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A scale invariant coupling of plants, water, energy, and terrain[1]

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Abstract: Compelling evidence from studies of stream channel density supports the hypothesis that terrain and vegetation are coupled via water and energy fluxes. The slope of a classic power law relation between drainage density and water availability reverses sign and changes value where precipitation equals potential evapotranspiration. The change of slope indicates a "phase transition" from water- to energy-limited vegetation. To initiate a common biophysical theory for these power-law relations and for the phase transition, we partitioned precipitation into an infiltrated fraction available to plants and a fraction available for flow and thus erosion. To estimate infiltration we exploited invariance with respect to spatial scale at the transition. We tested the invariance hypothesis by analyzing the spatial distribution of energy-limited vegetation over length scales between 8,000 and 256,000 m in the Columbia River Basin of the northwestern US, which has a mixture of both phases. We observed a power law relation for the occurrence of energy-limited vegetation based on annual fluxes. We defined two dimensionless parameters that describe excess available energy for photosynthesis and surplus liquid water for terrain formation. Specification of the conditions under which neither parameter changed with spatial scale, in conjunction with a steady-state water balance model, enabled the formulation of an equation of soil infiltration at scales between 8,000 and 256,000 m. In water-limited vegetation, the equation enables the estimation of soil infiltration rates at arbitrary spatial scales for a given plant cover as a function of the ratio of precipitation to potential evapotranspiration. This work represents a first step towards the articulation of a biophysically sound theory about the ecology and hydrology of broad landscapes that respects a conservation law and scale invariance.
Keywords: Columbia River basin, drainage density, evapotranspiration, fractal dimension, hydrology, infiltration, landscape, scale invariance, water balance.

Résumé : Les résultat concluants d'études sur la densité des cours d'eau appuient l'hypothèse que le terrain et la végétation sont liés par des flux d'eau et d'énergie. La pente de la courbe exponentielle classique entre la densité du drainage et la disponibilité de l'eau s'inverse et change de valeur lorsque les précipitations égalent l'évapotranspiration potentielle. Ce changement dans la pente indique une transition pour la végétation : l'énergie remplace l'eau en tant que facteur limitatif pour les plantes. Pour élaborer une nouvelle théorie biophysique au sujet de ces relations exponentielles et de la phase de transition, nous avons divisé les précipitations en deux parties : la première correspond à l'eau qui s'infiltre dans le sol et qui est disponible pour la croissance des plantes, alors que la seconde est l'eau qui s'écoule en surface et qui érode le substrat. Pour estimer l'infiltration, nous avons utilisé l'absence de variabilité selon de l'échelle spatiale à la transition. Nous avons testé l'hypothèse d'absence de variabilité en analysant la répartition spatiale de la végétation limitée par l'énergie sur des distances de 8000 à 256 000 m dans le bassin de la rivière Columbia dans le Nord-Ouest des États-Unis. Nous avons observé une relation exponentielle pour la présence de végétation limitée par l'énergie en fonction des flux annuels. Nous avons défini deux paramètres non-dimensionnels qui décrivent les excès d'énergie disponibles pour la photosynthèse et les surplus d'eau liquide responsables de la formation du terrain. La description des conditions sous lesquelles l'un ou l'autre des paramètres change avec l'échelle spatiale, ainsi que l'élaboration d'un modèle fixe de bilan hydrique ont permis la formulation d'une équation sur l'infiltration d'eau dans le sol à des échelles de distance variant entre 8000 et 256 000 m. Pour la végétation limitée par l'eau, l'équation permet d'estimer des taux d'infiltration dans le sol à des échelles spatiales arbitraires pour un couvert végétal donné, les taux d'infiltration étant fonction du rapport entre les précipitations et l'évapotranspiration potentielle. Cette étude représente un premier pas vers l'élaboration d'une théorie biophysique traitant de l'écologie et de l'hydrologie de vastes paysages qui respecte la loi de conservation et l'absence de variabilité pour une échelle donnée.
Mots-clés : bassin de la rivière Columbia, densité de drainage, évapotranspiration, dimension fractale, hydrologie, infiltration, paysage, absence de variabilité pour une échelle donnée, bilan hydrique.

Introduction

The most compelling, yet unexplained, evidence for the coupled partitioning of water and energy by terrain and vegetation is the nonlinear relationship between drainage density, defined as total stream channel length per unit area, and a measure of surplus water in the landscape (Figure 1). In this classic example, the measure of surplus water is the sum, over 12 months, of ten times the mean monthly precipitation divided by the mean monthly potential evapotranspiration (Thornthwaite, 1933). Thus, a unitless measure, called *TI* for "Thronthwaite Index", of 120 results when the

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mean monthly precipitation equals the potential evapotranspiration in each month. Values below 120 signify annual water budgets that are water limited and values above 120 reflect energy limitation. The transition from arid and semi-arid to humid environments corresponds to a shift from water-limited to energy-limited vegetation as evidenced by the reversal in the slope of the drainage density relationship (Figure 1).

The relationship can be understood in terms of a general water balance equation. Even though the water balance applies everywhere, a crucial issue is to investigate the spatial relationships among locations at various scales. Spatial relationships are central to explaining the dependence of terrain surfaces and drainage networks on the partitioning of precipitation into runoff and evapotranspiration. In this paper we first test for evidence of a spatial manifestation of the transition from water- to energy-limited vegetation. The observed power law relation in the relevant variables reflects the persistent partitioning of water over long distances in a scale-invariant manner. Scale invariance or "scaling" can be viewed as a fundamental symmetry in nature that manifests under a scale change. Therefore, a major focus for us is to derive power laws from principles of conservation and biophysics. Here we show how scale invariance manifests in biophysical variables that govern water- and energy-limited vegetation across multiple spatial scales. The invariance, in conjunction with a mass conservation equation, produces a new biophysically based infiltration equation that describes the fraction of the precipitation that is available to plants at arbitrary scales.

Early documentation of power laws or scaling behavior led to the recognition that processes at fine scales propagate over vast distances, thereby creating new patterns and complexity (Mandelbrot, 1982; Meakin, 1993). To understand scaling consider the functional equation $f(xy) = f(x) f(y)$, where $f(.)$ is a function of variables x and y. It is well known that a general solution to this equation is a power law given by $f(x) = cx^{\theta}$, where θ is a scaling exponent (Stauffer & Stanley, 1996). Thus, if a system is known at some reference scale x then the behavior is known at any multiple of x within the valid domain. The term scale invariance applies when the scaling exponent is constant across a wide range of x. The origin of scaling behavior appears in the theory of critical phenomena associated with phase transitions (Stanley, 1971; Binney *et al.,* 1993) and in the theory of the renormalization group (Wilson, 1979; Creswick, Farach & Poole, 1992; Loreto *et al.,* 1995; Barenblatt, 1996). These theories predict the scaling exponent from detailed physical characterizations.

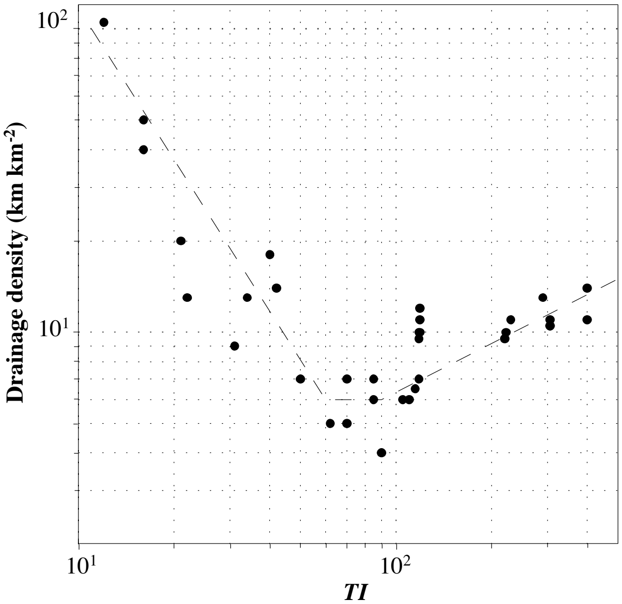

FIGURE 1. Drainage density and excess precipitation measured as the Thornthwaite Index, *TI*. Dashed lines indicate linear trends on doubly logarithmic axes. After Abrahams (1984).

Empirical scaling relations have been known for decades in biology and hydrology. For example, allometric power laws describe how quantitative traits of organisms vary with body mass raised to an exponent (Peters, 1983; Calder, 1984; Charnov, 1993). Similarly, in the "downstream" hydraulic geometry of river networks, velocity, depth, width, slope, and friction vary as powers of stream discharge (m^3 s^{-1}; Leopold, Wolman & Miller, 1964). These relations hold across the multiple spatial scales of a river network. A recent biological theory explains that the universal 3/4 scaling exponent pertaining to metabolic rates is due to an invariant capillary size, network geometry, and minimization of work in fluid transport (West, Brown & Enquist, 1997; 1999). However, a basic explanation of downstream hydraulic geometry from fundamental fluid-mechanical and other physical principles remains a very important open problem.

Further progress in elucidating the origin of scaling behavior in landscapes requires analysis of the coupling between terrain and vegetation due to their effects on the partitioning of precipitation into surface and subsurface runoff, evapotranspiration, and soil-water storage. Our goal is to test the null hypothesis that the spatial distribution of energy-limited vegetation is random, or more specifically, it is spatially independent and identically distributed (i.i.d.), versus scale invariant. Rejection of the null hypothesis would imply that the biophysical constraints that govern water balance at the fine scale propagate in a scale invariant manner over vast distances.

In this paper we (1) explain Figure 1 in terms of a general water balance model that defines the water- and energy-limited phases of vegetation; (2) compare the power law scaling of the spatial distribution of energy-limited vegetation against an analytical null hypothesis; (3) use an analysis of spatial connections motivated by the theory of renormalization groups to understand the observed scaling; (4) use the scale invariance of water and energy parameters to derive a soil infiltration equation that applies at many scales; and (5) suggest several implications for further research directed towards a comprehensive theory of ecohydrologic scaling.

MOTIVATION AND BACKGROUND

The nonlinear relationship between drainage density and surplus water (Abrahams, 1984; Figure 1) suggests that vegetation and terrain are coupled because a finite amount of water is partitioned between evapotranspiration and stream flow. Landscapes with low excess precipitation have low plant cover and therefore little resistance to erosion.

Consequently, high runoff produces high drainage densities. Increasing precipitation relative to evapotranspiration lowers drainage density to a minimum because the added moisture favors higher plant cover that increases infiltration, thereby leaving less water for erosion (Rietkerk *et al.,* 2000). The gradient of excess precipitation creates a dichotomy between water-limited vegetation at the low end and energy-limited vegetation at the high end of the *TI* gradient (Figure 1). The transition from water- to energy-limitation corresponds to a reversal in the slope of the drainage density relation.

We examined the slope reversal via a water balance equation given by

$$dS/dt = P - ET - Q \qquad [1]$$

where d*S*/dt is the rate of change of soil moisture storage, *P* is precipitation, *ET* is evapotranspiration, and *Q* is runoff that produces stream flow and erodes terrain. In semi-arid lands, plants play a major role in the water balance, primarily by modulating infiltration and runoff rates (Elwell & Stocking, 1976). Generically, we define infiltration, $f(p)P$, as the fraction of precipitation *P* that infiltrates soils. Infiltration is denoted as a function of the vegetation that occupies a fraction *p* of the land surface. Precipitation can be partitioned into infiltration, $(f(p)\,P)$, runoff, $Q(p) = (1 - f(p))P$, and evapotranspiration rate, $\tau(p)\,S$. It is a product of soil-water storage, *S*, and a "loss rate" coefficient, $\tau(p)$, which denotes evaporation from bare soil and/or plant uptake rate as a function of the plant cover *p*. Substituting these terms into equation [1] gives

$$dS(t,p)/dt = f(p)\,P - \tau(p)S \qquad [2]$$

Assuming that soil water changes more quickly than plants can grow, the equilibrial or steady-state soil moisture, $S^*(p)$ is, by definition, independent of time and is the value of $S(t, p)$ in the limit as $t \rightarrow \infty$. An annual time scale is the shortest relevant scale over which a steady state can exist. Over large basins and due to inter-annual climate variability, much greater time scales than annual may be required to meet the steady-state assumption. $S^*(p)$ can be obtained by substituting $S^*(p)$ for $S(t, p)$ in equation [2]. The left hand side drops out and the right hand side gives

$$S^*(p) = Pf(p)\,/\,\tau(p). \qquad [3]$$

Given that the water available for flow is $Q = P - ET$, we invoke Stephenson's (1990) definition of *ET* as the minimum of ecologically available soil moisture and potential evapotranspiration (*PET)*:

$$ET = \min(\,\tau(p)S^*(p), PET\,). \qquad [4]$$

In equation [4], we have equated available soil moisture with equilibrial-soil water $S^*(p)$. Annual *PET* is the energy available for plant growth under ideal conditions of unlimited water and nutrients (Stephenson, 1990; Frank & Inouye, 1994). *PET* has units of mm/year water if the energy is multiplied by the latent heat of vaporization (Jensen, Burman & Allen, 1989).

Moving from left to right along the *TI* axis in Figure 1, we expect strong interactions among parameters of the model such that some conditions lead to $Q > 0$ and others lead to $Q = 0$. The latter corresponds to moisture deficits (*PET* > *ET*) characteristic of arid and semi-arid landscapes at the left hand side of the *TI* axis. For illustration purposes, we define $f(p) = q + ap$, where *q* is the fractional infiltration on bare soil and *a* is the gain in infiltration with increasing cover *p* (Rietkerk *et al.,* 2000). Similarly, we define $\tau(p) = S(\,e + up)$, where *e* is the specific loss rate of water from the soil and *u* is a plant uptake rate coefficient (van de Koppel, Rietkerk & Weissing, 1997). Thus, a slice through the hyperspace defined by *PET*, *P*, *p*, *q*, *a*, *e*, and *u* will reveal transitions from water-limited to energy-limited vegetation and from conditions of positive to negligible flow. We illustrated this transition through a numerical example.

With fixed *PET* = 1,200 mm, $a = 1$, and evaporative and transpirative efficiencies $e = 0.5$ and $u = 0.7$, respectively, we compared two different bare soil infiltration rates *q* and showed that the water available for flow changes abruptly with plant cover in different environments. We computed $S^*(p)$ by equation [4] for combinations of *p* and *P* and obtained the runoff $Q = P - ET = P - \tau(p)S^*(p)$ (Figure 2). By definition, water- and energy-limited domains are separated by the *PET* = *ET* isopleth (Figure 2). Low bare soil infiltration ($q = 0.2$) produced water-limited vegetation and $Q > 0$ under most combinations of cover and water input (Figure 2a). High bare soil infiltration ($q = 0.8$) increased the prevalence of energy-limited vegetation and drastically reduced flow in the water-limited domain. As expected from Figure 1, the model produced flow in energy-limited vegetation when water input was greater than *ET*. Negative values for flow constitute an evapotranspirative deficit (Stephenson, 1990) or subsurface storage. Thus, the potential for erosion should be high in arid or semi-arid landscapes with sparse plant cover and low water input, leading to the proliferation of drainage networks characterized by the negative slope in Figure 1. The crossover to energy-limited conditions should favor increased erosion once the water input exceeds the potential evapotranspiration. Otherwise, the vegetation simply consumes the water input to an extent determined by *PET*.

In general, over areas larger than small plots, the forms of $f(p)$ and $\tau(p)$ are unknown. Moreover, there is no known principle by which to elucidate them, nor can these parameters be measured directly over large areas. To make progress, our next step is to test the hypothesis that relevant invariant properties hold both across a wide range of spatial scales and in the relationship between relevant variables. The following sections illustrate how a functional form for $f(p)$ can be obtained.

SPATIAL SCALING OF ENERGY-LIMITED VEGETATION

The water balance equation (equation [1]) applies to any domain with length scale *L* and area proportional to L^2. In particular, if we consider another domain with scale λL, where $\lambda > 1$ or $\lambda \leq 1$ is a dimensionless scale factor, then equation [1] also applies to this domain. In general, equation [1] applies to a sequence of domains of different λ. To represent the scale dependent consequence of equations [3] and [4], we define energy-limitation as $Q(\lambda L) > 0$ and water-limitation as $Q(\lambda L) = 0$. To evaluate these criteria, we would need to specify how flow varies as a function of scale for nested subnetworks within a river basin, rather than in cells of a square lattice. Unfortunately gauged

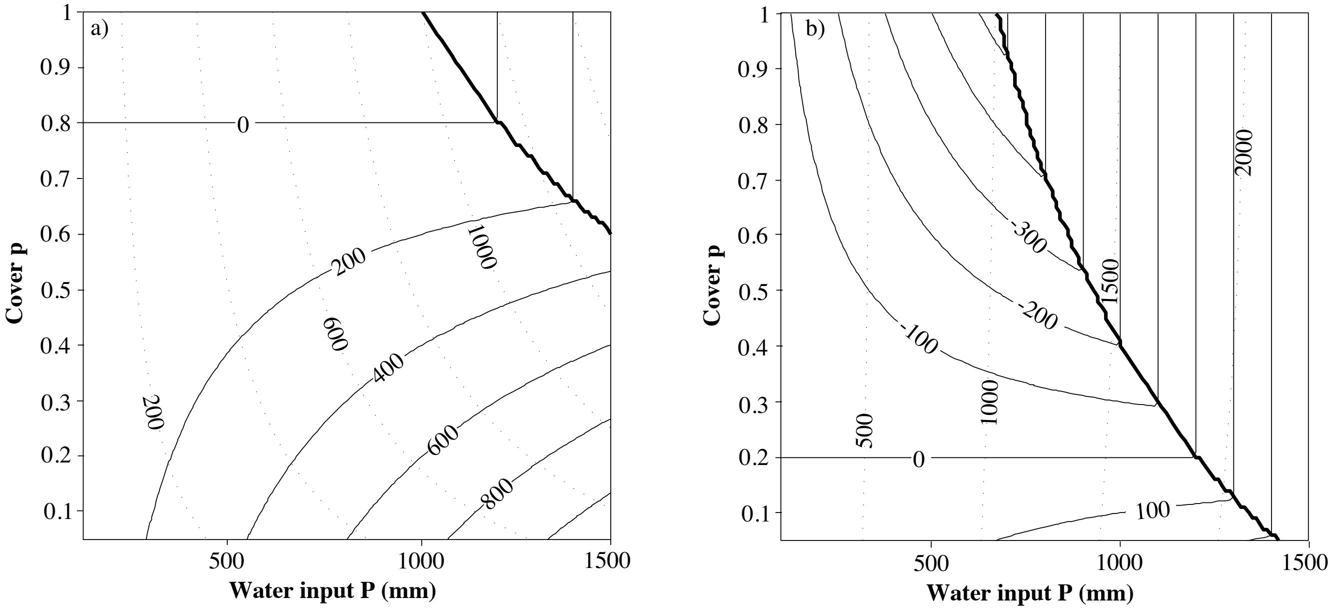

FIGURE 2. Water available for flow (thin solid lines) in environments of varying plant cover and water input. Bare soil infiltration a) $q = 0.2$ and b) $q = 0.8$. Equilibrial soil moisture content $S^*(p)$ (dashed). The heavy solid line demarcates the transition from water- (lower left) to energy-limited conditions (upper right).

streamflows are too sparse to conduct this kind of analysis. Rather, the transition from water- to energy-limited vegetation can be examined directly on a square lattice without requiring streamflow measurements.

We examined the spatial distribution of energy-limited vegetation by obtaining maps from the National Center for Geographic Information Systems and Analysis of annual *PET*, *ET* for 1989, and annual precipitation in 2,000-m-wide square cells over a 262,144-km^2 region in the Columbia River Basin (CRB). The study area was centered at the intersection of Idaho, Oregon, and Washington states, U.S.A. (Everett *et al.*, 1994; Table I). We classified vegetation as energy-limited where *ET* equaled *PET* (equation [4]). However, in the available data, evapotranspiration had been calculated for 1989, an extreme year with respect to the El Niño Southern Oscillation, which made the region water limited and precluded a straightforward definition of energy-limited locations. To approximate typical conditions that have a mixture of water- and energy-limited areas, we developed a subjective transformation of the data that effectively "binned" the data (reduced precision) and rendered some locations equal in *ET* and *PET*. Specifically, we rescaled measurements by a factor α and performed a logarithmic transformation. We computed the ratio of the integers of $\log_2 \alpha\, PET$ and $\log_2 \alpha\, ET$. By ignoring the decimal parts, some values of the transformed *PET* and *ET* were equal, thereby indicating energy-limitation. We explored different α ranging from 1 to 1,000 and found that $\alpha = 50$ maximized the range of the ratio. Cells were classified as energy-limited if the ratio was unity and water-limited if greater than unity.

Under the null hypothesis that energy-limited vegetation cells are independent and identically distributed (i.i.d.), we specified the expected occupation rate at each scale (Gupta & Waymire, 1993; Milne & Johnson, 1993; Milne & Cohen, 1999). Let $p(\lambda L)$ be the probability that a cell of length λL is occupied and $q(\lambda L) = 1 - p(\lambda L)$ be the probability of being empty. For simplicity of notation, take $L = 1$. It follows from the i.i.d. assumption that

$$q(2\lambda) = q^4(\lambda) \qquad [5]$$

because for a cell to be unoccupied at scale 2λ, all four cells at scale λ must be empty. In general for an integer $m > 0$, it follows that

$$\log(q(m\lambda)) = m^2 \log(q(\lambda)) \qquad [6]$$

Equation [6] describes renormalization of empty cells at different scales by relating the probabilities of being empty. This equation has a solution under general analytical conditions:

$$\log(q(\lambda)) = -k\lambda^2, \text{ or}$$
$$p(\lambda L) = 1 - q(\lambda L) = 1 - \exp(-k\lambda^2 L^2) \qquad [7]$$

where k is a constant (Gupta & Waymire, 1993). Note that for small λL equation [7] can be approximated by a linear relationship with a slope of 2 on a doubly logarithmic graph of $p(\lambda L)$ versus λL.

We tested the null hypothesis that energy-limited locations obey equation [7]. The procedure was to divide the map into boxes of length L, then count the number of boxes that contained any amount of the set (Feder, 1988; Voss, 1988; Milne, Johnson & Matyk, 1999; Figure 3). The frac-

TABLE I. Descriptive statistics for water balance variables over the study region of the Columbia River Basin. All variables are in meters of water per year.

Parameter	Precipitation	Potential evapotranspiration	Actual evapotranspiration (1989)
Minimum	0.152	1.411	0.034
Maximum	2.228	2.224	0.845
Mean	0.644	1.795	0.317
SD	0.361	0.169	0.121

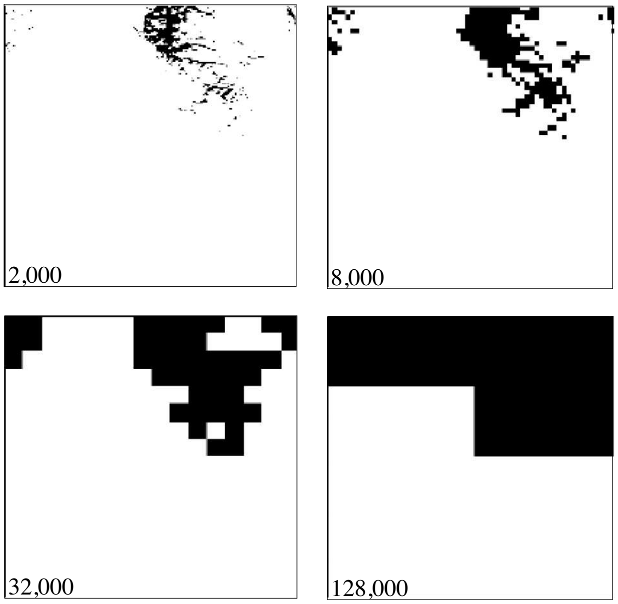

FIGURE 3. Real-space renormalization of energy-limited vegetation in the Columbia River Basin (black). The number in each panel is the cell length in meters.

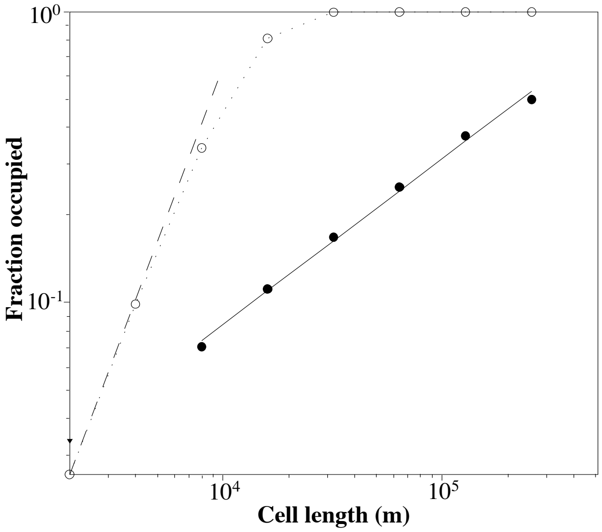

FIGURE 4. Scaling of the fraction of the Columbia River Basin landscape occupied by energy-limited vegetation (solid dots). Extension of the solid fitted curve predicts that a fraction 0.336 of the landscape was occupied at the original scale of 2,000-m cells (triangle). Expected occupation rates under the null hypothesis of no spatial correlation (open circles) had an initial scaling behavior governed by a slope of 2 (dashed line) and an overall behavior given by equation [7]; the curve originates at the observed occupancy.

tion of the area occupied is $p\ (\lambda L) = N(\lambda L)/(\ E^2\ /\lambda^2 L\ ^2)$, where E is the extent or width of the original square map and $N\ (\lambda L)$ is the number of occupied cells. The observations led us to reject the null hypothesis (Figure 4).

The number of occupied cells was fitted with a power law, $N\ (L) = cL^{-D}$, where c is a constant and D is the box fractal dimension (Voss, 1988; Milne, 1997) ranging from D = 0 for a point to D = 2 for a uniformly or randomly occupied plane; the latter is the case predicted by equation [7]. In general, $p\ (L) = c/E^2\ L^{\ 2-D}$. Under the null hypothesis with $D = 2$ and large L, $p\ (L) = c/E^2 = 1$ (Figure 4). The fitted model

$$p\ (L) = c/E^2\ L^{\ 2-D} = 0.00044\ L^{\ 0.57} \qquad [8]$$

gave a box fractal dimension of 1.43. The fitted curve evidenced modest systematic deviations in the residuals, perhaps due to the crude way in which energy-limited cells were defined and because the set was truncated at the map boundary. A second caveat relates to the range of scales over which the fit was made. Ideally, two or more orders of magnitude in measurement scale should be used, but such a range can be very demanding of the available data.

A subtle consideration applies to the domain of scales over which to estimate D. Like all such maps, the map of energy-limited vegetation at the original scale ($L = 2{,}000$ m) was subject to cartographic errors. One pertinent error stems from arbitrary thresholding, rounding, and averaging procedures that affected the maps that were used to calculate the water balance parameters. For example, when constructing a map of vegetation types used to model transpiration, it is customary to classify a cell based on the majority rule. In the majority rule, a certain type of vegetation is treated as the only type present if it covers more than 50% of the cell (Milne & Johnson, 1993). The majority rule can lead to an abrupt divergence in apparent composition of vegetation types after just a few changes of scale. Thus, using empirical estimates of $N\ (L)$ for small L subjects the analysis to errors at scales close to those of the original map. By using large λL to estimate D, we effectively remove those degrees of freedom (*i.e.*, cells on the map) most subject to error, thereby filtering the data to focus on the smaller degrees of freedom that contain the signal (Wilson, 1979). Strategic elimination of degrees of freedom is the essence of renormalization.

According to the scaling relation, the expected density of the original map was $p\ (2{,}000) = 0.0336$ (Figure 4). In contrast, the empirical occupancy at the original scale was $p = 0.0257$, 30% lower than the fractal estimate. The deviation reflects several possibilities. First, the discrepancy could obtain from extrapolating the regression outside the calibration domain. However, in this case the scaling relation is primarily a measure of how the area of energy-limited vegetation varies with scale. Consequently, we can use the scaling relation to infer densities at unmeasured scales, under the assumption that the scaling law is valid. Ideally, the assumption should be verified with independent data collected at finer scales than currently available (Kunin, 1998). Second, it is possible that the spatial filtering accomplished by the renormalization, or equivalently the box counting, has successfully ignored errors at the fine scales and provided a more robust characterization of the parametric geometry of the set. If so, then $p\ (2{,}000) = 0.0336$ can be considered a less biased estimate of the set. Given the standing problem of locating the missing carbon sink in the global carbon balance (Field, 2001), it is worth considering that current mapping and estimation methods may have underestimated pools at fine scales (Milne, 1997).

As expected, the renormalization function (equation [7]) overpredicted the portion of occupied cells at broad scales because the i.i.d. assumption does not account for connections between neighboring cells (Figure 4). Ultimately, the curve flattened as L became large because the function converges to $p = 1$ for all initial $p > 0$. Comparison of the renormalization predictions and empirical scaling clearly falsified the null hypothesis that the energy-limited regions were random. Moreover, the scaling pattern persisted to distances of 256,000 m. The persistence supported our interpretation that the macroscopic distribution of energy-limited environments entailed ecological and hydrological interactions over vast distances spanned by drainage networks. Such interactions involved large catchments and elevation fluctuations that affect precipitation, soils, temperature gradients, net radiation fluxes, and wind fields (Daly, Neilson & Phillips, 1994). Ecologically speaking, the scaling relationship given by equation [8] suggests that instabilities in the water balance may originate with the effect of plants on infiltration and transpiration rates (equation [3]) and propagate over large spatial distances in a scale invariant manner. We explore this idea more explicitly in the following section.

DERIVATION OF A SCALE INVARIANT INFILTRATION EQUATION VIA RENORMALIZATION

The observed scale invariance (Figure 4) implies that under certain combinations of water and energy supply the vegetation comes into an equilibrium according to a principle that does not change with spatial scale. To relate the water balance to scale invariance, we defined new water balance parameters and analyzed how they changed under a change of spatial scale. Our strategy was very similar to the renormalization analysis in physics, which has been used to elucidate scaling relations (Wilson, 1979; Creswick *et al.,* 1992; Milne *et al.,* 1996; Milne, 1998; Dodds & Rothman, 2000).

We defined two absolute measures: the energy available for photosynthesis and the water available for terrain formation, given by PET - ET and $P - ET$, respectively. In order to find a relationship between these parameters we nondimensionalize them in the spirit of dimensional analysis, which is a powerful technique to find functional relationships from experiments or observations (Barenblatt, 1996). We define the relative excess energy as $U = (PET - ET)/PET$, which makes Stephenson's (1990) water deficit relative to PET. The second parameter is relative excess precipitation, $W = (P - ET)/P$. Excess precipitation will be negative where riparian vegetation transpires water supplied by the stream channel rather than from the atmosphere. The parameters reflect the coupling of biotic and abiotic processes in the landscape

In the style of real-space renormalization, we examined the behavior of the parameters U and W in U-W phase space as the cell size was changed from 2,000 to 6,000 m. First, we spatially averaged PET, ET, and P in 3 × 3 cell neighborhoods (representing 36 km^2) and calculated U and W at the new scale. Scale invariance was defined by $\mathrm{d}U/\mathrm{d}\lambda = 0$ and $\mathrm{d}W/\mathrm{d}\lambda = 0$. For graphical clarity, we displayed one-ninth of the original $\{U(L = 2{,}000), W(L = 2{,}000)\}$ coordinate pairs and the corresponding renormalized pairs $(\{U(\lambda L = 6{,}000),\ W(\lambda L = 6{,}000)\}$ with an arrow that showed the direction of change (Figure 5). Under the null hypothesis that the spatial averages converge directly on the centroid, we would expect all the arrows to point to the grand means. Instead, however, there was a broad band in parameter space where little or no change occurred with scale. The band of scale invariance was shown by the $\mathrm{d}W/\mathrm{d}\lambda = 0$ contour for changes in excess precipitation, which coincided with the $\mathrm{d}U/\mathrm{d}\lambda = 0$ contour for excess energy (Figure 5). The band divided the U-W phase space into regions of increasing and decreasing excesses in the lower left and upper right corners, respectively.

To study the band of scale invariance, we used all the data and averaged the changes observed for $\lambda = 3$ within bins of width 0.05 and 0.1 in U and W, respectively (Figure 6). The bin means were used to calculate the expected changes in the parameters under successive changes in scale given by $\lambda = 3, 9, 27, 81$, and 243, corresponding to 6,000 ..., 486,000 m, respectively. The band of invariance was robust to penetration by trajectories that originated some distance away.

Derivation of an infiltration parameter $f(p)$ begins by parameterizing the band as the line $U = 0.9 - 0.36\ W$ (Figure 6) and then relating it directly to P, ET, and PET by expanding U and W:

$$(PET - ET)/PET = 0.9 - 0.36\ (P - ET)/P \qquad [9]$$

Rearranging terms in equation [9] gives

$$0.46\ P\ PET = ET(P + 0.36\ PET) \qquad [10]$$

According to equation [5], ET is $\tau S^{*}(p)$ in water-limited vegetation. Substituting for ET in equation [10] gives

$$S^{*}(p) = \{0.46\ /\ (\ 0.36 + P/PET)\}\ P/\tau\,(p) \qquad [11]$$

Finally, equation [11] can be compared with the equilibrium solution of the mass balance equation [4] which gives

$$f\,(p) = 0.46\ /\ (\ 0.36 + P/PET) \qquad [12]$$

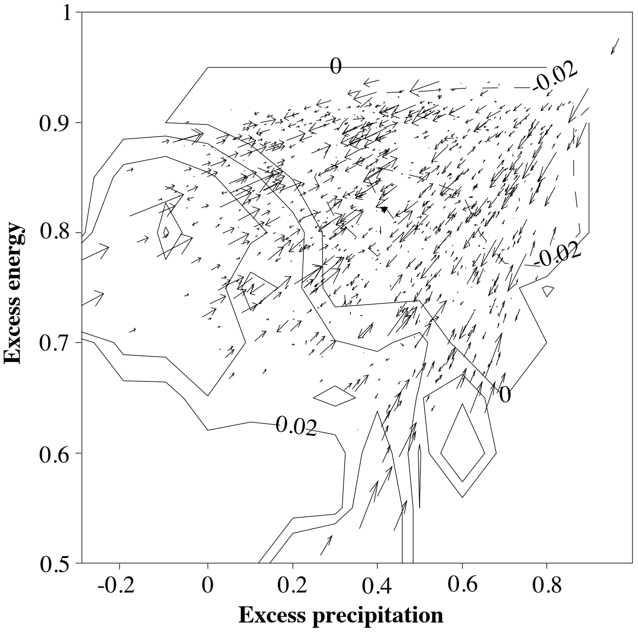

FIGURE 5. Renormalization trajectories of excess energy and excess precipitation observed with a three-fold increase in cell length over the Columbia River Basin. Arrows represent changes in parameters for 1/9 of all the original 2,000-m-long cells. Grand means of both parameters are given (triangle). Contour lines indicate rates of change in excess precipitation with a change of scale. The 0 contour along the diagonal identifies a broad band of conditions where the arrows reverse direction.

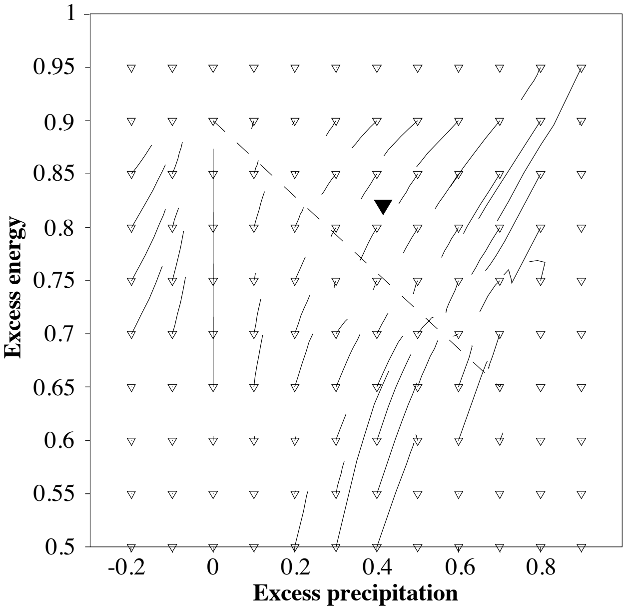

FIGURE 6. Renormalization trajectories obtained by averaging rates of change within small bins. Solid lines are trajectories away from initial conditions (open triangles) due to a 243-fold change of scale. The band of scale invariance had a slope of –0.36 (dashed line). The grand mean of both parameters is given (solid triangle).

Equation [12] shows that the fraction of precipitation rate P that infiltrates, $f(p)$, for a given plant cover is related to the ratio of precipitation and energy supply at all scales within the domain of scale invariance (Figure 4). Three insights obtain directly from this equation. First, infiltration rate can be estimated for a given plant cover from measurements of P and PET integrated over an area of any arbitrary size within the scaling domain. There have been no measurements or theories that predict infiltration over large regions. Over the broad scales of drainage basins, the estimation of infiltration is confounded by spatial variability in the infiltration parameters. Consequently, infiltration over regions larger than a plot has remained a seminal unsolved problem. Second, applications of the water balance in biogeography (Stephenson, 1990) use two variables, ET and moisture deficit ($PET - ET$), together, to predict biome distributions. By focusing on infiltration rather than ET, equation [12] expresses plant abundance (p) as a function of water and energy rather than with a cryptic combination of the two. The emergence of the ratio P/PET as the relevant factor suggests that plants must trade off investments in water and energy gathering tissues, *e.g.,* roots versus shoots. The infiltration equation could guide studies of how plants allocate fixed carbon to various tissues and organs. Third, plant cover often varies as a power of spatial scale (Figure 4, Krummel *et al.,* 1987; Milne, 1992; Milne, 1997; Kunin, 1998). Consequently, edaphic parameters must also vary with scale to maintain the equality with the ratio P/PET at each scale (equation [12]). Conversely, a fluctuation in P/PET must be balanced by a change in plant cover or infiltration rate. The coupling between plants, terrain, atmosphere, water, and energy is indicative of a self-organizing system governed by the infiltration equation (equation [12]) that creates scale invariant landscape patterns (Figure 4).

Concluding remarks and future directions

The reversal of drainage density (Figure 1) suggested a transition from water- to energy-limited environments. Our finding that a spatial scaling relation holds in such environments points to the existence of a new biophysical object, namely an ecotone at the interface of water- and energy-limited environments. The ecotone is similar to the phenomenon of spatial phase transitions widely studied in physics, where interactions between neighboring locations and dynamical instabilities give rise to macroscopic scaling relations (Stauffer & Aharony, 1992). The scaling relation (Figure 4, or equation [8]) is also predicted by the theory of random cascades, which has been applied to modeling turbulence and precipitation fields (Lovejoy, Schertzer & Tsonis, 1987; Gupta & Waymire,1993). The relation comes about due to long-range spatial correlations.

In the spirit of real-space renormalization, the observation of a band of scale invariant conditions (Figure 5) implies the existence of an instability (Creswick, Farach & Poole, 1992). In our case, such an instability pertains to the partitioning of water, or the fate of a raindrop, which may flow either through plants into the atmosphere or down the stream channel. Thus, the use of relative measures of excess energy and excess water appear sufficient to capture the instability.

The ratio P/PET is central to the definition of TI on the abscissa of the drainage density curves (Figure 1), although TI is based on monthly ratios rather than annual. The independent appearance of the ratio in our derivation of the infiltration equation (equation [12]) suggests a central role of the ratio in an ecohydrological view of the landscape. Equation [12] was derived from equation [9], which describes conditions under which the dimensionless variables for excess energy and water are constant with a change of scale. Invariance is central to the independent appearance of P/PET as the relevant parameter for drainage density and for water balance.

Tests of the infiltration equation (equation [12]) require landscapes that contain mixtures of water- and energy-limited vegetation in order to reveal combinations of the U-W parameters that are invariant with changes in scale. Future studies of infiltration over broad scales should be based on nested subbasins within large basins, rather than on blocks of pixels, because of the natural topology of flow. Stream discharge is predicted from equation [12] by $(1 - f(p))P$, which can be compared against observed stream discharges on a drainage network. The use of stream discharge provides an independent test of our theory.

Ultimately, a biophysical theory is needed to describe the empirical constants of the scaling band (equation [9]) so that the infiltration equation can be applied globally. A promising avenue would be to express plant cover in terms of plant mass, thereby providing an allometric basis for a purely biophysical theory of infiltration. In this context it is intriguing that the box fractal dimension of 1.43 is similar to the 4/3 power that governs plant mass and density in energy-limited environments (Enquist, Brown & West, 1998; Niklas & Enquist, 1999). With plants in steady state with resource supply rates, we expect energy-limited areas to saturate with plant mass and to have stem number vary as the 4/3 power of mass.

In general, we suggest that ecological measurements should be evaluated in a scaling context for two reasons. First, the expected values of relevant parameters change with scale. Rather than expecting a value obtained at one scale to represent an entire ecological system, it is better to characterize precisely how parameters vary with scale. The scaling relation itself may be more relevant than an estimate at a fixed scale. Second, renormalization is an extremely powerful tool with which to develop new theory that may apply at many scales, thereby solving the challenge of extrapolating measurements from one scale to the next.

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