area is basically invariant with respect to body size. Thus the rate of use of resources per unit area is usually not limited by plant size but rather by resource supply (15). In evaluating river basin metabolism, however, different subbasins of similar size frequently exhibit strong gradients in precipitation, and the above observation is not applicable without considering suitable averages. This is indeed accomplished through the dendritic structure and its accompanying subbasins by linking the metabolic activity of a river basin with its spatial organization.

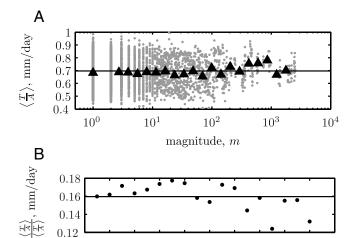
Organizational Principles of Equal Average Metabolic Rate.

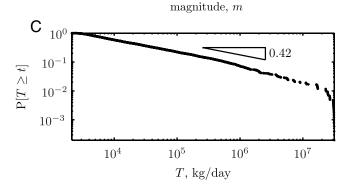
The average metabolic activity per unit area of a subbasin j of magnitude i is defined as the representative value of the metabolic rate of that subbasin. When such rates are averaged over all subbasins of the same magnitude, we obtain the mean metabolic rate per unit area for subbasins of magnitude i. The organizational principle of equal metabolic rate per unit area states that on the average this rate is the same for all magnitudes. This

principle is suggested to be applicable to both green and blue metabolic activity and represents a fundamental unification of the hydrologic dynamics of the river basin in the presence of vastly heterogeneous conditions of precipitation, geomorphology, soil and vegetation cover. Moreover, it carries important consequences regarding the spatial organization of the hydrologic dynamics throughout the basin. The principle of equal rate of metabolic activity per unit area was tested through a detailed analysis of the hydrologic dynamics of the Upper Rio Salado basin near Sevilleta in New Mexico (see Materials and Methods). The basin exhibits pronounced heterogeneity in vegetation along a strong topographical gradient with highly nonuniform precipitation. These characteristics make it appealing for a stringent test of the proposed principle. A detailed description of the basin is given elsewhere (16) where the hydrologic dynamics have been studied at a 30-m pixel resolution accounting for differences in soil, vegetation, and precipitation characteristics. The climate regime is typical of a semiarid environment with a pronounced growing season from May through September when the mean rainfall increases according to elevation from 220 to 325 mm/yr. It is during the growing season when most of the green metabolism takes place, although in the lower elevations there is a small amount of assimilation taking place outside this period (17). This is also the case for blue metabolism, with most of the runoff occurring from spring time snowmelt and strong summer storms (18). All our study of the hydrologic dynamics refers to the growing season (16). A detailed description of the extensive modeling carried out to estimate the fine spatial structure of the different components of the hydrologic balance is synthesized in Materials and Methods.

Fig. 1B shows the probability distribution of the upstream contributing area at a randomly chosen point in the network of the Upper Rio Salado . It displays the well-known power law behavior with the typical exponent -0.43 ± 0.01 over an extended range of values of area (2). The pronounced geographical impact on the hydrologic regime is seen in Fig. 1C, which shows the mean daily evapotranspiration averaged over all pixels located at the same distance x from the basin outlet measured along the network flowpaths. A strong topographical gradient exists in ET, which reflects the one existing in precipitation. The upper regions of the basin have an average evapotranspiration 55% larger than those sites located near the basin outlet. Using the same model results one can compute the average transpiration per unit area, say $\langle T/A \rangle$, for all subbasins of the same magnitude (as well as the corresponding coefficient of variation). Fig. 2 A and B shows the result of these calculations. The mean value is indeed remarkably constant for an extended range of subbasin magnitudes, and the coefficient of variation is quite small and relatively constant. This provides reassuring grounds for the principle of equal green metabolism per unit area (averaged within the network structure). From this principle it follows that the probability distribution of the green metabolism taking place in any subbasin, say P[T > t], should be identical to that of P[kA > t] where A is total cumulative area of a randomly chosen subbasin, and k represents $\langle T/A \rangle$, a random variable with the same mean and variance throughout all the subbasins as shown in Fig. 2. If k may be assumed as constant, then P[T > t] would be described by a power law with the same scaling exponent as the statistics of total cumulative area, P[A > a]. The Upper Rio Salado basin shows an excellent agreement with this prediction, as seen in Fig. 2C.

Blue metabolism involves the transport of runoff from all sites to the basin outlet. The drainage network results from the organization of a tree-like structure, which minimizes (2, 5, 6) the total energy expenditure as given by the concave functional $E \sim \sum_i Q_i^{1/2}$ where Q_i is the mean annual discharge through link i and the sum is over all links of the network. The resulting configurations are known as Optimal Channel Networks (OCNs) (5, 6) and are statistically undistinguishable from real river networks





10 12 14 16 18 20

Fig. 2. Constant green metabolism per unit area averaged within the subbasin structure. (A) Mean transpiration per unit area within subbasins of the same magnitude. Here the notation $\langle \cdot \rangle$ represents the mean values across all subbasins of the same magnitude. Fluctuations around the mean are generally small as shown by the coefficient of variation (B). As predicted, the probability distribution of green metabolism in any randomly chosen subbasin, shown in C, follows a power law with the same exponent of Fig. 1B. All calculations are for the upper Rio Salado Basin.

(2, 3). OCNs are constructed in practice by using area, A_i , as a surrogate variable for the landscape-forming discharge Q_i , which is hardly known otherwise for every link of the basin (2). The concept of OCNs is of crucial importance for the organizational structure of drainage networks in river basins, and it is supported by numerous geomorphological studies of basins around the world under a wide range of climatic and geological conditions. We now show that the equivalence between Q_i and A_i finds further justification when the same average blue metabolism per unit area within the network structure applies. Thus $Q_i^{(j)} = \beta_i^{(j)} A_i^{(j)}$ where $Q_i^{(j)}$ is the mean annual runoff of subbasin j of magnitude i, $\beta_i^{(j)}$ is the mean annual runoff per unit area of subbasin (i,j), and $A_i^{(j)}$ is the area of subbasin (i,j). If $\beta_i^{(j)}$ is assumed to be a random variable identically distributed across all magnitudes (i.e., within the network structure), then for any randomly chosen subbasin $Q_i = \beta_i A_i$. Thus $E \sim \sum_i (\beta_i A_i)^{1/2}$ where the β_i s are realizations of the same random variable, say β , which yields $E \sim \sum_{i} A_i^{1/2}$ provided its variance is small. The fact that this minimization has been shown to yield OCNs with excellent agreement with the statistical characteristics of real river networks (2, 3) provides strong support to the principle of equal blue metabolism per unit area—within the network structure—although a detailed analysis of the statistical structure of $\beta_i^{(j)}$ should be carried out for many basins with different climates and geomorphology. Thus the principle of equal average blue metabolism is linked to the minimization of energy expenditure

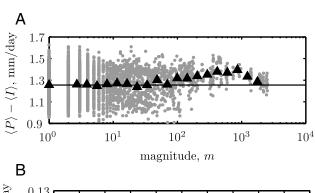
responsible for OCNs, which in turn is seen as an exact property of the solutions to the steady-state landscape evolution equations (9).

The principle of equal green and blue metabolic rates per unit area within the network structure is intimately connected to the spatial distribution of rainfall, P, over the basin, thus implying a unifying organization linking the basin structure and the precipitation it receives. For a given subbasin labeled by (i,j) the longterm average of the water balance per unit area can be written as (neglecting soil evaporation): $P_i^{(j)}/A_i^{(j)} = Q_i^{(j)}/A_i^{(j)} + T_i^{(j)}/A_i^{(j)} +$ $L_i^{(j)}/A_i^{(j)} + I_i^{(j)}/A_i^{(j)}$, where I is the canopy interception lost by evaporation and L is the leakage out of the subbasin, which in the long-term is assumed as part of Q. Taking averages over all subbasins *j* of magnitude *i* one gets $\langle P_i^{(j)}/A_i^{(j)} - I_i^{(j)}/A_i^{(j)} \rangle = \beta + k = \alpha$, constant independently of magnitude. Fig. 3 *A* and *B* shows the mean and coefficient of variation of $P_i^{(j)}$ for the Upper Rio Salado basin after interception has been subtracted. Both variables are again remarkably constant and the coefficient of variation is quite small, a surprising and suggestive result. Fig. 3 A and B results from the spatial disaggregation of rainfall based on six meteorological stations existing in the basin through the procedure described in Materials and Methods.

The results obtained are very encouraging in relation to the hypothesis that the metabolic activity of a river basin is intimately linked with its spatial organization through the principle of an equal average metabolic rate per unit area when the averages are computed through subbasins of the same topological magnitude. Although the Upper Rio Salado basin was chosen because of its high degree of vegetation heterogeneity, strong precipitation gradient, and nonuniform evapotranspiration characteristics, we wish to emphasize the need to test the principles discussed before in other river basins with different climatic, geomorphologic, and vegetational characteristics.

Allometric Scaling and River Basin Metabolism.

Obviously there exists a strong connection between green and blue metabolisms, because runoff production is closely linked to transpiration rates. This linkage—e.g., a synthesis of river basin



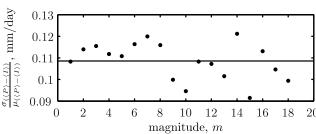


Fig. 3. Linkage between basin topology and rainfall input. (*A*) The average rainfall per unit area (minus interception) is constant when calculated across basins of the same magnitude. Moreover, the coefficient of variation of $\langle P \rangle - \langle I \rangle$ for subbasins of the same magnitude is quite small as shown in *B*.

metabolism—may be provided by allometric scaling relations of the Kleiber's law type (19–27) relating metabolic rates B of an organism to its body size M—i.e., $B \propto M^{\chi}$ (where χ is the allometric scaling coefficient, widely speculated to belong in the range 2/3-3/4) (20, 25, 28). The role of the metabolic rate had been previously (19) taken by total contributing area, $B(x) \sim A_x$, at any site x within the basin, thus considering each nested subbasin as an organism and addressing intraspecies scaling behavior. This interpretation was suggested by the ansatz on the role of the network structure distributing metabolites in the above scaling features (25). At any location x, area is defined by the recursive relation $A_x = \sum_{j \in nn(x)} A_j + 1$ where nn(x) indexes all nearest neighbors of x that drain into it through steepest descent directions (2), and 1 is the unit area (the pixel size). Whereas the early work on hydrologic allometry focused only on blue metabolism (19), the proposed extension examines the allometric scaling of green metabolism as well (i.e., by substituting area as a proxy of metabolism with total transpiration upstream of x; i.e., $T(x) = \sum_{j \in y(x)} T(j)$ where y(x) indexes all sites ultimately connected to x through downstream links). The analog of body mass is maintained as in the literature (19). To that end we link to the transpiration, T(x), the sum of total contributing areas $(M(x) \sim \sum_{i \in y(x)} A_i)$ at every site *i* upstream of the given outlet *x* (that is, indexed by y(x) as before). The above quantity, which is rather different from A(x), serves as a proxy of body mass of the basin closed at x because it surrogates the flow volumes (proportional to the sum of fluxes) and in turn landscape-forming events (2, 29) by the local values of total contributing area (19, 20). Thus allometric scaling of basin-scale green metabolism namely, total transpiration T(x) upstream of x—is compared over several orders of magnitude against M(x).

Fig. 4 shows the resulting scaling relation, indeed well represented by a power law with exponent χ very close to 2/3 $(\gamma = 0.65 \pm 0.03)$. Significantly, the exponent agrees well with the theoretical value of D/(D+1) = 2/3 predicted (20, 30) for directed planar (D=2) networks acting as means of transport of metabolites to every element of a body when the transport velocity can be assumed constant throughout the network (20) (for an assessment of the relevance of the latter assumption in the biological context see ref. 28), which is indeed the case (29) when mean annual flow is considered to be present in all links of the river network. Furthermore, we verify empirically the direct relations that exist (19) between the scaling exponent ξ of P[T > t] $\propto t^{-\xi}$ (Fig. 1C), the allometric scaling coefficient (χ) from $T(x) \propto M(x)^{\chi} = (\sum_{i \in x} A_i)^{\chi}$ (Fig. 4), and Hack's morphological exponent (2, 19, 29) h relating channel lengths to basin area $(\xi = 0.43, h = 1 - \xi = 0.57, \chi = 1/(1+h) \sim 0.64)$. The above suggests that allometric scaling of metabolic rates within a river network may indeed be regulated by the constant metabolic needs per unit area regulating hydrologic fluxes, which are observed in (and probably shape) the organization of the river basin.

Materials and Methods

The upper portion of the Rio Salado basin is located near the Sevilleta Long-Term Ecological Research (LTER) site in central New Mexico. The basin exists within and adjacent to the Cibola National Forest, and covers an area of 464 km2. Elevation in the basin ranges from 1,985 m above mean sea level (a.s.l.) to 2,880 m a.s.l. The stream network was derived from 30-meter resolution US Geological Survey (USGS) digital elevation maps available from the seamless data distribution system (http://seamless.usgs.gov). The US Department of Agricultire STATSGO soil database (31) was used to determine the pattern of soil texture within the Rio Salado basin; soil texture was related to specific values of saturated hydraulic conductivity, porosity, field capacity, and the hygroscopic point according to commonly used relationships (32, 33). The distribution of vegetation composition (tree/shrubland/grassland) was taken from the USGS 28.5 m National Land Cover Dataset (NLCD) based on Landsat imagery (34), which was resampled at 30-meter resolution using a nearest neighbor technique (16). By using 12 years of rain gauge data (1990-2001) recorded in six meteorological stations located in the Sevilleta

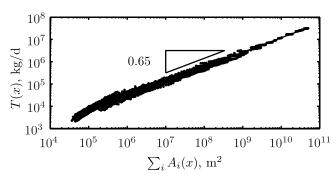


Fig. 4. Allometric synthesis of river basin metabolism. Total amount of runoff (surrogated by the nested sum ot total contributing areas) (19) present on the average in the network of a subbasin versus total transpiration in the same subbasin. The exponent is close to 2/3, which corresponds to directed planar networks transporting metabolites with constant velocity to every element of a body (20).

research area and the Rio Salado basin, linear relationships were developed between elevation and rainfall frequency and depth (16). There currently exist no methods available for direct estimation of plant transpiration at landscape scales. Therefore, the estimates of plant water use within the Rio Salado basin are taken from a detailed model previously implemented (16) based on the derivation of the steady-state probability distribution of soil moisture at each location in the basin and the resulting spatial patterns of the steady-state water balance. The rainfall input driving the model is characterized at the daily time scale by the frequency of rainy days, λ , and the mean value of rainfall in a rainy day, α . A marked Poisson process is then used where the arrivals of rainy days follow a Poisson process with rate λ and the rainfall marks are exponentially distributed with mean α . By using the previously developed linear relationships between elevation and rainfall frequency and elevation and mean depth, values of λ and α were estimated for each pixel of the basin to characterize the spatial structure of the rainfall dynamics throughout the upper Rio Salado river basin. Canopy interception was accounted for by assuming a threshold of rainfall depth below which no water effectively penetrates the canopy (35). This threshold controls the storage capacity of the vegetation according to the type existing at each pixel (16). The starting point of the model is the stochastic differential equation for the daily soil water balance (35, 36) where plant transpiration is assumed to linearly increase in response to soil moisture; from zero at the plant wilting point to $E_{\rm max}$ (mm/d) when the soil moisture level is at or above the point at which the plant begins to close stomata in response to water stress. The specific values of plant wilting point and the point of incipient stomatal closure depend on both the soil texture and vegetation type at each site (16). The spatial pattern of $E_{\rm max}$ within the Rio Salado basin depends on many factors, the most critical of which are plant physiology, canopy structure, and the prevailing climatic conditions during the growing season. The value of E_{max} at each site was estimated using the Penman–Montieth equation (16). For this calculation meteorological data from Station 45 in the Sevilleta LTER were used to determine characteristic values of daytime average incoming shortwave radiation, mean air temperature, and mean vapor pressure during the growing season. A linear relationship was then established between elevation (in meters a.s.l.) and mean growing season daily air temperature based on meteorological observations from 6 meteorological stations within the Rio Salado basin. Based on these relationships the saturation vapor pressure and the vapor pressure gradient were estimated at each pixel in the Rio Salado basin (16). The net radiation was calculated assuming that the temperature of the vegetation canopy and the atmosphere are equal (33). The product of the vegetation maximum stomatal conductance and leaf area index determined the total canopy conductance under well-watered conditions. Field observations (17, 18) provided the maximum stomatal conductance of shrub and tree vegetation, and a characteristic value of desert grassland vegetation (37) specified the grass maximum stomatal conductance. Based on the range of observed leaf area for shrubs and grasses in the Sevilleta LTER (37), it was assumed that the leaf area of grasses and shrubs during the growing season are constant and equal to 0.25 and 0.50, respectively (16). The leaf area of tree vegetation were inferred by using a remotely sensed image of LAI acquired by the MODIS sensor at 1-km resolution (MOD15A2, 8-day, 1-km LAI/FPAR product) (16). The aerodynamic conductance term in the Penman-Monteith equation was estimated as a function of vegetation height and wind speed. The average daily value of E_{max} (mm d⁻¹) was determined by scaling the value of E_{max} obtained from

the Penman–Monteith equation by the average day length during the growing season (16). The average rate of daily plant transpiration was then determined using the resulting basin-wide patterns of $E_{\rm max}$ and the steady-state probability distribution of soil moisture. The different components of the steady-state water balance were estimated using an analytical model of stochastic soil moisture balance (35, 36).

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