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Spatial Scale Dependence of Ecohydrologically Mediated Water Balance Partitioning: A Synthesis Framework for Catchment Ecohydrology

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Abstract. The difficulties in predicting whole-catchment water balance from observations at patch scales motivate a search for theories that can account for the complexity of interactions in catchments. In this paper we suggest that the spatial patterns of vegetation may offer a lens through which to investigate scale-dependence of hydrology within catchments. Vegetation patterns are attractive because they are observable drivers of evapotranspiration, often a dominant component in catchment water balance, and because the spatial distribution of vegetation is often driven by patterns of water availability. We propose that non-trivial, scale-dependent spatial patterns in both vegetation distribution and catchment water balance are generated by the

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presence of a convergent network of flow paths and a two-way feedback between vegetation as a driver of evapotranspiration, and vegetation distribution as a signature of water availability. Implementing this hypothesis via a simple network model demonstrated that such organization was controlled by catchment properties related to aridity, the network topology, the sensitivity of the vegetation response to water availability, and the point-scale controls on partitioning between evapotranspiration and lateral drainage. The resulting self-organization generated spatial dependence in areally averaged hydrologic variables, water balance and parameters describing hydrological partitioning, and provided a theoretical approach to connect water balances at patch and catchment scales. Theoretical and empirical studies aimed at understanding the controls of vegetation spatial distribution, point scale hydrological partitioning and the implications of complex flow network topologies on the spatial scale-dependence of catchment water balance are proposed as a research agenda for catchment ecohydrology.

1. Introduction

Hydrologists are increasingly concerned with predicting the effects of global change on water scarcity, water quality, water-related natural hazards and ecosystem service provision [*Jackson et al.*, 2001; *Wagener et al.*, 2010], as well as the potential feedbacks between land surface hydrology and the global climate system [*Montanari et al.*, 2010; *DeAngelis et al.*, 2010]. There are a number of features of catchment hydrology which continue to hamper predictability, including the tremendous heterogeneity in landscape properties and climatic inputs; the highly interconnected nature of hydrological response with climatic, ecological, geomorphological, pedological and anthropological processes, all of which are subject to imposed change [*Istanbulluoglu and Bras*, 2005; *Vitousek*, 1994]; and the multi-scale variability of resulting hydrological responses. Monitoring of hydrological responses occurs primarily at the whole catchment scale, where simplified lateral boundary conditions and flow aggregation through the river network facilitate water balance closure [*Gupta and Dawdy*, 1995]. However, detailed understanding of physical hydrological processes is often most applicable at point scales where environmental parameters may be approximated as homogeneous. Point based predictions are notoriously difficult to relate to catchment responses [*Blöschl and Sivapalan*, 1995] leading to a gap between the scales at which processes occur and are understood, and the scale at which observations are made and hydrological prediction is needed. The interconnectedness of catchment processes further complicates prediction, because changes to any aspect of the system may propagate to others in complex ways, ultimately affecting the whole system's response. Therefore, predicting hydrological responses to global change poses a major challenge to hydrologists and earth system scientists and requires a new generation of theories and descriptive principles. These principles must link local change to whole catchment response, and confront the challenges posed by the high dimensionality of the catchment system and the nonlinearity and complexity of relationships amongst its components [*Dooge*, 1986].

Fortunately, the form and function of catchments results from long-term coevolution between water, soils, landforms and ecosystems, and catchments consequently display a large degree of self-organization in hydrological and biophysical properties [*Hopp et al.*, 2009; *Wagener et al.*, 2004; *Koster et al.*, 2000]. An attractive approach for simplifying the problem of hydrological prediction is to use this organizational structure to identify emergent properties or patterns that constrain relationships across processes and scales [*Koster et al.*, 2000; *Ducharne et al.*, 2000; *McDonnell et al.*, 2007; *Blöschl*, 2006; *Sivapalan*, 2003]. Catchment hydrology has made great strides in prediction through utilizing two such emergent patterns: the geomorphological instantaneous unit hydrograph or GIUH [*Rodriguez-Iturbe and Valdes*, 1979; *Mesa and Mifflin*, 1986], which uses the characteristics of the channel network to predict catchment storm response; and the topographic wetness index, which uses topographic features to characterize spatial patterns of soil wetness and forms the basis for many current models (e.g. TOPMODEL and RHESSYs [*Beven and Kirkby*, 1979; *Band et al.*, 1991, 1993]). Both cases draw on emergent relationships between geomorphological patterns and hydrological response. Using such emergent properties for 'dimension reduction' [*Holmes*, 2005] simplifies prediction and helps to overcome some of the issues of heterogeneity [*Blöschl and Sivapalan*, 1995; *Viney and Sivapalan*, 2004]. More fundamentally, emergent properties are outcomes of the co-evolution of catchment features and consequently offer a window into understanding the response of the entire catchment system to imposed change.

The introduction of the GIUH and TOPMODEL, both in 1979, led to significant improvements in our ability to make hydrological predictions and advances in hydrological research. Both discoveries coincided with the wider availability of topographic information in the form of DEMs. There is potential for other emergent patterns in catchment properties to be identified and used in a similar manner. In particular, the wide availability of high resolution aerial photography, as well as advances in aerial and ground based LIDAR [*Lefsky et al.*, 2002], now offers unprecedented levels of information about the spatial distribution of vegetation in catchments. This paper is motivated by the prospect that spatial organization of vegetation might form the basis for a new set of emergent relationships to constrain hydrological processes at catchment scales. Linking vegetation distribution to hydrological function is attractive for several reasons:

1. Vegetation cover is a surface feature of catchments, and as such is readily observable [*Boggs*, 2010]. Vegetation mapping suggests that vegetation cover and type in many catchments are influenced by patterns of water availability. These patterns may even persist in highly disturbed environments (see Figure 1). Thus, hydrological relationships inferred from vegetation patterns can be usefully applied across a wide array of sites and scales.

2. Secondly, vegetation is an important driver of evapotranspiration fluxes, which comprise 62% of terrestrial water balance [*Shiklomanov*, 1998], and often approach 100% of rainfall in arid climates [*Budyko*, 1974]. Removal or change in catchment vegetation, or even the diurnal variation of vegetation water use, are observed to alter the magnitude and

temporal pattern of streamflow [*Brown et al.*, 2005; *Bond et al.*, 2002; *Gribovszki et al.*, 2010]. Consequently, understanding vegetation water use and its scale-dependence has the potential to explain a significant proportion of the water balance and its variability.

3. Furthermore, advances in ecohydrological science have progressed in pace with the availability of remote sensing vegetation data. Point-scale controls on water balance and soil moisture due to vegetation are increasingly well understood [*Guswa et al.*, 2002; *Rodriguez-Iturbe et al.*, 2007] and can be envisaged as driving the partitioning between vertical and horizontal water fluxes (or 'green' and 'blue' water) at a point [*Falkenmark*, 1997]. In the absence of spatial variation in precipitation inputs or soil hydraulic properties, spatial organization and scale-dependence arise primarily due to spatial variation in the horizontal components of the flux, which, via either surface or subsurface redistribution subsidizes downstream or downslope points with additional water to rainfall [*Puigdefabregas et al.*, 1999; *Yu et al.*, 2008; *Valentin et al.*, 1999]. The lateral subsidy reflects and integrates upslope or upstream structures and processes, including connectivity, slope, convergence and water balance partitioning. Although such subsidies are likely to be quite spatially variable, the probability that water balance is influenced by such subsidy processes should increase down-gradient in catchments. Spatial structures in vegetation are known to naturally arise in response to water availability [*Caylor et al.*, 2005; *Scanlon et al.*, 2007; *Rietkerk et al.*, 2004; *Kefi et al.*, 2007], at least in arid or semi-arid environments. Because of the two-way coupling between the lateral subsidy (as a driver of moisture availability) and the presence of vegetation (as a driver of local partitioning), vegetation spatial organization is hypothesized to be both a control and a signature of hydrological processes. The link between vegetation pattern and hydrological process

will vary in strength depending on the significance of other drivers of spatial variation in water balance (for instance in soil hydraulic properties) and vegetation distribution (for instance, energy or nutrient availability, or disturbance regimes) within a particular watershed [*Boisvenue and Running*, 2006].

4. Finally, vegetation exhibits the potential for rapid, widespread change in response to changing environmental drivers [*Jackson and Overpeck*, 2000; *Allen and Breshears*, 1998; *Clark*, 1998; *Clark et al.*, 1998; *Barbier et al.*, 2006]. Consequently, vegetation patterns can also act as tractable indicators of system-wide change.

The need for water balance predictions to be underpinned by improved understanding of the link between hydrological partitioning at point and catchment scales was a key finding of the 2009 Hydrologic Synthesis Summer Institute, as reflected in many of the papers presented in this special section of Water Resources Research [*Sivapalan*, 2010]. The papers included in this special section explore patterns in water balance at both whole catchment and point (or patch) scales, developing deeper insights into the controls and complexities of water balance prediction. The difficulties experienced in reconciling point level predictions with catchment scale observations provide a strong motivation for addressing the scaling challenge in water balance partitioning, especially as they are influenced by vegetation. In this review paper we aim to combine advances in the quantification of catchment-scale water balance made during the Summer Institute with current understanding in catchment hydrology and ecohydrology. These ideas are synthesized in a network model which is used to test the plausibility of linking scale-dependence in catchment water balance and catchment vegetation distributions, given a presumed two-way feedback between water and vegetation. The model immediately highlights a number of relationships between climate, topography and vegetation within catchments. We focus on these as the drivers of scale dependent behavior in ecohydrology and to outline a set of broad research opportunities and challenges in catchment ecohydrology.

2. Scaling of ecohydrologically mediated partitioning

As outlined above, vegetation spatial organization at catchment scales can be viewed through two lenses: ecologically, in which the focus is on the links between spatiotemporal vegetation dynamics and environmental drivers, including water availability; or hydrologically, in which the focus is on the spatial structure of hydrological partitioning in a catchment, and the consequences for catchment scale hydrology. The ecological approach offers insight into the controls of spatial organization of vegetation and inference from observed vegetation patterns [*Scanlon et al.*, 2007; *Caylor et al.*, 2005; *Franz et al.*, 2010; *Caylor et al.*, 2009; *Hwang et al.*, 2009; *Stephenson*, 1998]. The latter approach links water balance partitioning to the distribution of vegetation through space and time. Vegetation alters the partitioning of water balance at both patch and whole-catchment scales. However, the role of vegetation in controlling the spatial and temporal dependence of water balance partitioning within catchments remains challenging to elucidate. Effectively linking patch and catchment scales requires both bottom-up approaches that aggregate established process understanding, and top-down approaches which utilize catchment-scale observations and emergent patterns in water balance to constrain and guide conceptual model development.

2.1. How do plants mediate water partitioning at different spatial scales?

2.1.1. Patch scales

Vegetation control of hydrological fluxes at patch scales (i.e. those associated with individual trees or shrubs, or near-homogeneous vegetation assemblages) is one of the best understood aspects of ecohydrology, and a comprehensive review lies beyond the scope of this paper. Instead we provide a brief overview of the relevant processes of hydrological - ecological interaction.

Mechanistically, vegetation alters aboveground hydrologic fluxes through canopy and litter layer interception, stemflow and infiltration modification [*Thompson et al.*, 2010a; *Durocher*, 1990; *Levia and Frost*, 2003; *Vetaas*, 1992; *Crockford and Richardson*, 2000; *Putuhena and Cordery*, 1996]. These effects can be highly spatially variable, and can result in directed transport of water in vertical or lateral directions, for example through interactions of stemflow with macroporosity in the rootzone, runon-runoff effects or snow redistribution [*Marks et al.*, 2002; *Martinez Meza and Whitford*, 1996; *Ludwig et al.*, 2005]. In the subsurface, vegetation modifies hydrological transport by altering soil structure, notably through macropore formation, by hydraulic redistribution, but perhaps most overwhelmingly by root uptake [*Angers and Caron*, 1998; *Burgess et al.*, 1998; *Scott et al.*, 2008; *Oliveira et al.*, 2005]. The relationship between soil moisture and transpiration, which determines root water uptake from the soil and its subsequent vaporization in the canopy, has been a primary focus of ecohydrologists.

Water uptake is physiologically critical to plants because of its intimate coupling to photosynthesis and carbon gain through the stomata [*Berry et al.*, 2005]. The trade-off between carbon gain and water loss within individual plants has been hypothesized to drive the rapid dynamics of stomatal opening and closing [*Katul et al.*, 2009, 2010]. Plants are hypothesized to function 'on the edge' of cavitation [*Sperry*, 2000], implying that the optimization of such controls may be critical to survival. On longer timescales, carbon-water tradeoffs are also hypothesized to control variability in root:shoot ratio and biomass allocation [*Givnish*, 1986; *Schenk and Jackson*, 2002; *Schenk*, 2008; *Zerihun et al.*, 2006]. *Nemani and Running* [1989] showed that plant water availability could predict the leaf area index at the stand scale in water limited forests. The response of stomata to atmospheric and soil moisture conditions allows soil water potential to be related to transpiration [*Feddes et al.*, 1976]. By linking water uptake dynamics with stochastic rainfall, *Rodriguez-Iturbe et al.* [1999] derived analytical solutions of the 1D stochastic soil water balance in the absence of a water table [*Rodriguez-Iturbe et al.*, 1999; *Laio et al.*, 2001] allowing important progress to be made in quantitative ecohydrology e.g. [*D'Odorico and Porporato*, 2006]. More recently these stochastic approaches have been extended to systems with dynamic water tables [*Rodriguez-Iturbe et al.*, 2007; *Laio et al.*, 2009; *Tamea et al.*, 2009] and applied to streamflow prediction in simple catchments [*Botter et al.*, 2008, 2007].

These developments in theory have been simultaneously inspired and supported by improvements in monitoring and measuring fluxes within individual plants (primarily using sap flow approaches [*Smith and Allen*, 1996]) and at the canopy level, particularly using eddy covariance techniques [*Shuttleworth et al.*, 1988; *Baldocchi et al.*, 2001]. These approaches allow a coupling of hydrological fluxes across the whole soil-plant-atmosphere continuum by linking atmospheric conditions to evaporative demand, and the satiation of that demand to moisture availability and plant status [*Tuzet et al.*, 2003]. Despite this progress, simple prediction of the dynamics of evapotranspirative fluxes and soil moisture throughout a vertical profile remains challenging, requiring detailed meteorological, edaphic and vegetation data. Although many models reasonably represent patch-scale ET and CO_2 exchange over certain timescales [*Drewry et al.*, 2010a, b], completely predicting these fluxes at all relevant timescales (seconds to inter-decadal) remains challenging [*Siqueira et al.*, 2006].

In summary, although there remains a need to refine understanding of the role of vegetation in locally modifying water balance partitioning at point scales, 'classical' ecohydrology at patch scales has developed a large body of empirical evidence and maturing theory, which can be applied to the estimation of water balance at least when climatic, edaphic, ecological and hydrological forcing can be assumed to be homogeneous.

2.1.2. Intermediate scales

Moving from patch scales to hillslope or small watershed scales requires knowledge of the distribution of water availability and flux partitioning through space, and the role of vegetation in determining and reflecting that partitioning. Although many upscaling approaches (at least for the evapotranspiration component of catchment water balance) are based on superposition of patch-scale processes [*McCabe and Wood*, 2006; *Li and Avissar*, 1994], these approaches ignore the potential for contributions of water ('subsidies') from one patch to another. The existence of such non-local controls on local water availability complicates the upscaling water balance dynamics and indeed, water balance measurements made at point scales are often poor indicators of watershed scale response [*Oishi et al.*, 2010]. Before examining the implications of non-local controls on point-scale water availability for vegetation distribution and water balance, we discuss the kinds of hydrological processes that can result in non-local water subsidies.

Lateral connections within catchments and effects on water balance scaling: An obvious form of non-local water contribution is overland flow, which can induce significant lateral hydrological connectivity in mountainous or arid ecosystems where rocky terrain or crusted soils reduce infiltration capacity [*Descroix et al.*, 2007]. This localized and transient hydrological connectivity is responsible for structuring patchy or patterned landscapes [*Valentin et al.*, 1999; *Ludwig et al.*, 2005; *Rango et al.*, 2006]. However, the strong scale dependence of infiltration capacity in arid landscapes means that beyond the size of typical runon - runoff zones [*Puigdefabregas et al.*, 1999], overland flow is unlikely to induce further scale dependence in catchment water balance.

Surface flow in channel networks forms an equally obvious subsidy process by connecting upstream and downstream areas along a river network. Subsidies from the channel to the landscape may arise from surface flow processes (e.g. overbank flow or flooding), for example in humid regions, flooded conditions may persist in bottom-land forests, sustaining a high rate of evapotranspiration and long residence times and certainly influencing local ecology [*Hupp*, 2000]. Studies addressing the significance of these dynamics for catchment scale water balance partitioning, however, are scarce [*Lesack and Melack*, 1995]. Subsidies from the channel to the landscape may also be mediated by subsurface transport in 'losing' reaches, sustaining high rates of evapotranspiration in the riparian zone with potentially significant implications for water balance partitioning, particularly along arid rivers [*Scott et al.*, 2008]. Similar transfers of water from inundated sites in wetlands into vegetated islands are locally important in structuring these ecosystems [*McCarthy*, 2006; *Wassen et al.*, 1990], but again these transfers are unlikely to generate significant scale dependence in catchment water balance (despite their importance for water quality and ecological function).

Subsidies may also be generated in the subsurface. At very local scales, contrasts in water retention properties (associated with e.g. inclusions) or soil depth may be sufficient to result in subsidies. In the case of shallow (transient) perched water tables, downgradient flow-path convergence is likely to lead to accumulation and increased water availability. This accumulation broadly follows the surface catchment topographic network structures, but is also influenced by the topography of confining units, variability in hydraulic properties and the presence of preferential flow paths. For example, spatially variable differences in soil depth determined vegetation water use at the Panola Mountain Research Watershed [*Tromp-van Meerveld and McDonnell*, 2006]. When present, downslope accumulation of subsurface lateral subsidies may result in spatial gradients in evapotranspiration under otherwise uniform vegetation conditions, as observed by several authors in monocultural forested stands [*Mackay et al.*, 2010; *Ford et al.*, 2007; *Yeakley et al.*, 1998]. Similarly, lateral subsurface redistribution of snowmelt in a mountainous catchment increased soil moisture availability and reduced downslope plant water stress [*Tague*, 2009; *Tague et al.*, 2010]. The importance of subsurface redistribution in generating spatial-dependence of water balance partitioning is temporally variable: for instance an increasing downslope spatial trend in ET disappeared under periods of high vapor pressure deficit when all trees shut their stomata, eliminating the spatial pattern [*Loranty et al.*, 2008].

A third form of non-local transport relates to regional groundwater flows. This form of subsidy is characterized by relatively long transport timescales between recharge and discharge sites, an effective sequestration of flow from evaporation or transpiration, and a behavior which is often decoupled from surface topography and may cross watershed boundaries [*Freeze and Witherspoon*, 1967]. These subsidies may form important contributions to catchment water balance at seepage faces and discharge sites [*Genereux and Jordan*, 2006; *Thorburn et al.*, 1993]. For instance, the growth of xeric phreatophytic vegetation in regions where rainfall is too low to sustain plant growth provides an indicator of groundwater-driven lateral subsidies [*Naumburg et al.*, 2005]. In several arid rivers where groundwater contributions drive flow, declining aquifer depth may simultaneously impact riparian vegetation and river flows [*Stromberg et al.*, 1996].

Some additional forms of subsidy, which we do not consider in further detail here, are those provided by human modification of watersheds and those provided by long distance teleconnections between watersheds. Such anthropogenic processes include artificial drainage networks, inter-basin transfers, and artificial exchanges between aquifers and surface water (e.g. aquifer injection, irrigation etc) [*Weiskel et al.*, 2007]. Climatic processes include the links between synoptic and local microclimate and “convective recycling” of rainfall [*Ruddell and Kumar*, 2009a, b; *Dominguez and Kumar*, 2008].

This wide array of subsidy processes generate non-local controls on patch-scale water availability. The significance of these non-local controls on point scale water balance varies between catchments, patches, and through time, depending on the magnitude of the lateral contribution relative to the water contributed by rainfall at that site (the local control). Thus, non-local controls should be most significant when the subsidies are large (e.g. regular inundation of floodplains, regional aquifer discharges), when local rainfall contributions are low (e.g. arid or seasonally arid sites), or both.

Vegetation response to lateral subsidies: Numerous eco-physiological features of vegetation may respond to changing water availability. At the simplest level, changes in fractional cover or presence-absence may arise where contrasts in water availability induced by subsidies are sufficiently striking: examples abound in arid environments where groundwater availability [*Naumburg et al.*, 2005], riparian zones [*Scott et al.*, 2008] or runoff-runon processes [*Valentin et al.*, 1999] all generate sharp and striking contrasts in the location of vegetation in the landscape. Similarly striking changes in plant-functional-type are also often observed in drylands (runon-runoff and root-zone redistribution), in the contrasts between upland and bottomland vegetation, and between vegetation zones in wetlands (where water availability is altered by both shallow-subsurface and in-channel lateral connections, and vegetation distributions impacted by both oxygen and water stress) [*Hupp*, 2000; *Stromberg et al.*, 1996]. Local hydrological context as driven by lateral subsidies may also induce patterns at a species level [*Huang et al.*, 2008; *Nippert and Knapp*, 2007]: for instance, a combination of water and oxygen stress controlled largely by groundwater availability drove the spatial pattern of species distribution in alpine meadows [*Lowry et al.*, 2010] (this issue); while patterns in species abundance, canopy diversity and mortality rate in Mexican dry rainforests were shown to correlate to a hillslope gradient in water availabilty [*Segura et al.*, 2003]. Beyond organization at species level, vegetation may also demonstrate spatial patterns in physiological properties: *Hwang et al.* [2009] showed that leaf area index and soil moisture availability both increased downslope in the Coweeta Experimental Forest. These examples illustrate cases where vegetation properties reflect patterns of water availability, which in turn reflect (at least in part) trends in non-local controls on water availability. Caution must be employed however before interpreting vegetation patterns in purely hydrological terms because vegetation responds to other environmental gradients (e.g. in disturbance, nutrient availability or elevation) and covariation across these gradients often exists [*Webb and Peart*, 2000; *Valencia et al.*, 2004].

In summary, water balance at hillslope or small watershed scales is most likely to exhibit spatial scaling when lateral subsidies of water introduce a non-local control on the point-scale water balance. A range of empirical examples illustrate the potential for lateral subsidies of water to generate distinctive spatial patterns in a range of vegetation properties. Although these cases are rarely linked to the scaling of catchment water balance, they provide ‘stepping stones’ towards understanding ecohydrology at catchment scales.

Additional Drivers of Vegetation Spatial Distribution: Water availability is not the only driver of vegetation spatial organization, and hydrological inference from vegetation patterns requires isolating the signal of water availability. Confounding factors in water-limited ecosystems include energy and heat (e.g. ecotones may be driven by slope aspect in desert ecosystems [*Istanbulluoglu et al.*, 2008]), as well as disturbance regimes, particularly fire [*Odion and Davis*, 2000]. In energy-limited ecosystems, vegetation spatial distribution is likely to be strongly determined by light and temperature availability [*Vajda et al.*, 2006]. Temperate ecosystems often experience multiple limitations in different seasons, and the expression of these multiple limitations in the spatial distribution of vegetation is complex [*Boisvenue and Running*, 2006]. Over large scales landscapes may transition from energy- to water- limited conditions, with changes in climate and topography providing first order controls on vegetation [*Churkina and Running*, 1998]. Thus, the application of these ideas to a specific location requires a detailed interrogation of the processes driving vegetation behavior at a particular site, and modification of estimations and models to account for multiple, and potentially confounding processes.

2.1.3. Whole catchment scales

The ability to close the water balance and thus to obtain spatially lumped water balance data at catchment scales allows the examination of two separate but important features of catchments. Firstly, these data can be used to empirically verify the importance of vegetation cover as a control on the water balance. Secondly, by examining trends in the properties of the water balance as driven by different climatic, topographic or ecological properties, we can obtain emergent signatures of hydrological behavior across environmental gradients in space or time.

Vegetation controls on catchment water balance: A vast body of empirical evidence supports the importance of vegetation for water balance. This evidence includes paired catchment studies [*Brown et al.*, 2005], observations of change in water balance associated with shrub encroachment [*Wilcox and Huang*, 2010], tree mortality [*Guardiola-Claramonte et al.*, 2010], deforestation [*Cramer and Hobbs*, 2002; *Hatton et al.*, 2003] or afforestation [*Farley et al.*, 2005], and suggests that both the mean water balance and its variability are related to vegetation [*Peel et al.*, 2002]. Symmetries in the patterns of mean annual water balance between catchments (spatial variation) and inter-annual variability within individual catchments (temporal variation) are suggestive of patterns of acclimation and adaptation of vegetation [*Brooks et al.*, 2010b]. Broad patterns in the presence and function of vegetation have been elucidated at regional - global scales. *Zhang et al.* [2001] demonstrated that total evapotranspiration in 250 catchments was explained by the vegetation type (forest versus grasses) and the aridity index. *Donohue et al.* [2010] showed that incorporating observations of vegetation LAI improved predictions of inter-annual variability of streamflow in catchments on the order of 300 - 3000 km^2 in scale. Primary production has been shown to globally scale as a saturating function with climatic humidity [*Huxman et al.*, 2004], while total woody vegetation cover tends to saturate at 100% at precipitation values of 600-1000mm across African savannah ecosystems [*Sankaran et al.*, 2005]. Actual evapotranspiration and water deficit were shown to correlate strongly to plant functional type in the Sierra Nevada [*Stephenson*, 1998]. Near-linear increases in fractional vegetation cover and function with measures of water availability, prior to saturation at some point where water is no longer limiting, seems to be a general phenomenon.

Variation of water balance with environmental gradients: The catchment scale water balance may be parsimoniously modeled by assuming that long-term ET depends on climatic averages, vegetation and soil conditions [*Budyko*, 1974]. At less than geologic timescales, soil and vegetation may be reasonably assumed to depend on average precipitation (P) and energy (represented as potential evapotranspiration PE [*Dooge*, 1992]). Under these circumstances dimensional analysis yields [*Fu*, 1981; *Yang et al.*, 2008]:

$$\frac{AE}{PE} = \phi\left(\frac{P}{PE}\right) \tag{1}$$

Equation 1 is known as the Budyko hypothesis [*Budyko*, 1974], and offers an initial framework for examining the sensitivity of catchment water balance to mean climate and vegetation conditions. *Milly* [1994] showed that measured values of plant-available water holding capacity (driven by e.g. rooting depth) approximately maximized evapotranspiration (minimizing runoff) for given climatic conditions, suggesting that the rooting depth of plants reflects ecologically optimized responses to the relative timing and magnitude of water and energy supplies.

Within individual catchments, the temporal variability in water balance appears to be buffered by the role of natural vegetation. This buffering was first proposed by *Horton* [1933] who observed that in a forested river basin in Delaware, North-East USA, the ratio between vaporization (evaporation plus transpiration) and catchment wetting (difference between precipitation and quick flow) defined as the Horton index, H [*Troch et al.*, 2009] was remarkably constant from year to year, despite the large inter-annual variability of growing-season precipitation. This result was confirmed by *Troch et al.* [2009] based on analysis of a further 92 catchments across the United States. Horton hypothesized that *"the natural vegetation of a region tends to develop to such an extent that it can utilize the largest possible proportion of the available soil moisture supplied by infiltration"* (p. 456).

In practice, H as a water balance metric can usefully reflect both topography and ecology. *Voepel et al.* [2010] (this issue) analyzed the spatial controls on H in over 400 catchments across the conterminous USA, and found that climate, catchment slope and catchment elevation explain $\approx 90\%$ of the variability in observed mean H. Given that H is the ratio of vaporization versus subsurface water availability to plants, we can consider this index as the climate (aridity index) filtered through the landscape. Slope and elevation control the annual amount of precipitation that can be retained sufficiently long in the catchment for plant water uptake. *Voepel et al.* [2010] also showed that the mean H was the best predictor of spatial variation in vegetation cover (measured as NDVI). The strong covariation between topography, ecology and H is suggestive of the co-evolution of and tight coupling between geomorphic, hydrological and ecological features of catchments.

Although the links between catchment water balance and vegetation distribution can be demonstrated empirically, as in *Voepel et al.* [2010] and *Brooks et al.* [2010b] , mechanistically accounting for the role of vegetation at these scales remains challenging. *Zanardo et al.* [2010] (this issue) used a simple bucket model to derive the probability density function of the Horton Index for a set of 431 catchments with $> 70\%$ natural vegetation cover. The mean of H was well predicted by this approach, allowing a good understanding of inter-catchment differences to emerge. Inter-annual variability of individual catchments was poorly represented, presumably in part because the dynamic response of vegetation to sub-annual climatic variability was not accounted for. Unfortunately, mechanisms underlying such intra-annual vegetation response are best understood at patch scales, and translating this behavior to larger scales is not straightforward. *Brooks et al.* [2010b] showed that vegetation response to climate variability was strongly influenced by vegetation type: agricultural, grasslands or forests, and it is unsurprising that a single lumped model fails to capture these different responses. Despite the broad trends in vegetation fractional cover at large scales [*Sankaran et al.*, 2005], such bulk trends disguise fine-scale spatial patterning within catchments as well as intra-annual variation, both of which may be dramatic (see Figure 3). Again, scaling relationships in vegetation mediated water partitioning from patch to catchment scales, and their response to temporal variation in climatic drivers, are needed for hydrological prediction.

Thompson et al. [2010b] found that predicting catchment scale H from patch-scale observations of vegetation-driven water partitioning was confounded by lack of knowledge about hydrological connections and vegetation properties throughout the catchment. In particular, *Thompson et al.* [2010b] compared estimates of a local Horton Index H_L derived from eddy correlation measurements at small scales with H determined from whole catchment scale rainfall-runoff data for 5 sites where this could be reliably estimated from 30 year data records (1961-1990, see Figure 4). The H index was computed for each water year at these sites and averaged. These data assume that in the mean $dS/dt << Q$ and V, a reasonable assumption on 30 year timescales. At these five sites the mean values of H_L underestimated the mean H by 25% and displayed three times the inter-annual variability (as measured by the CV) of H. One site displayed $H_L > 1$ for some years, indicating that evapotranspiration exceeded rainfall and fingerprinting the role of a water subsidy to this site. The systematic underestimation of H by H_L is likely a reflection of the siting requirements for using eddy correlation, in addition to the inability to account for fast runoff generation processes at patch scales.

In summary, the scale gap between our detailed process knowledge about vegetation and water balance partitioning (patch scales) and evidence of its bulk effect on hydrology (catchment scales) continues to confound prediction of water balance and hydrological variations. Relationships between these scales are likely to be nonlinear, reflecting the presence of connections between patches, resulting in the generation of subsidies which may or may not be organized around the catchment topographic network. Several studies suggest that the spatial variation in vegetation fractional cover, species distributions or even physiological responses may reflect optimality principles, potentially resulting in a covariation between vegetation fractional cover and water availability. In the next section we will focus on the specific case where subsidies are organized around the catchment topographic network. Using a simple network model we explore whether a two-way coupling between water availability, vegetation cover and vegetation water uptake can generate spatial scale-dependence in water balance and vegetation cover. Should scale-dependence arise it may form an initial basis for a coupled scaling theory between water balance and vegetation distribution.

3. A simple model of water balance and vegetation coupling on a hierarchical flowpath network

3.1. Model formulation

In this section we present a simple network water balance model. The model has two key features which create the potential for non-trivial spatial organization: i) the network defines a potential energy gradient and thus a direction of water accumulation, and (ii) vegetation cover and transpiration are treated as being co-dependent, allowing the patterns of vegetation organization and water balance along the imposed network structure to arise naturally along the network. The water balance partitioning model used in here is a modification of that developed by *L'Vovich* [1979]. The original model partitions rainfall into three components: vaporization V, equivalent to ET, the rapid runoff response Q_S which may be taken as consisting of overland flow , subsurface stormflow and interflow, and the slow runoff response Q_U, which approximates baseflow. Partitioning is treated as the outcome of competing demands for water in the catchment , e.g., between subsurface drainage and evapotranspiration, or between infiltration and overland flow: rainfall is firstly partitioned into wetting $W = Q_U + V$, and Q_S, and the wetting fraction is then partitioned between Q_U and V (see Figure 2). For example, *Ponce and Shetty* [1995a] described the partitioning in terms of assumed functional forms with associated coefficients that determine the potential for wetting W_P and vaporization V_P, and the thresholds needed to generate runoff ($= \lambda_{Q_S}\ W_P$ and $= \lambda_{Q_U}\ V_P$). In this model the Ponce and Shetty formulation is extended to allow an explicit treatment of vegetation, and investigation of water balance partitioning along a network. Note that this model has been developed primarily as a way of exploring the hypotheses outlined in qualitative terms in the preceding literature review. While it offers a framework for the future development of predictive models, the current version aims to capture relevant processes in a minimal way, and is not intended for immediate application to a specific catchment.

Figure 2A illustrates the network structure applied in the model, which is assumed (for simplicity) to be a simple bifurcating network. The 'network' here is phenomenological in nature and should be thought of as representing the connectivity of all flow paths in the catchment, and not solely the channel network. The different process controls on water balance that apply on hillslopes, in the riparian zone and within the channel network are not explicitly resolved, and left for future research. The water balance equation for any link in the network at any level in the hierarchy is:

$$\frac{dS}{dt} = W + \sum Q_{U_s} - Q_U - V \tag{2}$$

where S is the local storage (a lumped term incorporating both saturated and unsaturated stores), W is the wetting due to rainfall, $\sum Q_{U_s}$ is the subsidy from links located immediately upstream of the local link, V is the local vaporization, and Q_U is discharge from the local link, which provides a water subsidy to the downstream link. In a bifurcating network, as used here, each link contributes Q_U to one downstream link and receives it from the two up-gradient links. For simplicity, we solve the model at steady state, neglecting the dynamics of Q_S or transients in the storage dynamics, giving:

$$Q_U = \sum Q_{U_s} + W - V \tag{3}$$

The steady-state water balance may be solved iteratively on the network by imposing a no flux boundary condition at the exterior links (corresponding to the condition at the catchment divide) so that $Q_{U_s} = 0$, and propagating the subsidy term Q_U down gradient. W is externally prescribed for the whole network, and the subsidy $\sum Q_{U_s}$ is generated from the upstream links, leaving 2 unknowns in the water balance: Q_U and V. Constitutive relations for Q_U and V are needed to close the system of equations. The flow and vaporization are treated as functions of the storage S in the link:

$$V = V_{max} B \times \begin{cases} \dfrac{S}{S_m} & 0 < S < S_m \\ 1 & S \geq S_m \end{cases} \tag{4}$$

$$Q_U = k_U S \tag{5}$$

We approximate vaporization V as transpiration, neglecting bare soil evaporation and interception as a first order assumption. V has an upper limit given by the product of the fractional cover of perennial vegetation, B ($0 < B < 1$) and a maximum specific transpiration rate, V_{max}, set by atmospheric demand. Neglecting evaporative fluxes in this way slightly exaggerates the dependence of B on V, but does not substantially alter model predictions. We allow water stress to limit transpiration when storage S falls below a threshold value S_m. Under water-stressed conditions (i.e. when $S < S_m$), transpiration scales linearly with the fraction S/Sm. Similarly, we express Q_U as a linear function of S, which is often considered as a reasonable representation of the slow component of discharge [*Palmroth et al.*, 2010]. The drainage parameter k_U is best interpreted as arising from the combination of local topographic slope and soil properties.

To complete the specification of the governing equations, we relate the fractional vegetation cover B to vaporization V at each link. This coupling represents the control of water availability for vaporization on carbon assimilation [*Sankaran et al.*, 2005; *Huxman et al.*, 2004]:

$$B = \frac{V}{V + V_B} \tag{6}$$

Here V_B is a half-saturation parameter determining the water availability at which canopies close (lower for water tolerant species e.g. C4 grasses, or under strongly light limited conditions e.g. at high latitudes).

Equations 3 to 6 form a closed set of equations linking water balance and vegetation cover. W is the main climatic driver, and is externally specified. Following non-dimensionalization of these equations, three dimensionless parameters can be identified as controlling the dynamic behavior of the model: the aridity index $R = V_{max}/W$; an index of the drainage competitiveness, $D = k_U S_m/V_{max}$; and an index of the vegetation adjustment to climate $G = V_B/V_{max}$. The Horton index at any point is defined as: $H_L = V/W$.

In order to implement the model on a network, a further non-dimensional parameter β (where $0 < \beta < 1$) must be defined to control the network structure. A network with N links is generated by starting from the outlet and moving to the next confluence.

At a confluence the remaining links are divided into two parts containing $\beta(N-1)$, and $(1-\beta)(N-1)$ parts, each assigned to one upstream branch of the confluence. This process is repeated recursively until the links are exhausted, generating a deterministic network that ranges from perfectly bifurcating when $\beta = 0.5$, to perfectly feathered (one main-stem surrounded by first-order channels) when $\beta = 0$ or 1. Once the model is considered on a network we can also define a 'locality index' for any given point as $L = \sum Q_{U_s}/W$, representing the relative importance of inputs of drainage from up-gradient.

3.2. Solution of governing equations in a link of the network

At point scales there are three solutions to the system of equations. The first is a trivial solution that arises when vegetation is absent ($B = 0$) and transpiration is zero ($V = 0$). Drainage in this case is simply equal to the sum of the inputs: $Q_U = W + \sum Q_{U_s}$, or in dimensionless terms: $Q_U/W = 1 + L$.

The other solutions correspond to the stressed and unstressed transpiration cases. Stressed transpiration occurs below a threshold water input from wetting and upslope subsidies given by $1 + L < R(1 - G + D)$. In this case the following solutions hold:

$$\frac{Q_U}{W} = \frac{D}{1+D} \cdot (1 + L + G \cdot R) \tag{7}$$

$$\frac{V}{W} = \frac{1 + L - D \cdot G \cdot R}{1+D} \tag{8}$$

$$B = \frac{1 + L - D \cdot G \cdot R}{1 + L + G \cdot R} \tag{9}$$

In the unstressed case the solution is much simpler, and V and B are independent of the subsidy L:

$$\frac{Q_U}{W} = 1 + L - R\,(1-G) \tag{10}$$

$$\frac{V}{W} = R\,(1-G) \tag{11}$$

$$B = 1 - G \tag{12}$$

3.3. Solving the model along the network

The model equations can be solved numerically on the network by iterating the solution to Equations 3 to 6 down-gradient from the exterior links to the outlet. For the special case of a symmetrically bifurcating network (i.e. $\beta = 0.5$) the network model may be solved analytically. In such a network every link of stream order k has two links of order $k-1$ upstream of it, for a total accumulated upstream area of $2^k - 1$. L in a link of order k is twice the value of Q_U/W in links of order $k-1$, i.e. $L = \sum Q_{U_s}/W = 2Q_{U_{k-1}}/W$, generating a geometric series. For water-stressed conditions, this series can be solved to give Q_U, V and B as a function of scale k:

$$\frac{Q_{Uk}}{W} = \frac{1-\left(2\frac{D}{D+1}\right)^k}{1-D} D\,(1+GR) \tag{13}$$

$$\frac{V_k}{W} = \frac{\left(2\frac{D}{D+1}\right)^k (GR+1) - DGR - 1}{D-1} \tag{14}$$

$$B_k = 1 - \frac{(D-1)GR}{\left(\left(2\frac{D}{D+1}\right)^k - 1\right)(GR+1)} \tag{15}$$

The ‘catchment’ Horton index H at scale k, is determined by the ratio of mean vaporization over all up-gradient links to the wetting. This is simply one minus the ratio of the drainage Q_{Uk}, normalized by the up-gradient area $(2^k - 1)$ and the wetting W:

$$H_k = 1 - \frac{Q_{U_k}}{W(2^k-1)} = 1 - (GR+1)\left(\frac{\left(\frac{2D}{D+1}\right)^k - 1}{2^k - 1}\right)\frac{D}{D-1} \tag{16}$$

Expressions 13 to 16 are only valid under water stressed conditions where V is explicitly dependent on ΣU_S and consequently the network structure. The patterns that arise from this model are explored in the next section.

3.4. Vegetation and water balance patterns along the network

The network model generates patterns of increasing vegetation cover (B) and vegetation water use (expressed by the catchment Horton index H) in the down-gradient direction. Examples of such patterns are shown in Figure 5 (model parameters are given in the caption) which compares model output at each catchment scale to that obtained in the absence of the subsidy, and thus isolating the effects of the subsidy on catchment water balance. Figure 5 (A) shows a histogram of up-gradient contributing areas of a range of sizes, (B) shows the vegetation cover B, both in terms of its local value (computed numerically and analytically using Equation 15) and its spatial average over the up-gradient area, and (C) shows the local and catchment Horton index (V / W) computed using the numerical model and the analytical solution in Equations 14 and 16.

This example illustrates characteristic patterns driven by the subsidy of water down-gradient. The local value of the Horton index in the external links in this case is quite low at 0.5, indicating that only 50% of W is used locally for vaporization, and the rest is passed down the network. Vegetation at this point is also relatively low, at $B = 0.5$, and is in the water stressed regime. In the case shown in Figure 5, these small order links comprise most of the catchment area. Further down the network, B increases as the subsidy effects increase water availability. Storage S also increases down-gradient, reducing water stress and increasing V, leading to a rapid increase in the local Horton index. The catchment Horton index also increases and approaches 1. In the higher-order links ($k > 4$), the increased storage due to the up-gradient subsidy leads to a transition to unstressed transpiration, and local values of B and V stabilize.

Generalizing from the cases in Figure 5 it can be shown that if the drainage efficiency is low ($D < 1-G$) and the system is sufficiently arid ($R > 1/(1-D-G)$), the subsidy effect slowly increases down-gradient, asymptotically approaching a maximum value where the wetting and subsidy balance the increased vaporization due to the expanded vegetation cover. Otherwise, in wetter or more rapidly draining conditions, the system eventually transitions to a locally unstressed condition. By definition, the flow in unstressed conditions must exceed the flow at the moisture threshold. That is, at the threshold scale k_t, the equality Q_U/W, $Q_U/W = D \cdot R$ holds, allowing k_t to be defined for $\beta = 0.5$ as:

$$k_t = \frac{\log\left(\frac{R(D+G-1)+1}{GR+1}\right)}{\log\left(\frac{2D}{D+1}\right)} \tag{17}$$

The importance of the spatial scale dependence in vegetation is illustrated in Figure 5C which shows that if B were spatially uniform and determined only by the available rainfall, then the spatial dependence of H at both the local and the catchment scales is greatly reduced. A greater proportion of the system would operates under well-watered conditions (i.e. k_t is reduced). The smaller value of H suggests the intriguing possibility that without the capacity for vegetation to organize, the catchment operates ‘sub-optimally’, in the sense that less of the available water is utilized by vegetation to enable carbon fixation.

These patterns have clear implications for the relationship between catchment and point-scale water balance patterns. There is a large difference between the value of Horton index in the unsubsidized exterior links and the value at the catchment outlet. We refer to this difference as ΔH and investigate it in more detail in the next section. There is an even larger difference between the values of the local Horton index near the outlet, which are affected by the subsidy, and the values in the exterior links, which are not. This behavior recapitulates the empirical difficulties associated with attempting to relate patch scale observations to catchment level responses (see Figure 4), and suggests a possible rationale for this discrepancy.

3.5. Controls of landscape and vegetation parameters on subsidy-based patterns

The patterns observed over various scales in the previous section are dependent on the parameters of the system, R, D, G, and β. Solving the model numerically over a wide range of parameter values reveals that the subsidy has the greatest effect for arid climates (large R), and intermediate values of drainage efficiency D and vegetation sensitivity G. This is shown in Figure 6, in which contours of ΔH (the difference in H at the network outlet and at the unsubsidized exterior links (c.f. Figure 5 C)) are shown as a function of R, D and G. This behavior can be readily understood as arising from the combination of parameters at which the presence of vegetation is sensitive to local storage. Where G is small or large, the vegetation cover is uniform across the catchment, saturating everywhere for small G ($B \sim 1$) or unable to establish for large G ($B \sim 0$). Similarly, where D is small, slow drainage favors vaporization, generating large H independently of the vegetation organization. Large D favors drainage, so V and H are small everywhere. For intermediate values of these parameters the vegetation can spatially organize and alter water balance. This 'maximum organization in intermediate environments' is qualitatively reflected in the images of US pre-colonization vegetation cover in Figure 1, where the imprint of hydrological organization on vegetation pattern is most obvious in the Mid-West where forest cover transitions to grassland, driven in part by climatic factors.

Three regimes of model behavior can be identified in the ΔH plots in Figure 6. Firstly, for low D and high G, the catchment system is globally unstressed. In these circumstances subsidy effects do not alter the behavior of V and thus ΔH is zero. Secondly, for low G and low D, subsidy effects are not strong enough to alleviate water stress at any scale. Outside of these regions, H and the controls on V are both sensitive to the down-gradient subsidy. The boundaries of these regions are indicated by dashed lines in Figure 6. Although we have focused on the case with $\beta = 0.5$ in order to capitalize on the analytical results available in that case, the results presented are broadly representative of other bifurcating networks. An approximately 30-fold variation in the length of the main stem (as β deviates from ~ 0.5 to ~ 1 or ~ 0) results in variations in the peak values of ΔH of only $\sim 10\%$.

3.6. Effects on climate sensitivity of water balance

The model allows us to investigate the suggestion made by *Troch et al.* [2009] that variability in H_k is damped by the dynamic response of vegetation to available water. This phenomenon was investigated at a whole-catchment level in the context of the L'vovich-Ponce and Shetty water balance model [*L'Vovich*, 1979; *Ponce and Shetty*, 1995a, b] by *Sivapalan et al.* [2010], and *Harman et al.* [2010] expanded that approach to investigate the sensitivity of the water balance to variations in the precipitation. In the network scaling model the mutual dependence of V and B describes a plausible response of vegetation to climate, and can provide insight into how the properties of the landscape determine the sensitivity of the water balance to climate.

We can quantify this sensitivity with the derivative of H_K with respect to the aridity index R. In the analytical case this is obtained by noting that:

$$\frac{dH_k}{dR} = \frac{dH_k}{dV_{max}} \frac{dV_{max}}{dR} \tag{18}$$

From the definition of R, the second term on the right hand side is simply W. The first term can be obtained by differentiating Equation 16, giving finally:

$$\frac{dH_k}{dR} = \left(G + \frac{1}{R}\right) \frac{D}{(D+1)} \left(\frac{D + 1 + \left(\frac{2D}{D+1}\right)^k (D(k-1) - k - 1)}{(D-1)^2 \, (2^k - 1)} \right) \tag{19}$$

The interpretation of this climate sensitivity is slightly different from the inter-annual variation explored by *Troch et al.* [2009]; *Sivapalan et al.* [2010] and *Harman et al.* [2010] in that it can be applied only over timescales long enough that the transient dynamics associated with vegetation self-organization have decayed and a steady state can again be assumed. The sign of the sensitivity is consistent with H_k having a positive relationship to aridity [*Troch et al.*, 2009]. Note that G and $1/R$ simply amplify the effects of scale k and drainage D, so that where G is small (that is, vegetation cover is able to saturate when water is available) and R is large (the maximum vaporization rate is much larger than the available water) the sensitivity of the water balance to R is damped, since the vegetation is able to respond dynamically to changes in available water. This is broadly in accordance with the suggestions of *Troch et al.* [2009]. The relationship suggests a close link between the effects of scale and lateral flows on the water balance sensitivity. Dividing the above equation by $(G + 1/R)$ isolates the effects of D and k. The resulting values of $(\frac{dH_k}{dR})/(G + 1/R)$ from this analytical model, (valid for the stressed condition) and for the numerical model (including both stressed and unstressed cases), are shown in

Figure 7. Numerical results are shown for the subsidized case in a network with $\beta = 0.5$ and $k = 5$, and for the unsubsidized case (i.e. $k = 1$).

The sensitivity of H to climate is greatest for intermediate values of D. For the unsubsidized case ($k = 1$) $(\frac{dH_k}{dR})/(G+1/R)$ reduces to $D/(D+1)^2$, which is maximized for $D = 1$. The maximum sensitivity to climate for intermediate D arises due to the dominance of topographic and soil factors in determining partitioning when $D \gg 1$ and $D \ll 1$. In the former case, drainage is so efficient that vaporization is negligible, and thus insensitive to climate. In the latter, drainage is highly inefficient compared to vaporization, and so vaporization dominates the water-balance regardless of R. It is only when the vegetation controls on vaporization can compete with drainage - i.e. $D \approx 1$ that a change in R translates to a significant change in the water balance. In the subsidized case ($k > 1$) the maximum sensitivity arises for $D > 1$. This reflects the increase in vegetation cover downgradient due to the accumulation of drainage. Thus when $D > 1$ (drainage tends to dominate) an increase in R (towards a more arid climate) produces a comparatively larger increase in V because the downstream vegetation uses the lateral subsidy more efficiently to sustain transpiration.

The sensitivities captured in the analytical results are swamped, however, by the effects of transitions to alternative transpiration behavior (stressed versus unstressed conditions) along the network. These transitions cause the apparently erratic behavior of the unsubsidized case. As D increases, the subsidy to links at the downstream end of the network provides sufficient water that they become unstressed. In unstressed conditions V/W scales directly with R (Equation 11) and so sensitivity to variations in R becomes 1 for these parts of the network, and the sensitivity of the whole network jumps up. As D

increases further, links at the upstream end of the network drain so efficiently that they cannot sustain vegetation, and transpiration drops to zero. Consequently they become insensitive to variations in climate. The number of links where these thresholds are crossed increases with D, leading to the complex behavior observed in Figure 7. The precise values of D at which the thresholds are crossed depends on the values of G and R, and the structure of the network. The effects of the transition are amplified in the given example by the symmetry of the network used here, as the switching of either threshold induced by a change in D occurs synchronously at all links of a given order. In a more realistic network these transitions would be less abrupt.

3.7. Model Interpretation

This model aimed to test the hypothesis that a convergent network that allowed the accumulation of excess water, coupled with a two-directional feedback between vegetation and vaporization, would generate spatial organization of vegetation and of catchment water balance properties. Indeed, this simple model generated spatial scale-dependence in hydrological and ecological state variables and also in higher order metrics such as the Horton Index. Three features of the model results are promising from the point of view of improving our understanding of spatial scale-dependence in catchments. The first is that the combination of lateral fluxes of water with a vegetation-vaporization feedback leads to interdependence between the spatial organization of vegetation and hydrological partitioning. Although this model is far too simplistic to conclude that observations of vegetation spatial distribution are sufficient to infer local hydrological states, it suggests that as more complex and robust representations of plant-water feedbacks are accounted for, observations of vegetation may provide a way to improve predictions of scale-dependence of water balance. Second, these effects are most significant in intermediate environments, where assumptions about the primacy of vertical water fluxes between the atmosphere and land surface must give way to a more nuanced understanding of the controls on the partitioning between vertical and lateral fluxes. Thirdly, we have developed a basic theory that incorporates the vegetation-vaporization feedback for a perfectly bifurcating network, and shown that it exhibits the expected scale-dependence.

Four dimensionless numbers dictated the sensitivity of the response. While R (aridity) and β (network bifurcation parameter) are observable at catchment scales, the drainage competitiveness parameter D and the vegetation sensitive parameter G reflect relationships between slope, evapotranspiration dynamics, and the adaptations and acclimations of vegetation communities. Intriguingly, the locality index L has strong affinities to the topographic wetness index utilized in TOPMODEL. The strength of TOPMODEL is its ability to relate local measures of wetness to global properties of the catchment (at least in some cases - see *Grayson et al.* [1997] and *Western et al.* [1999] for counterexamples). The modeling approach suggests that it might be possible to define similar local - global relationships for other aspects of the water balance.

We recognize that the model presented here is simplistic, and that only broad key conclusions can be drawn from it. These conclusions — that self organization driven by lateral subsidies resulted in strong spatial scale-dependence of both vegetation and water balance — motivate us to pursue refined investigations of the processes represented in this simple model. Extending the model framework to assist the analysis of real catchments requires several key alterations, including explicit partitioning of evapotranspiration into bare soil evaporation and transpiration (recently shown by *Kochendorfer and Ramirez* [2010] to be primarily dictated by soil type in the Great Plains region of the USA); separating hillslope from channel processes; applying the model during transient conditions rather than solely at steady state; and allowing runoff generation at a point to respond to variable soil and topographic features. We have attempted to address the major shortcomings in the modeling approach as we develop a broader research agenda in the following section.

4. Key research challenges and questions

The challenge of relating the theoretical advances in understanding of point and patch scale ecohydrology to catchment scales represents a frontier in ecohydrological science: one which explicitly addresses the spatial connections between water and plants, and which offers the potential to use these connections to develop important insights into water balance partitioning through space. Although the modeling work presented above is rudimentary compared to this goal, it highlights that there are several key features which influence the emergence of spatial scale-dependence. These features are broadly related to the dimensionless numbers defined above, and form the basis for the discussion below. The goal of future research in each of these areas is the refinement of the catchment water balance framework to the point where it can be used to address three coupled questions: i) how will vegetation respond to changes in hydrological regime, ii) how will hydrological regimes respond to changes in vegetation, and iii) how do these responses result in observable changes in vegetation distribution?

4.1. Drainage - evaporation partitioning

The capacity for non-local subsidies to alter water balance through a feedback to vegetation depends on the partitioning of local water stores between drainage and evapotranspiration fluxes. Physical (slope, soil hydraulic properties, soil depth) and vegetation features (rooting depth, canopy cover and energy balance) are expected to influence this partitioning. However there are several outstanding questions regarding the ability of non-local subsidies to generate vegetation responses. Recent work in the Oregon Cascade Mountains suggests that water routed to rapid runoff rarely mixes with the pools of water used by plants for transpiration [*Brooks et al.*, 2010a], suggesting that these subsidies are largely decoupled from vaporization, at least in these steep, highly connected, well-watered sites. However, the observed differences in runoff behavior in the presence or absence of vegetation in arid sites [*Puigdefabregas et al.*, 1999] suggest that there can be important coupling processes between vegetation and the fast runoff response. Teasing out the feedbacks between vegetation and fast runoff response remains an important challenge. Not all potential subsidy processes are equally well studied, and further attention to the role of riparian zones, floodplains and regional groundwater discharge sites in altering evapotranspiration and catchment-scale water balance is needed to quantify the role of these subsidy processes in generating scale dependence.

4.2. Vegetation Sensitivity

Although we have only considered the fractional cover of perennial vegetation as providing a hydrological feedback, a wide array of biophysical, physiological and ecological factors could (and do) respond to changing water availability. Not only are further observational studies needed to determine these modes of vegetation response to water availability, but improved models of vegetation and ecosystems that can account for these responses are also needed. At these ecosystem scales, a growing body of work uses optimization principles based on maximization of primary production given a constraint of minimizing water (and other) stresses as 'closure models' to constrain predictions about vegetation community responses [*Schymanski et al.*, 2008, 2007; *Franz et al.*, 2010]. Optimality approaches offer an appealing framework for several reasons: they link back to a rich theoretical literature on plant physiology [*Givnish*, 1986], they allow an explicit treatment of co-limiting factors such as energy and nutrient availability [*Hwang et al.*, 2009], and they represent a semi-mechanistic approach to predicting vegetation distributions. Optimization models have been used to link drainage network properties and soil moisture spatial organization to observed vegetation patterns in semi-arid ecosystems [*Caylor et al.*, 2005]; to link shifts in vegetation community on humid hillslopes with shallow groundwater to the spatial locations where evapotranspiration is maximized [*Brolsma and Bierkens*, 2007; *Brolsma et al.*, 2010]; and to explain the organization of species and carbon allocation along a catena in response to downslope redistribution of water and nutrient availability [*Hwang et al.*, 2009]. However, optimality approaches are valid only to the extent that ecosystems are able to optimize their function (i.e. we would expect many systems to behave sub-optimally), and they may also require extension to incorporate other relevant ecological paradigms such as competitive interactions.

4.3. Network Topology

Although the structure of a river network is readily observable via remote sensing, the relevant topology of water flow in a catchment is more complex and bidirectional than implied by the form of the channel network alone. The 'flowpath network' needs to be disaggregated to include an explicit representation of hillslope, riparian and channel processes (missing in the toy model), and the connectivity between these zones. For instance, bidirectional connections, e.g. associated with water fluxes from the channel into the riparian zone and hillslope (either through saturated flow, or in association with flood events) may need to be included. In arid areas, such contributions can determine the width of the riparian zone [*Muneepeerakul et al.*, 2007], where vaporization regularly exceeds rainfall inputs, and $H > 1$ [*Scott et al.*, 2008]. Such bidirectional feedbacks could induce a significant anisotropy in scale-dependence perpendicular to the channel (reflecting hillslope partitioning) versus parallel to the channel (reflecting channel - riparian interactions), and merit further investigation. Completely different topologies arise for different forms of non-local water subsidies, and will be reflected in spatial patterns of vegetation response to water availability. For example, in Figure 1 C a residual pattern in greenness distribution persists in the highly modified Kaskaskia River Basin despite the presence of preferential flow paths (in the form of artificial drainage) between 'hillslopes' and the river channels. In such modified catchments, the relative controls of human-induced land use change on water balance versus the underlying natural structure of the catchment are not known. The extent to which the residual vegetation distribution pattern influences catchment scale water balance depends in part, on the degree to which flow paths traverse or bypass this vegetated riparian zone. Consequently, inference about water balance partitioning based on observations of vegetation patterns must be predicated on an understanding of the connectivity induced by different subsidy processes.

4.4. Climate

Model results suggested that climate (in the form of the aridity index for the catchment) acts as a major control on the emergence of spatial patterning in vegetation or water balance partitioning. This prediction can be tested empirically using aerial photography and measured climatic data, presuming that topographic, vegetation and network properties can be controlled for. Such a data synthesis would allow the predictions of the minimal model to be tested, and would: 1. enable a broad survey of the kinds of vegetation patterns that occur; 2. motivate the development of suitable metrics of such patterning, potentially similar to the width function described by *Caylor et al.* [2005], and 3. allow new signatures of catchment function to be developed (analogous to the Budyko Curve [*Budyko*, 1974], the Abrahams Curve [*Abrahams and Ponczynski*, 1984], or the fractional vegetation cover - rainfall relationships described above [*Sankaran et al.*, 2005]).

4.5. Coevolution

The issues identified above characterize the relationships between the local environmental setting, hydrological context and vegetation response, but ignore the slower dynamics of landscape evolution as influenced by both water availability and vegetation cover [*Rasmussen et al.*, 2010]. Understanding the relationships between vegetation cover, landscape evolution and water status may yield a tractable approach toward developing improved theories of process coupling in catchment systems. In semi-arid catchments in New Mexico, differences in vegetation between north and south facing slopes in association with different soil moisture status posed a dominant control on basin geomorphology [*Yetemen et al.*, 2010]. Landscape evolution models confirm a dominant role of vegetation in water limited climates [*Collins and Bras*, 2010; *Istanbulluoglu and Bras*, 2005], suggesting that vegetation response to climate gradients affects drainage density, relief and channel concavity, reproducing empirical patterns in drainage density with climate [*Abrahams and Ponczynski*, 1984]. *Rasmussen et al.* [2010] used catchment data from different climates and common lithology to demonstrate that energy and mass fluxes associated with primary production and effective precipitation explain substantial variance in catchment structure and function. Their analysis suggests that an integrated framework based on energy and mass transfers across catchment boundaries, constrained by governing principles such as minimum energy expenditure [*Rinaldo et al.*, 1992] or maximum entropy production [*Kleidon et al.*, 2009], may provide a first order approximation of non-linearity and feedbacks in catchment processes that control catchment evolution. There may be considerable scope to unify theories of catchment evolution across many disciplines by continuing to elucidate functional relationships across scales and processes.

5. Conclusions

The research undertaken through the Hydrological Synthesis Project, under the Biosphere - Hydrosphere Interactions theme, examined patterns in catchment water balance (quantified by the Horton Index) and worked at patch scales to investigate the relevant process controls on the water balance. The attempts to connect these issues within the Synthesis Project identified the complexity of scale relationships in water balance within catchments, and highlighted the need for theoretical and empirical research to address this connection. By employing a consistent framework that explicitly considers the role of subsidies and non-local controls on water supply, and implementing this framework in a simple network water balance model, spatial scale-dependence in catchment water balance and vegetation distribution emerge, at least for the case where non-local subsidies are structured around the channel network. The controls on spatial scale-dependence were related to the dimensionless parameters that drive the model: climate (R), soil, plant uptake rates and topography (D), vegetation properties (G) and the topological structure of the network (β). Elaborating on the relationships of each of these factors to catchment organization and consequently to the development of models that capture the spatial scale-dependence of water balance require a new research effort. The specific avenues for future research span hydrology, geomorphology and plant physiology, and suggest that synthesis of knowledge across sites, scales and disciplines will continue to be critical for moving this field forward. The network water balance model presented here is merely a first step in the development of a more comprehensive theories for the emerging field of catchment ecohydrology.

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Table 1. Model parameter definitions

Parameter	**Definition**	**Dimensionless Group**	**Definition**
B	Vegetation cover	$R = V_{max}/W$	Aridity
V_B	Half saturation of vegetation cover	$D = k_U \cdot S_m/V_{max}$	Drainage competition
V	Transpiration	$G = V_B/V_{max}$	Vegetation adjustment
V_{max}	Maximum transpiration rate	$L = \Sigma Q_{U_S}/W$	Nonlocal contribution
k_U	drainage rate		
S	Storage		
S_m	Storage threshold for V		
ΣQ_{U_S}	Upslope water subsidy		
W	Wetting (local water supply)		
N	Network links		
k	Link 'order'		
k_t	Link order where V becomes unstressed		
β	Network bifurcation parameter		

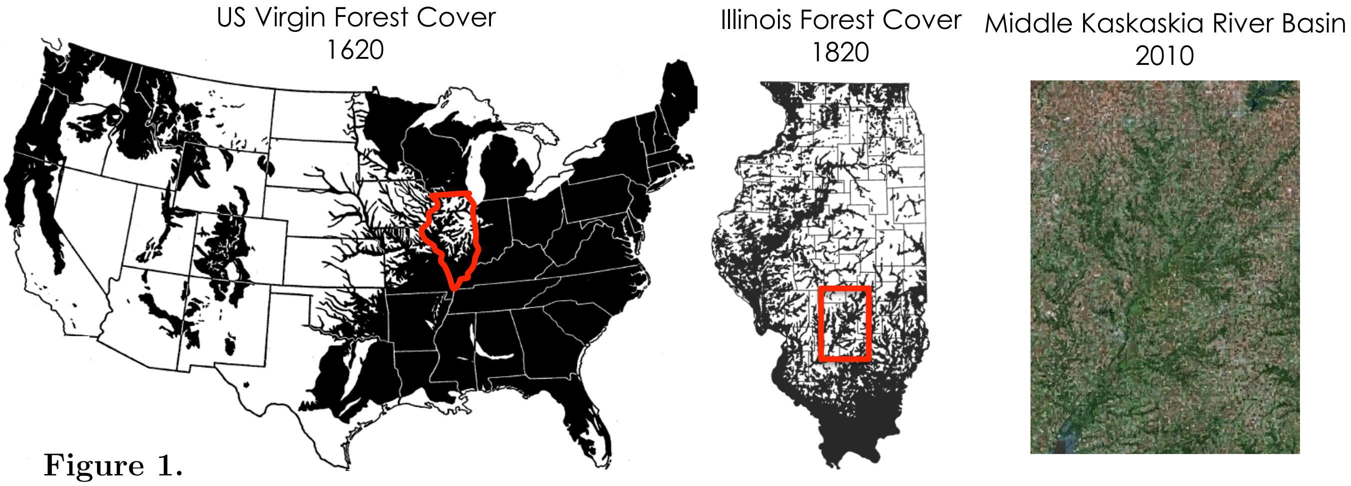

Figure 1.

Virgin forest cover in the US at the time of colonization appears to follow a gradient from complete absence to complete presence across the continent, and was strongly organized by the river network in mesic climates. The self-similarity of this vegetation coverage is reflected in the historical forest cover of the state of Illinois. Interestingly, despite the high level of clearing and land disturbance in Illinois, contemporary patterns also preserve the remnants of this spatial pattern, although the degree to which this reflects water availability, the suitability of riverine land for agriculture or deliberate land management practices is unclear. Images sourced from *Greeley* [1925], *Iverson* [1991] and Google Earth (USDA Farm Service Imagery, ©2010 Digital Globe, ©2010 Google)

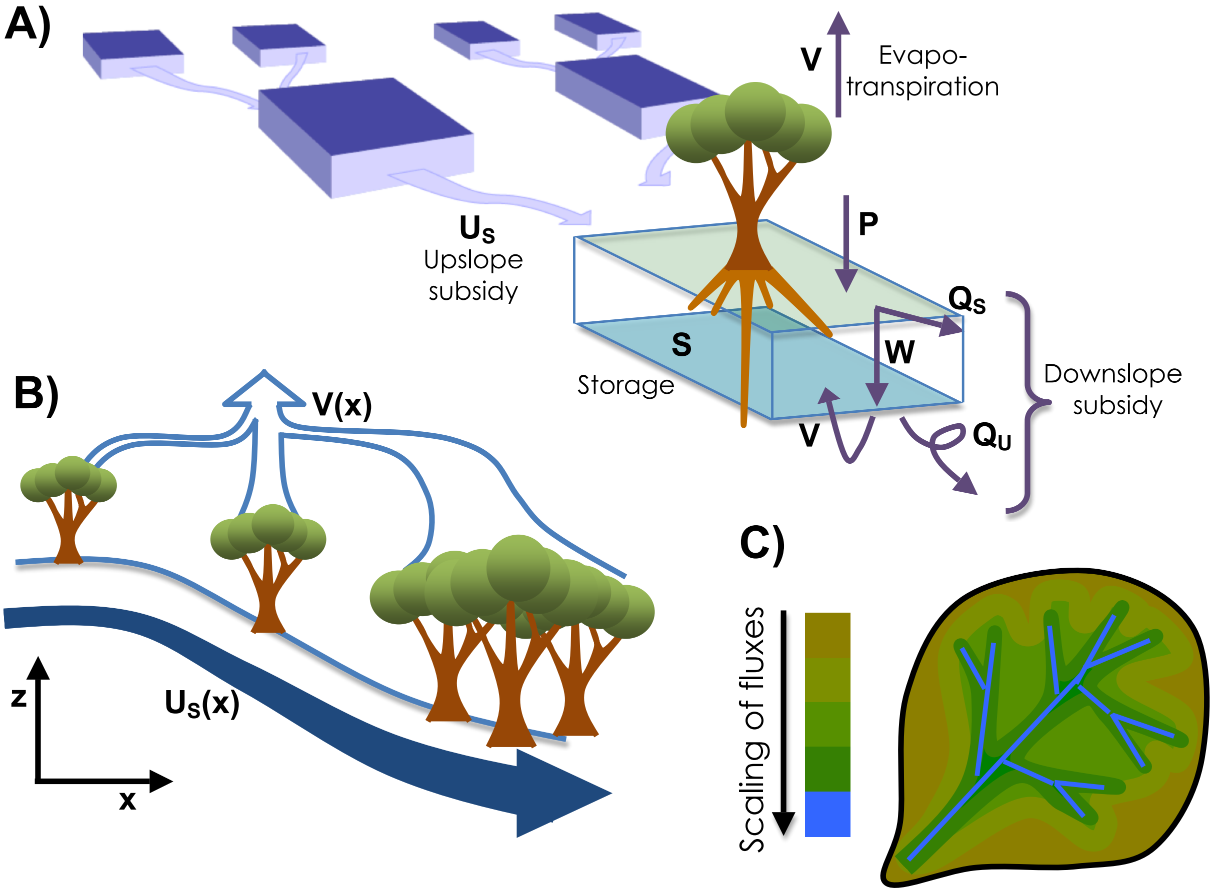

Figure 2. A) Vegetation mediates partitioning at a point. Flow paths in the catchment may be visualized as a network of links (each represented by a 'slab' in this figure). A downslope subsidy U_S provided by the sum of Q_U and Q_S from upslope contributing areas. The subsidy and the local wetting W are partitioned into vaporization V and an additional downslope contribution as mediated by local vegetative cover and properties. B) Along a hillslope, vegetation (potentially cover, vegetation type and vegetation physiology) changes in conjunction with scale-dependence in vaporization V and changes in the lateral subsidy U_S contributed from site to site. In the riparian zones, up-network contributions from the channel provide an additional subsidy. C) Conceptually, this scale-dependence generates non-uniform spatial variations in water fluxes and water balance partitioning in directions both perpendicular and parallel to the network throughout the catchment.

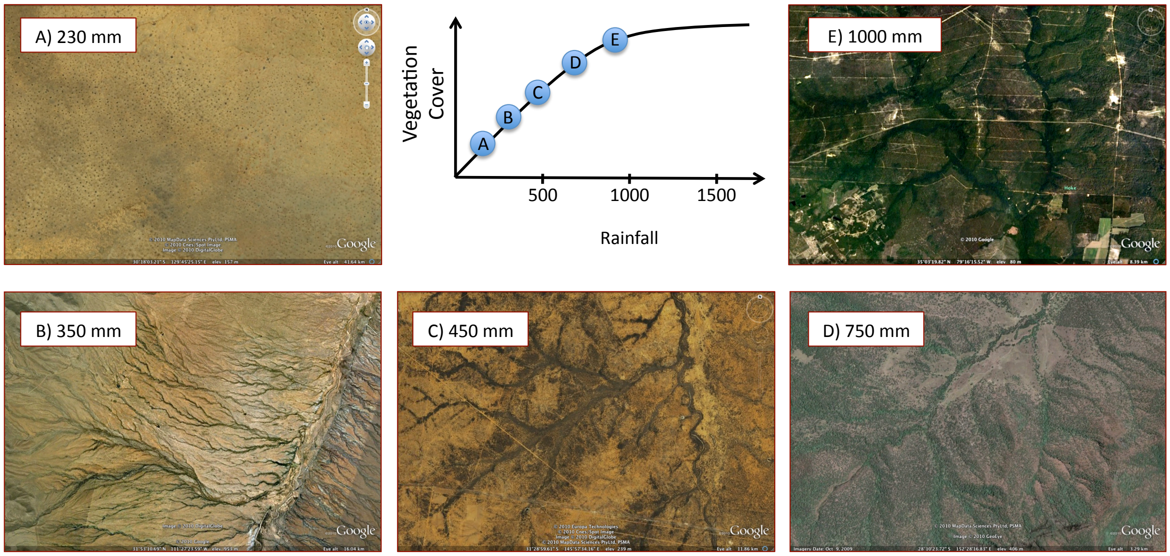

Figure 3. Catchment-scale trends in vegetation indices with rainfall are well known [*Sankaran et al.*, 2005; *Huxman et al.*, 2004], but hide information about spatial organization of vegetation within the catchments. A) Under sufficiently arid conditions almost all rainfall evaporates and hydrological processes are essentially vertical, precluding the formation of spatial patterns associated with hydrological transport; B, C) As rainfall availability increases, perennial vegetation emerges in association with a drainage network; D, E) At higher rainfall rates canopies close and woody vegetation occupies $\sim$ 100% of the catchment. Spatial patterns in vegetation with water availability can still arise: in D) dry sclerophyllous woodland occupies uplands and slopes but rainforest grows in the drainage lines. In E) xeric long-leaf pine savannas grow on the uplands and denser broadleaf forests grow near the stream channels. Images from Google Earth: A) Forrest Station, Western Australia, $30^{\circ}18'03.21''\ S$, $129^{\circ}45'25.15''\ E$. ©2010 MapData Sciences PtyLtd, PSMA, ©Cnew/Spot Image, Image ©2010 DigitalGlobe; B) South of Tucson, Arizona, $31^{\circ}53'10.69''\ N, 111^{\circ}27'23.59''\ W$. Image ©2010 DigitalGlobe ©Google. C) East of Cobar, New South Wales, $31^{\circ}28'59.61''\ S$, $145^{\circ}57'34.16''\ E$. ©Europa Technologies ©Cnes/Spot Image, Image ©2010 DigitalGlobe, ©2010 MapData Science PtyLtd, PSMA. D) Near Emu Vale, Queensland, $28^{\circ}10'23.72''\ S, 152^{\circ}28'16.83''\ E$. ©2010 MapData Sciences PtyLtd, PSMA. Image ©2010 GeoEye. E) Camp Lejeune North Carolina, $35^{\circ}03'19.82''\ N$, $79^{\circ}16'15.52''\ W$. ©2010 Google

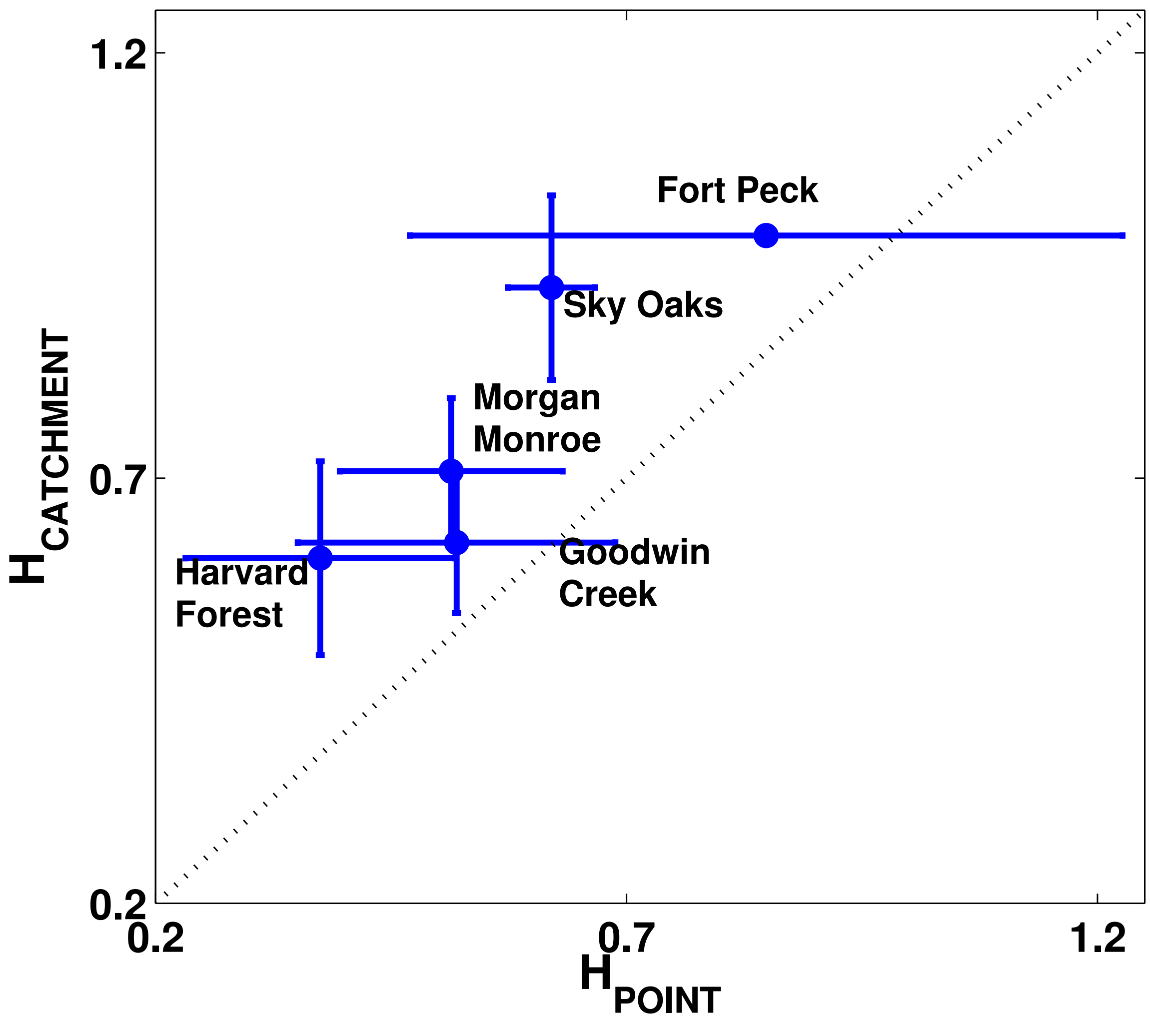

Figure 4. Comparison of point and catchment based estimates of *H* for Sky Oaks (CA), Morgan Monroe (IN), Harvard Forest (MA), Fort Peck (MT) and Goodwin Creek (MS) Ameriflux sites. Dashed line shows the 1:1 line.

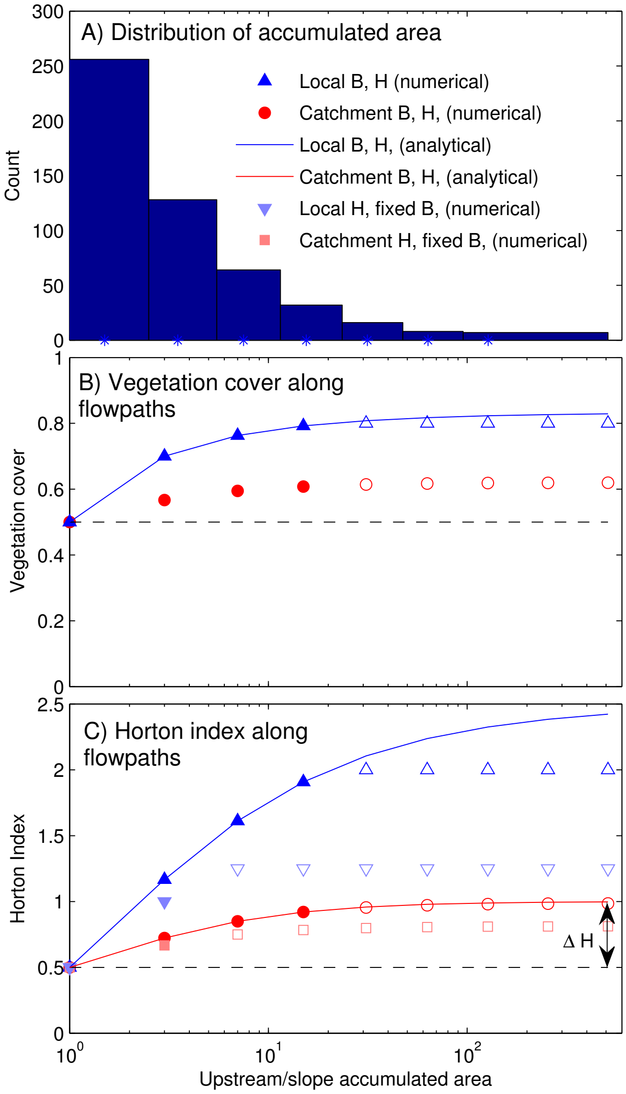

Figure 5. Model output for a system with $N = 511$ links, and $\beta = 0.5$, $R = 2.5$ (a dry system), $D = 1.5$ (Q_0/V_{max}), and $G = 0.2$ (V_B/V_{max}). (A) The proportion of the area with up-gradient contributing areas of different amounts (from 256 external links with area 1 to a single link with area 511 at the outlet), (B) vegetation index B, locally and averaged over the accumulated areas, as a function of accumulated area (closed symbols: water limited, open symbols: energy limited), and (C) Horton index for the accumulated areas (total V / total W) as a function of the accumulated area along the flowpath leading to each link in the system

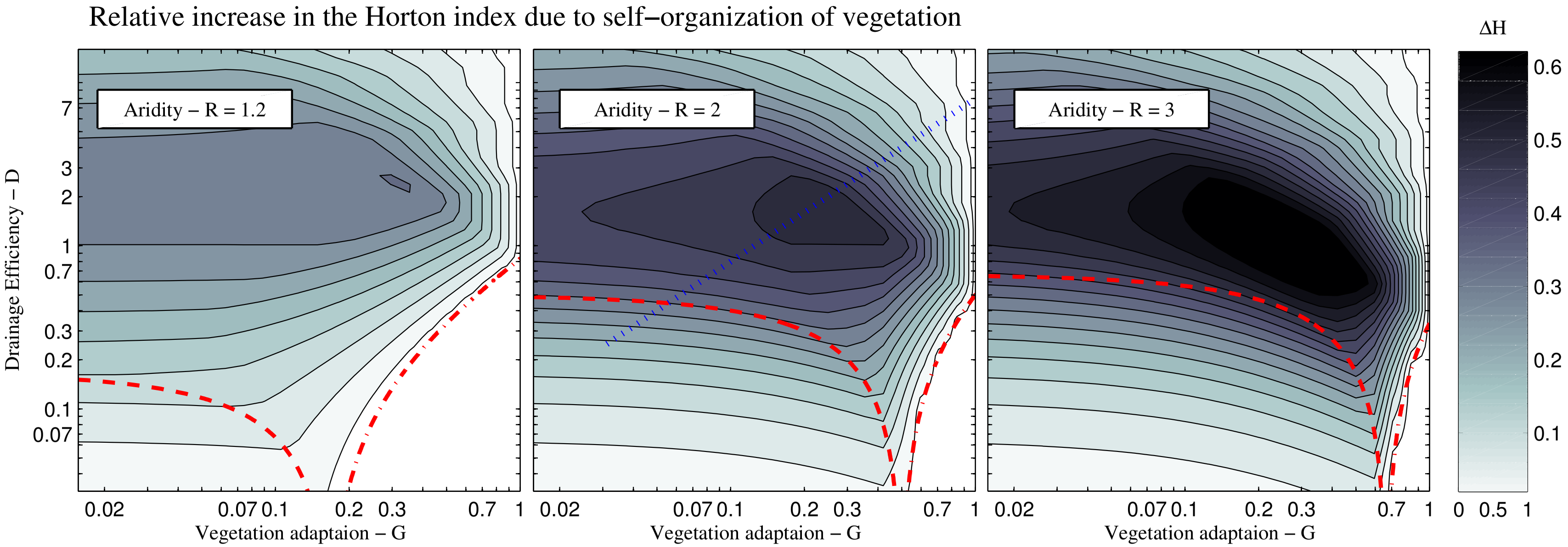

Figure 6. Contours of the difference in Horton index H (calculated at the system outlet) between the case with self-organized vegetation and the case with uniform vegetation, as a function of the three dimensionless ratios that determine the dynamics.

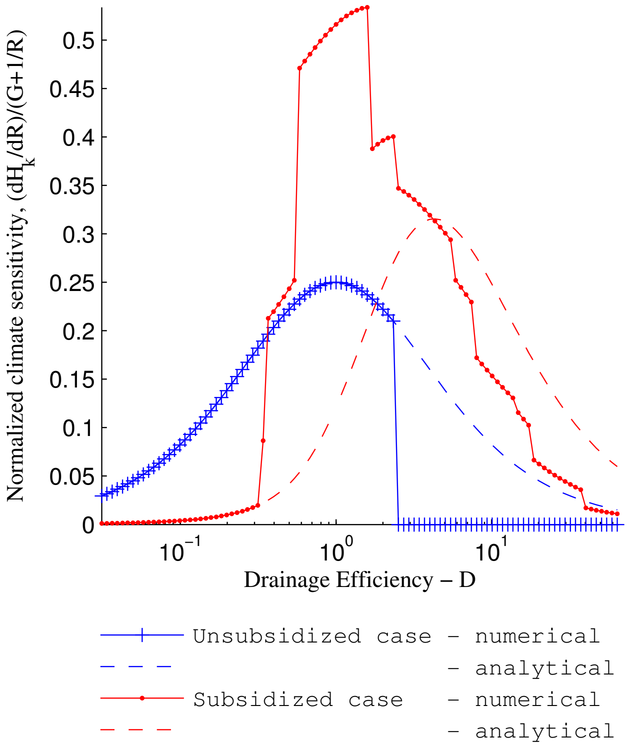

Figure 7. Sensitivity of the Horton Index to changes in aridity as a function of the drainage efficiency D and catchment scale k. The sensitivity is normalized by vegetation and climate properties to isolate the topographic controls (see Equation 18). Analytical solutions apply to the water stressed transpiration regime and indicate that water balance is most sensitive to climate for intermediate values of the drainage sensitivity ratio (D) at point scales, and that the subsidy down-network shifts this peak sensitivity to higher D at the watershed scale. Numerical solutions include the effects of discrete transitions between stressed and un-stressed transpiration regimes, resulting in multiple thresholds in the sensitivity response.