Climate and vegetation water use efficiency at catchment scales

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Effects of Climate Variability on Water Balance Dynamics: Role of Vegetation

Global change is affecting the hydrologic response of landscapes in various ways. Understanding and predicting these effects on the water cycle are becoming increasingly critical (Jackson et al., 2001), but to date, there has been little progress in generating mechanistic relationships between climate, land use and hydrologic partitioning that can be broadly applied. Projected changes in surface temperature and precipitation dynamics will undoubtedly alter the runoff regime (Barnett et al., 2005) as well as runoff extremes (Milly et al., 2002; Dai et al., 2004). The sensitivity of annual stream flow (runoff) to changes in temperature and precipitation has been investigated empirically as well as theoretically (Arnell, 1996). Runoff sensitivity to climate change derived from the observational record has limited predictive capacity in light of non-stationarity of interdependent hydroclimatic variables and landscape features in a changing environment (Milly et al., 2008). Water balance models (Schaake, 1990; Dooge, 1992) usually consider the landscape to be invariant and their application to specific river basins relies on observations to calibrate the model parameters (Wagener, 2007).

Both climate and land use are altering the landscape with concomitant changes in ecosystem structure and function (Walther et al., 2002) and regional hydrological cycles (Breshears et al., 2005). Although the hydrologic impacts of land use change imposed by humans have received considerable attention by hydrologists (e.g. Hurkmans et al., 2009), the impacts of natural large-scale vegetation shifts as a consequence of climate change are unclear (Allen and Breshears, 1998). Vegetation shifts are an important climate-ecosystem-hydrology feedback through their alteration of carbon, water and energy exchanges at the land surface (Adams et al., 2009). Although recent ecohydrological studies have focussed on understanding interactions between hydroclimatic variables and ecosystems response (e.g. Rodriguez-Iturbe and Porporato, 2004), as well as the effects of ecosystem structure on local-to-regional hydroclimate (e.g. Rinehart et al., 2008; Veatch et al., 2009), we lack a comprehensive theory of how vegetation will respond to changes in the water and energy balance of a region.

Over short timescales, vegetation can respond adaptively to variations in climatic factors. Vegetation productivity, measured as net carbon uptake by the landscape or estimated from patterns of above-ground net primary production (ANPP), and growing-season actual evapotranspiration are strongly related (Webb et al., 1986). Since actual evapotranspiration typically is the largest component of many ecosystem water balances (Zhang et al., 2001), the inter-annual variability of catchment hydrologic response should be strongly related to ecosystem function and productivity. Thus, understanding vegetation response to inter-annual variability of climate and water availability should be central in any attempt to predict hydrologic change.
The nature of this response at the catchment scale depends on the physiological traits of the collection of organisms inhabiting the catchment, including their interactions with each other (such as through competition for water). Over the long term, the differing ability of species to respond adaptively to short-term variability of resources in a resource-limited environment may create selection pressures that drive shifts in the species composition. Huxman et al. (2004) showed that while average rain-use efficiency (RUE; defined as the ratio of ANPP over annual precipitation) decreases across biomes as mean annual precipitation increases, the RUE at individual sites converges to a common value (similar to that of arid ecosystems) during the driest years. Within individual biomes, however, both the strength and direction of the relationship between annual precipitation and RUE vary tremendously (Knapp and Smith, 2001). A possible explanation for these observations is that historical drought provides a productivity set-point defined by the mortality thresholds of dominant vegetation, while in wetter years, productivity is not limited by water, but by some other resource (e.g. temperature, radiation and nutrients).

One of the avenues to explore vegetation adaptation to climate variability and the resultant impact on water balance dynamics is to evaluate inter-regional and inter-annual variability of both water availability and vegetation productivity. Here, we investigate the effects of growing-season water availability on hydrological partitioning at the catchment scale across different ecoregions. We re-introduce an index, suggested by Horton (1933), relating estimates of actual evapotranspiration to estimates of catchment wetting (L’vovich, 1979) as a measure of catchment-scale vegetation water use. Specifically, we ask the question: Is inter-annual variability in hydrologic partitioning and catchment water balance across a range of ecosystem types and spatial scales consistent with the hypothesis that vegetation becomes more efficient in its water use as water availability decreases?

**Catchment Annual Water Balance: The Horton Index**

In 1933, Robert E. Horton published his now famous article on ‘The Role of Infiltration on the Hydrologic Cycle’ (Horton, 1933). Although mostly remembered for Horton’s in-depth discussion of the different factors affecting the infiltration capacity of natural and cultivated soils, this article has a much broader scope and discusses the role of catchment wetting through infiltration in the entire hydrologic cycle. The capacity of catchments to store infiltrated water, as a function of soil type, and evaporate it in return, controlled by the vegetation, plays a central role in Horton’s discussion of inter-annual variability of the water balance. For instance, he presents the growing-season water balance components of the West Branch of the Delaware River at Hancock and Hale Eddy, NY, from 1905 to 1929 (Horton, 1933, Table 3, p. 455). Besides listing total precipitation and stream flow, he also computes infiltration excess runoff and baseflow (by means of a baseflow separation method he develops in the article), as well as the ratio between actual evapotranspiration (precipitation minus stream flow) and catchment wetting (precipitation minus infiltration excess runoff). He observed that this ratio (from here on referred to as the Horton index, $H$) is remarkably constant from year to year (mean of $H = 0.78$ with standard deviation of 0.06), despite the large inter-annual variability of growing-season precipitation (minimum of 406 mm, maximum of 812 mm). Since the Delaware River was still largely covered with natural forest vegetation during the first decades of the 20th century, he 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).

Motivated by Horton’s (1933) stated hypothesis, we expand the analysis to a larger number of catchments and examine the inter-annual variability of the water balance across a range of climates. But first, let us re-examine the Horton index in terms of modern hydrology. In Horton’s days, runoff generation was thought to be solely related to the infiltration capacity of the soils (due in large part to Horton’s own work!). Now, we know there are many ways in which precipitation is quickly released from the landscape to the channel network (Beven, 2006). Therefore, the Horton index can alternatively be defined as follows:

$$H = \frac{V}{W}$$  \hspace{1cm} (1)

where $V$ is water vaporization through soil evaporation, interception and plant transpiration, and $W$ is catchment wetting (water available for vaporization), both calculated for the growing season. At the catchment scale, $V$ and $W$ are most easily computed from observed growing-season precipitation ($P$) and stream flow ($R$). $V$ can be estimated as $P - R$, but this will represent a lower bound of the actual evapotranspiration, since we neglect soil water storage depletion during the growing season, as well as storage carry-over from the dormant into the growing season. Thus, $H$ estimated with Equation (1) should be considered as an estimate of the lower bound of vegetation water use during the growing season. The computation of $W$ requires the separation of stream flow into baseflow ($U$) and storm runoff ($S$), which leads to $W = P - S$. The wetting ($W$) is thus defined as the sum of baseflow ($U$) and vaporization ($V$). Obviously, in regions with very limited available energy, most precipitation will leave the catchment as stream flow, leaving vaporization close to zero, and hence $H \equiv 0$. On the contrary, in water-limited environments (arid and semiarid catchments), total stream flow will be made up...
mostly of storm runoff \((R \cong S)\) and be less in volume than precipitation; thus \(H \cong 1\). In catchments with very limited storage capacity, \(P \cong R \cong S\) and thus \(H\) is undefined \((0/0)\). In humid catchments, \(R > S\), so we expect \(H < 1\).

We expect \(H\) to be constant \((\sim 1)\) in semi-arid environments where ecosystems sensitivity to annual precipitation is maximal (Huxman et al., 2004), such that more available water leads directly to higher ANPP and higher evapotranspiration (Scanlon et al., 2005). However, \(H\) should be low and more variable in more humid climates, where more precipitation during the growing season may not lead to increased evapotranspiration and vegetation productivity if other factors are limiting (e.g. Schimel et al., 1997). Moreover, Huxman’s et al. (2004) research suggests that when mesic vegetation experiences water limitations during drought conditions, it uses the available water more efficiently, similar to vegetation in semi-arid regions.

Given the previous observations, we investigate the variability of the Horton index between catchments on the basis of differences of climate, but also between different years in the same catchment. In other words, we analyze the between-catchment and between-year variability of the annual water balance to understand how vegetation communities are adapted to short-term climate variability to better understand how they may shift in response to longer-term climate change. More specifically, we postulate that (1) if the vegetation in a catchment ecosystem develops, as postulated by Horton, to use the maximum fraction of available water, given the constraints imposed by the limiting resource, then the \(H\) index should be relatively constant irrespective of inter-annual climate variability; and (2) if vegetation uses water more efficiently during drought, as postulated by Huxman, then the \(H\) index should tend towards unity in all catchments in the driest years.

Variability of Annual Water Balance:
Between-Catchments and Between-Years

The model parameter estimation experiment (MOPEX) data set (http://www.nws.noaa.gov/oh/mopex) was used to select 89 watersheds with minimal snow storage so that the effect of winter-to-spring water storage carry-over can be neglected. The majority of the catchments are located in the southeastern United States, but some catchments were selected in California, Oregon, and Washington (Figure S1 and Table S1 in Supporting Information), resulting in a wide range of humidity indices \(P/PE\), mean annual precipitation \(vs\) mean annual potential evapotranspiration; Budyko, 1974) from 0.25 to 2.5. Drainage areas vary between 80 and 10 328 km². Potential evapotranspiration climatology is provided in the MOPEX database and taken from National Oceanic and Atmospheric Administration’s free water evaporation atlas (Farnsworth et al., 1982).

An initial screening using 33 catchments demonstrated that the Horton index was not strongly sensitive to the method of baseflow separation (Figure S2 in Supporting Information); consequently, we continue the rest of our analysis using the physically based method of Huyck et al. (2005). Thirty years (1961–1990) of growing-season daily stream flow and precipitation data were analyzed for each basin. The growing season was defined to begin on May 1st and end on October 31st. Although actual start and end dates may vary between catchments and years, initial sensitivity analysis (Figure S3 in Supporting Information) suggests that these dates capture most of the vegetation activity during each year in the selected catchments and provide a consistent objective basis for our multi-year comparison.

Figure 1 shows the mean Horton index and its standard deviation as a function of the climatologic humidity index, for the 89 catchments. The semi-arid catchments \((0.25 < P/PE < 1.0)\) all have mean Horton indices close to 1, reflecting the ecosystems’ ability to respond efficiently to inter-annual variability in water availability. The variability of the Horton index in semi-arid climates is generally small \((<0.05)\), although some catchments exhibit larger variability. As the humidity index increases across catchments, the mean Horton index decreases while its variability tends to increase. This suggests that vegetation in energy-limited climates uses water less efficiently than vegetation in water-limited climates. A regression line through the data in Figure 1a has a linear trend with slope of \(-0.12\) and intercept of 1.02 (not shown). Our analysis further shows that the standard deviation of the Horton index is less than 0.06 for about 50% of the catchments analyzed, while in about 90% of the cases, the standard deviation is less than 0.10. This provides support for Horton’s observation of a constant Horton index in the Delaware River, and although the observed variability in our MOPEX catchments often exceeds the one suggested in Horton (1933), the variability is notably small considering the large number of catchments in our study.

Next, we examine the inter-annual variability of the Horton index. Figure 2a shows how the Horton index varies with seasonal humidity index (growing-season precipitation divided by the climatologic potential evapotranspiration during the growing season) for three catchments in Virginia, and Figure 2b shows the same information against annual humidity index (annual precipitation divided by climatological annual potential evapotranspiration). These results illustrate that the Horton index is related to growing-season precipitation (contrary to Horton’s assumption), and that the dependence of the Horton index to annual precipitation is more pronounced (steeper slopes of linear regression lines; the average value of these slopes for all catchments is \(-0.20\)). The stronger relationship with annual humidity index suggests that catchment wetting during the non-growing season

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Figure 1. Between-catchment variability: mean (a) and standard deviation (b) of the Horton index (based on 30 years of data; 1961–1990) as a function of the catchment’s humidity index. A regression line through the data (not shown) has a linear trend with slope of $-0.12$ and intercept of $1.02$.

Figure 2. Inter-annual variability of the Horton index as a function of the seasonal humidity index (a) and the annual humidity index (b) for three catchments in Virginia.

provides a variable water source to vegetation that is subsequently depleted during the spring and summer. Furthermore, when a significant portion of the annual precipitation falls outside the growing season, precipitation may exceed surface soil storage, the vegetation may be inactive when water is available or energy may limit the ability of vegetation to consume the available water and the catchment will release more baseflow. In all cases, we see that when the catchments experience climatologic drought (lowest annual humidity index in 30 years of observations), the Horton index tends to increase towards $1.0$, the value found in semiarid catchments.

Comparing Figures 1a and 2a, we notice a striking symmetry in the variability of the Horton index between-catchments and between-years. In both cases, the Horton index is strongly governed by the humidity index. In the first case (between-catchments), it is a measure of climate variability between regions. In the second case (between-years), it is a measure of the inter-annual climate variability. This suggests that vegetation across different ecoregions adapts in very similar ways to water availability. Note, however, that the average slope of the inter-annual Horton index trend is about twice ($-0.20$) that of the slope of the inter-catchment Horton index trend ($-0.12$).

Implications for Vegetation RUE

Since ANPP is closely related to annual actual evapotranspiration, we can compare the Horton index with catchment-scale vegetation RUE. We used the empirical relationship between ANPP and annual actual evapotranspiration derived for several grassland sites across the United States by Webb et al. (1986):

$$ANPP = 496 - 666e^{-0.0025V}$$

with ANPP in g m$^{-2}$ year$^{-1}$ and V in mm year$^{-1}$. The catchment-scale vegetation RUE is given by the following equation:

$$RUE = \frac{ANPP}{P}$$

with P in mm year$^{-1}$.
where $P$ is the annual precipitation. Figure 3 shows the catchment-scale vegetation RUE versus the inter-annual variability of the Horton index for several MOPEX catchments in Virginia, Kentucky and North Carolina. Obviously, both variables are related through Equation (2), but more important is the observation that the RUE tends towards values reported for semi-arid ecosystems (Huxman et al., 2004, reports a value of 0.42 g m$^{-2}$ yr$^{-1}$) as the Horton index tends towards 1.

These results indicate that the convergence of biomes towards a common maximum RUE across climates leaves a detectable signal in the catchment-scale water balance, and furthermore that this signal is consistent with observations from plot-scale ecological studies. This is an important conclusion, as it may help us to understand the role that vegetation plays in controlling large-scale hydrological partitioning (Donohue et al., 2007) and how hydrological and biogeochemical responses of the landscape may be altered due to global change. Specifically, Horton’s approach refines our estimate of the fraction of precipitation that is actually available to interact with both soil and vegetation processes, providing a mass balance constraint for quantitative models of water, carbon (C) and nitrogen (N) cycles.

Conclusions and Implications for Future Research

In conclusion, this analysis has focussed on the catchment water balance in an attempt to understand the role of vegetation on hydrological partitioning. We have indeed found that inter-annual variability in hydrologic partitioning across a range of ecosystem types and spatial scales seems to be consistent with the hypothesis that vegetation becomes more efficient in its water use as water availability decreases. We have revealed an interesting pattern in the response of vegetation water use to water availability, which suggests similarities in short-term adaptation strategies and long-term selection pressures on vegetation, and that vegetation adapts to changes in climate in similar ways, independent of ecosystem type. Our results further show that when water becomes the limiting factor for vegetation productivity, the catchment-scale vegetation RUE converges to a common maximum value, in agreement with earlier findings at the ecosystem level (Huxman et al., 2004).

Of course, the approach presented here has several limitations and will need to be tested against independent measurements of ecosystem response to inter-annual climate variability. One way to improve the analysis may be to use remotely sensed vegetation characteristics, such as normalized difference vegetation index and enhanced vegetation index, to relate growing-season vegetation activity to water availability in the catchments used in this study. Such information would also provide more accurate start and end dates for the growing season and would allow us to refine Horton’s method for estimating vegetation water use efficiency. Experimental watersheds such as long-term ecological research sites and flux tower data can offer additional opportunities to test our results at smaller spatial scales. To extend the analysis to other catchments (beyond the ones tested here), issues that will need to be considered include the effects of vegetation water use from root zone storage depleting the soil water content during the growing season, storage carry-over from winter into spring in snow-dominated systems, the effect of interception evaporation on the catchment water balance (Savenije, 2004) and data-driven hydrograph separation using stable water isotopic information. These and related issues are being explored in our ongoing research activities.

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