Quantifying regional scale ecosystem response to changes in precipitation: Not all rain is created equal

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[1] Primary productivity and vegetation cover are strongly related to how precipitation is partitioned into surface discharge, storage, and evapotranspiration (ET). Thus, quantifying feedbacks between changes in precipitation and vegetation at regional scales is a critical step toward predicting both carbon balance and water resources as climate and land cover change. We used a catchment-based approach to quantify partitioning of precipitation and compared these hydrologic fluxes to remotely sensed vegetation greenness (NDVI) in 86 U.S. catchments between 2000 and 2008. The fraction of precipitation potentially available to vegetation (catchment wetting; W) ranged from 0.64 to 0.99 demonstrating that up to 36% of precipitation was not available to vegetation. The ratio of ET : W (Horton Index (HI)), ranged from 0.07 to 1.0 demonstrating even greater variability in the fraction of catchment wetting used as ET. Negative slopes between annual Horton Index and maximum annual NDVI values indicated water limitation during dry years in most catchment ecosystems. Not surprisingly, grasslands were more sensitive to drying than forests. However, in nine of the wettest (HI < 0.66) catchment ecosystems, NDVI values increased as HI increased suggesting greater vegetation productivity under drier conditions. Our results demonstrate that catchment-scale hydrologic partitioning provides information on both the fractions of precipitation available to and used by vegetation. Their ratio (HI) identifies shifts between water and energy limitation, and differential sensitivity to drying based on vegetation type within catchment ecosystems. Consequently, catchment-scale partitioning provides useful information for scaling point observations and quantifying regional ecohydrological response to climate or vegetation change.


1. Introduction

[2] Predicting the response of terrestrial ecosystems to changes in precipitation and water availability is one of the greatest challenges associated with climate change [Bates, 2008; Denman et al., 2007; Fang et al., 2005; Huxman et al., 2004; Knapp and Smith, 2001]. In addition to direct effects on water resources, the response of vegetation to changing amounts and patterns in precipitation is expected to play a significant role in determining the magnitude of the terrestrial carbon sink. To date, efforts to address the role of changing precipitation on within-biome productivity have yielded conflicting results. Although primary productivity generally increases across biomes with increasing precipitation [Sala et al., 1988], the response within biomes appears to be variable in all but strongly water limited environments such as arid and semiarid ecosystems [Huxman et al., 2004; Knapp and Smith, 2001]. The uncertainty associated with how changes in precipitation will affect terrestrial ecosystems is a major contributor to the difficulties in predicting current and future regional carbon sinks.

[3] Water availability, together with temperature and nitrogen, is considered to be a primary control on terrestrial productivity at local to global scales [Boisvenue and Running, 2006; Gerten et al., 2008; Schimel et al., 2001; Webb et al., 1983], but translating changes in precipitation into changes in plant available water is not straightforward. Plant available water is related to the amount, timing, and partitioning of precipitation into soil water [Rodriguez-Iturbe, 2000; Sandvig and Phillips, 2006], but data to quantify spatial patterns in plant available water are limited in extent, subject to assumptions about the volume of the subsurface that can be accessed, and notoriously difficult to quantify directly over larger scales [Famiglietti et al., 1999]. Consequently, efforts to evaluate how productivity responds to changes in precipitation typically assume water availability is either directly related to, or varies consistently with, precipitation. These implicit assumptions likely contribute to the different conclusions reached in various studies. For example, remote sensing of vegetation structure combined with biogeochemical modeling suggest that productivity is sensitive to changes in precipitation [Fang et al., 2005; Katul et al., 2007], but long-term observations of field sites rarely exhibit clear trends [Knapp and Smith,
Explanations advanced for these different responses include complex feedbacks between water, carbon, and nutrient cycles [Schimel et al., 2001; Porporato et al., 2003], biome differences in diversity, phenology, and herbivory [Knapp and Smith, 2001], and, perhaps most importantly, the difficulty in estimating the amount of water that is actually available to vegetation over various spatial and temporal scales [Rodriguez-Iiturbe, 2000; Sandvig and Phillips, 2006].

Understanding how precipitation is partitioned into evapotranspiration, storage, and streamflow is a fundamental question in hydrology. From the catchment perspective, hydrologic partitioning is manifested in the various spatial and temporal scales of catchment runoff responses related to climatic forcing and catchment morphological and pedological characteristics [Wagener et al., 2007; Botter et al., 2007]. From a hydrometeorological and ecohydrological perspective, partitioning is represented by the characteristic time scales of evaporation and transpiration, controlled by climate, soil moisture storage, and vegetation dynamics [Rodriguez-Iiturbe et al., 1999; Laio et al., 2001; Porporato et al., 2001; Teuling et al. 2006]. An implicit coupling between catchment research, focused on lateral redistribution and runoff processes, and ecohydrological research, focused on vertical exchanges and vegetation processes, has long been recognized [Horton, 1933], but only relatively recently has the role of vegetation in buffering variability in runoff been demonstrated across multiple catchments [Botter et al., 2008; Troch et al., 2009]. Because runoff response appears to be strongly related to vegetation, these studies suggest that in-turn, catchment-scale hydrologic response can be used to infer how vegetation may respond to changes in climate.

L’vovich [1979] presented an empirical theory for the two-stage partitioning of water at the land surface describing an initial step at estimating plant available water at the scale of catchment-ecosystems. First, incoming precipitation is partitioned into a quick flow component and the rest infiltrates into the soils and wets up the catchments. This wetting component is then further partitioned into bare soil evaporation plus plant transpiration (also referred to as vaporization) and a slow flow component that can be considered base flow. The fraction of vaporization to wetting (termed the Horton Index) [see Troch et al., 2009] reflects the efficiency of catchment vegetation to use plant available water. Sivapalan et al. [2011] verified the ability of the L’vovich theory to predict regional patterns of mean annual water balance among 431 Model Parameter Estimation Experiment (MOPEX) catchments, as well as interannual variability in the individual catchments. Their analysis shows that there exists a close symmetry between spatial (regional) variability of mean annual water balances and general trends of temporal (inter-annual) variability in individual catchments. Given this symmetry in space and time, the L’vovich theory provides a promising framework to evaluate both how plant available water at the catchment scale varies from year to year, and how vegetation responds to this inter-annual variability.

Over 75 years ago, Horton [1933] used a similar approach in evaluating long-term annual water yield of the Delaware River, to postulate 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” Horton [1933, 446–460]. A significant body of modeling and observational research on plant water use and water limitation generally supports Horton’s postulate [Istanbulluoglu and Bras, 2006; Ridolfi et al., 2000; Vivoni et al., 2008; Borgogno et al., 2010], and recently similar patterns have been observed in catchments throughout the conterminous United States [Troch et al., 2009]. These observations suggest that climate forcing of runoff is buffered by vegetation responses to inter-annual variability in water availability during wet and dry years. If Horton’s [1933] inference is correct, variability in catchment water balance should leave a detectable signal in vegetation structure and productivity. Only recently, however, have multiyear records of catchment-scale land use and vegetation structure been available to evaluate this inference.

The objective of this paper is to evaluate vegetation response to variability in precipitation using catchment hydrologic data to uniformly and consistently quantify the relationships between precipitation, plant available water, and evapotranspiration. Specifically, we ask “Is there a detectable response in catchment vegetation to inter-annual variability in catchment-derived estimates of plant water availability?” To evaluate the ability of a catchment-derived index of water availability to capture responses in vegetation, we compared estimates of plant available water from catchment water balance to the Normalized Difference Vegetation Index (NDVI), a remotely sensed index of vegetation structure commonly used to estimate productivity [Running et al., 2004].

2. Methods

Our analysis includes nine years of climate forcing, seasonal maximum NDVI data, and hydrologic partitioning estimates from 86 temperate catchment-ecosystems. Catchments ranged in size from 80 to 10,328 km² and covered a wide range of biomes and ecosystem types identified by the National Land Cover Database [Homer et al., 2004]. All 86 sites were used by Troch and colleagues [Troch et al., 2009] to develop the Horton Index, which is a dimensionless number between 0 and 1 that describes the fraction of catchment wetting used in evapotranspiration. Both estimates of catchment wetting (W) and evapotranspiration (ET) were obtained from catchment surface water discharge

\[ W = P - S. \]  

\[ ET = P - Q. \]

where P is precipitation, Q is the total surface water (stream) discharge, and S is the increase in surface water discharge (alternatively termed “quick flow”) associated with precipitation events. Because most precipitation events result in an increase in surface water discharge, this index explicitly corrects for the amount of water that leaves a catchment ecosystem in response to a precipitation event, and thus is not available for vegetation. Following previous work [Horton, 1933; Troch et al., 2009], we relate ET and W in a term named the Horton Index (HI), defined as

\[ HI = ET / W. \]  

To minimize variability due to seasonal changes in soil water storage, we calculate HI on an annual, water-year
time step, assuming that base flow is proportional to recharge. By relating water use (ET) to available water (W), the HI provides a measure of vegetation water limitation in response to changes in precipitation. Voegel et al. [2011] demonstrated that HI values are significantly related both to climate as well as topographic characteristics and thus represent a competition for W between plant water use (ET) and drainage to base flow.

[10] The MOPEX data set (available at http://www.nws.noaa.gov/oh/mopex) contains hydrometeorological discharge (derived from USGS data, http://www.nwis.usgs.gov), and corresponding land cover data for 438 US catchments covering the period from 1948 to 2003 [Duan et al., 2006]. The primary goal of MOPEX is to develop techniques for the a priori estimation of the parameters used in land surface parameterization schemes of atmospheric and hydrological models. We selected 86 of these catchments for this study, all characterized by minimal seasonal snow cover. We excluded sites with extended seasonal snow cover to minimize the effects of inter-annual variability in both snow accumulation and ablation, which may affect hydrologic partitioning, vegetation response, and remote sensing reflectance. The majority of the catchments are located in the southeastern US, with a few located in California, Oregon, and Washington (Figure 1).

[11] We expanded the data record for these catchments to cover the 2000 to 2008 water years (1 October 1999 through 30 September 2008) to obtain data contemporaneous with remote sensing indices of vegetation. Daily streamflow data were downloaded from the U.S. Geological Survey (USGS) (available at http://waterdata.usgs.gov/nwis/dv/) and Parameter-elevation Regression on Independent Slopes Model (PRISM) data were obtained from the Oregon State University (available at http://www.prism.oregonstate.edu/) [Daly et al., 1994]. The monthly PRISM data at 4 km resolution were spatially averaged to create time series of precipitation and temperature for each catchment. The Hydrologic Index was calculated as P/PET. Monthly potential evapotranspiration (PET) was computed from the monthly average temperature using Hamon’s equation [Hamon, 1961].

[12] Daily streamflow values Q were partitioned into two components: base flow b which represents discharge from the groundwater storage to the stream; and direct runoff f which is a response of streamflow to rainfall and is affected by catchment characteristics and vegetation (Q = b + f). The one parameter recursive filter developed by Lyne and Hollick [1979], Nathan and McMahon [1990], and Arnold and Allen [1999],

\[
b_i = a b_{i-1} + \frac{1-a}{2} (Q_i + Q_{i-1}) \]

\[b_i \leq Q_i,\]  

and two parameter recursive filter developed by Eckhardt [2005],

\[
b_i = \frac{(1 - BFI_{max})a b_{i-1} + (1-a)BFI_{max}Q_i}{1 - aBFI_{max}} \]

\[b_i \leq Q_i,\]  

were used to compute base flow and direct runoff. BFI_{max} is a maximal value of base flow index (the ratio of base flow to total flow) and a is a filter parameter. The value of the filter parameter a was set to 0.925 for both filters and the maximal value of BFI was estimated from the base flow index grid developed by Wolock [2003]. Filters were passed over the streamflow data two times, backward and forward, to obtain more precise estimation of the base flow especially for the beginning of the time series. Daily values were summed to obtain annual streamflow (Q), base flow (B), and direct runoff (S) data which, together with annual precipitation data for each water year, were used to compute the Horton Index based on equations (1)–(3). Similar results presented by Troch et al. [2009] evaluated three base flow separation methods and indicated that inference drawn about hydrologic partitioning and the Horton Index were not highly sensitive to the method of base flow calculation.

[13] Time series of Normalized Difference Vegetation Index (NDVI) for the 86 selected catchments were extracted from NASA’s Moderate Resolution Imaging Spectroradiometer (MODIS) Land Products MOD13A2 distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the USGS Earth Resources Observation and Science (EROS) Center (available https://lpdaac.usgs.gov). MOD13A2 stores NDVI composites every 16 days at the spatial resolution of 1 km [Huete et al., 2002]. Although arguments can be made for different NDVI measures (e.g., mean, maximum, growing season sum), we chose maximum NDVI as a minimally biased method for the wide range of ecosystem types in our catchments. Because individual catchment ecosystems used in this study contain variable mixtures of deciduous and coniferous forests, grassland, agriculture, and other uses, TIN calculations would require multiple, subjective decisions to classify each catchment on a pixel by pixel basis for each year of study. In contrast, maximum NDVI can be objectively determined for each catchment and year. Perhaps most importantly, maximum NDVI typically is closely correlated with Time Integrated NDVI (TIN) [Reed et al., 1994; Jia et al., 2006], but does not require assumptions about growing season length, background NDVI values, and phonological issues associated with diverse ecosystem types [Reed et al., 1994].

[14] Only high-quality, filtered data were used in spatial analysis. This included filtering pixels with cloud cover and the few pixels with slopes steeper than 40% where high slopes may result in overestimating NDVI values. Missing or incomplete data, typically discharge but in a few cases time series of NDVI, precluded the use of some years in some catchments; the final data set contained 643, out of a possible 774, unique catchment-year combinations. All statistical analyses on the resulting data set were performed in JMP 8 statistical package (SAS Corporation, Cary, NC).

3. Results

[15] Mean annual temperature for all sites and all years was 15.4°C (standard deviation (SD) 2.5°C) and mean annual precipitation 1212 mm (SD 353 mm) (Table 1). Mean potential evapotranspiration (PET) was 835 mm (SD 117 mm) and the average Humidity Index (P/PET) was 1.32 (SD 0.29). Of the 643 catchment-year combinations, only 85 (~13%) had a Humidity Index less than or equal to 1.0, of these only three catchments had Humidity Indices less
than or equal to 1.0 in all years. These ratios suggest that water is available in excess of the energy to drive evapotranspiration in most catchments during most years. On an annual basis therefore, vegetation should not be water limited unless energy and water availability are strongly out of phase. Interestingly, the mean catchment-estimated ET value of 795 mm (SD 175 mm) was approximately 95% of mean climatological PET 835 mm (SD 117 mm). Temperature ($r^2 = 1.00$), precipitation ($r^2 = 0.95$), and runoff ($r^2 = 0.96$) during our study period were strongly correlated to values observed during the previous 30 years (Figure 2a, 2b, and 2c). The reasonable agreement between these values suggests that our catchment-based estimates of hydrological partitioning, including the assumption of no significant change in storage are reasonable over annual time scales.

Across all sites and years, the Horton Index averaged 0.76 (SD 0.14) (Table 1), indicating that 76% of catchment wetting ($W$) was used as ET. Values for individual catchments on individual years ranged widely, however, from a low of 7%–100%. $HI$ values generally were lower and more variable in the mountains and higher and less variable at lower elevations (Figure 3a). The mean
value of the maximum annual NDVI value across all catchments and years was 0.82 (SD 0.08) (Table 1). In contrast to the pattern observed in HI values, NDVI values were higher and less variable in mountains and lower and more variable at lower elevations, especially in Texas (Figure 3b). Although our estimated PET and ET values were similar across all sites and years, the humidity index was not a good predictor of ET in individual sites (Figure 4a). In contrast, the humidity index was related to the Horton Index (Figure 4b), presumably because the Horton Index normalizes ET for catchment wetting (W), which is the fraction of that precipitation retained in the catchment and potentially available to ET. Horton Index values converged to a value of 1.0 as Humidity Index decreased, indicating that a larger fraction of plant available water (W) is used as evapotranspiration as catchment-ecosystems become more water limited. In general, the scatter in the relationship decreases as humidity decreases, consistent with observations that vegetation uses water more efficiently as it becomes more limiting.

[17] Time series of NDVI values for three catchments illustrates variability in both the amplitude and seasonality of NDVI arising from differences in phenology associated with vegetation type (Figure 5). Because the majority of our sites contain a mixture of land cover and vegetation types, this variability precluded objective calculation of time integrated NDVI and led us to use maximum annual NDVI. Maximum annual NDVI values increased with precipitation up to ~750 mm yr⁻¹, and then varied randomly around 0.85 (Figure 6a). A plateau in NDVI values is even more apparent when maximum annual values are plotted against the Horton Index (Figure 6b). In general, NDVI values do not begin to decline until the Horton Index approaches 0.95, indicating that most potentially available water (W or catchment wetting) is being used as ET. Considered across all sites, these data demonstrate the ability of catchment vegetation to adapt to local water availability. This pattern initially might suggest that the HI is less able to detect changes in vegetation response to water limitation; however, the strength of the HI is in capturing the interannual variability within catchment ecosystems.

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[19] Within individual catchment ecosystems, the slopes of the regressions relating annual HI values to maximum annual NDVI are consistent with the sensitivity of catchment vegetation to variability in water limitation (Figure 7). Although promising, only 13 of the regressions describing the relationship of HI to maximum annual NDVI had p values less than 0.1, and only 8 had p values less than 0.05. The catchments-ecosystems with statistically significant relationships were distributed over the full range of climate with precipitation values ranging from 869 to 1489 mm and HI values ranging from 0.51 to 0.87.

[20] Cluster analysis of all HI-NDVI slopes identified three distinct, significantly different zones corresponding to thresholds in the Horton Index, or the fraction of available water used by vegetation (Table 2). Of the 86 catchments, eleven exhibited mean annual Horton Index values of less than 0.67, indicating that these ecosystems used less than two-thirds of available water as ET. The majority (N = 55) of catchments had Horton Indices between 0.67 and 0.83, and 20 catchments had values greater than 0.83. A negative relationship between the annual Horton Index and NDVI indicated some degree of water limitation in drier years in 67 of the 75 sites with mean Horton Indices greater than 0.67. In the eight catchment ecosystems with intermediate HI values where NDVI increased as the annual Horton Index increased, land use was dominated by actively managed systems (crops, pasture, and managed open space), which should not be expected to respond as predictably to local climate. Perhaps most surprisingly, NDVI values increased as the annual Horton Index increased in nine of the eleven catchment-ecosystems with the lowest ratio of ET/W (<0.67), suggesting that vegetation productivity
Figure 3. Mean and standard deviation of (a) the Horton Index and (b) maximum annual NDVI values across our study sites.
increased during drier years. These catchments were characterized by greater than 80% forest cover (Table 2) and tended to be located in montane environments (e.g., Cascade Range and Ozark Highlands).

21 At both the lowest and highest Horton Indices the response of vegetation seemed clear, but the majority of sites fall at intermediate HI values. Within catchment-ecosystems with intermediate HI values (Horton Indices between 0.67 and 0.83), we examined the role of land cover in the relationship between the Horton Index and annual maximum NDVI (Figure 8). Among these sites, the slope of the Horton-NDVI line was positively \( r^2 = 0.55, p > 0.001 \) related to the percent forest cover, and negatively \( r^2 = 0.21, p > 0.001 \) related to the percent grassland cover in the catchment. This observation is consistent with the expectation that forest vegetation is less sensitive to water limitation than grassland.

4. Discussion

22 To evaluate how changes in climate, especially precipitation, impact regional scale vegetation dynamics, we combined approaches from catchment hydrology to partition precipitation into catchment wetting (W) and vaporization (ET) with remote sensing methods to estimate ecosystem-scale vegetation response. By explicitly quantifying catchment wetting (W), we focused our analysis on the fraction of precipitation that may directly affect vegetation. Because the fraction of precipitation potentially available to vegetation varies due to both physical catchment characteristics and the intensity and distribution of precipitation [Voepel et al., 2011; S. Zanardo et al., Climatic controls on inter-annual variability of catchment vegetation water-use: a probabilistic approach, submitted to Water Resources Research, 2011], this approach allows us to evaluate both spatial and temporal variability in ecosystem response to climate.

23 Catchment-scale hydrologic partitioning at the annual time step in these 86 catchments yielded results consistent with the findings of Troch et al. [2009] who focused only on partitioning during the growing season. We chose to use annual, rather than growing season data to capture inter-annual variability in catchment wetting associated with winter/spring wet up of soils providing water potentially available to vegetation during the subsequent growing season. Our data has slightly greater variability than Troch et al. [2009], possibly because of the annual time step, but also because of the shorter record length in our study that only includes years with concurrent, high quality NDVI data. A consistent finding among related work is that drier catchments or drier years exhibit both higher and less variable Horton Indices [Horton, 1933; Troch et al., 2009; Voepel et al., 2011]. This direct link to climate forcing is consistent with long-recognized spatial patterns in hydrologic partitioning [Budyko, 1950; L’vovich, 1979] related to climate, but also includes information on landscape-controlled partitioning of plant available water [Thompson et al., 2011; Voepel et al., 2011]. Consistent patterns in both space and time [Sivapalan et al., 2011; C. J. Harman et al., Emergent climate-functional relations in annual water balance: Implications for sensitivity to precipitation change, submitted to Water Resources Research, 2011] suggest that dimensionless ratios, such as the Horton Index obtained from catchment-scale hydrologic partitioning, will be useful in predicting hydrologic response. From a vegetation perspective, because both catchment characteristics and the timing, intensity, and duration of precipitation affect the fraction of rainfall that exits a catchment quickly in response to rainfall events, the HI value represents a dimensionless number that captures both climate and landscape controls on water availability. In particular, because the Horton Index relates ET, which is largely under control of vegetation, to catchment wetting, which is an estimate of plant available water, it is reasonable to expect that changes in this ratio will result from, and be observable in, vegetation as originally postulated by Horton [1933] over 75 years ago.

24 Remote sensing of vegetation provides spatially extensive estimates of vegetation response both to climate forcing and to land cover change. We chose to use a freely available, standard product (MOD13A2 16 day, 1 km NDVI composite) that is widely accepted and either used to develop or closely related to more derived products of productivity or water limitation [Fang et al., 2005; Hicke et al., 2002; Zhou et al., 2003; Newman et al., 2006]. Results similar to those in Figure 6a have led to debates over the use of NDVI to assess vegetation response to changes in precipitation or water availability [Fang et al.,
This study however, presents one of the first comparisons between NDVI and a dimensionless index of hydrologic partitioning that relates water used as ET to water potentially available to vegetation. As such, we compared changes in an index of vegetation greenness to changes in an index of water limitation rather than to an amount or quantity of precipitation.

Overall, the fraction of potentially available water (W) used for evapotranspiration was relatively constant (mean 76%, SD 14%), similar to previous reports [Troch et al., 2009; Horton; 1933]. Catchment ecosystems with the highest mean annual HI values (>0.83) exhibited the greatest sensitivity of NDVI to inter-annual variability in HI (Figures 6b and 7). High HI values at these sites indicate that vegetation is using most of the available water during all years, and consequently any decrease in water availability is more likely to be associated with a decrease in productivity [Huxman et al., 2004; Knapp et al., 2001]. Vegetation reflects water limitation and these sites had the lowest fraction of forest cover and the highest fraction of shrub and grassland (Table 2). Although the importance of water availability is well-established at the plot scale for these drier ecosystems, the HI provides a metric for integrating water limitation at larger spatial scales. For example, comparing HI versus NDVI relationships in catchments with different levels of shrub and grass cover could be used to spatially extrapolate the effects of vegetation change on the coupling of water and carbon cycling [Scott et al., 2006].

Ecosystem-scale water limitation during drier years, evidenced by negative slopes for the regressions between the inter-annual variability in HI values and NDVI (Figure 7 (inset)), was apparent in catchment-ecosystems where 67% to 83% of available water was used for evapotranspiration. Within these sites, the sensitivity of vegetation to water limitation was related to vegetation cover, with forest vegetation less sensitive to drier years (Figure 8, top) and grassland more sensitive (Figure 8, bottom). Plot-scale studies have suggested that woody or forest vegetation is less sensitive to drought than grasslands [Scott et al., 2006], and our results demonstrate that this differential sensitivity is related to, and detectable in, catchment water balance. Although the regressions between vegetation type and response to drying are not strong, they are highly significant (p < 0.001). The ability to detect any relationship is surprising given the mixed land use in all these catchment-ecosystems. For example, these catchments contained an average of 23% agricultural use where productivity and greenness is actively managed and not dependent solely on precipitation. An interesting and likely productive area for future work would be to apply these techniques to catchments with single dominant land use and vegetation type to evaluate vegetation specific response to climate variability. Within these single land use sites, we anticipate stronger statistical relationships between HI and NDVI than found in our multiple land use MOPEX catchments.

The most surprising finding may be the increase in NDVI values associated with an increase in the Horton
catchment water balance, provides estimates of plant available water that are independent of, but related to, direct measurements of soil moisture or hydro meteorological estimates of energy and water balance. These approaches largely have proceeded independently, but changes in climate outside of our observational record [Milly et al., 2008] will require these types of coordinated analyses using data from multiple sources, perspective, and disciplines to infer ecosystem response to changes in climate. For example, ongoing and predicted changes in the amount and especially the intensity of precipitation [Bates, 2008; Groisman et al., 2005] can be expected to affect the partitioning of precipitation, increasing quick runoff, and resulting in a scenario where precipitation increases, but plant available water remains the same or decreases. Consequently, predictions of ecosystem response that do not consider differences in catchment-based partitioning of precipitation may miss both the magnitude and direction of vegetation response.

As both climate and land cover continue to change, the use of catchment-derived HI holds promise for evaluating how climate interacts with the terrestrial ecosystems. More specifically, both ET and W are primarily controlled by climate, but ET is secondarily mediated by vegetation, while W is secondarily mediated by landscape (H. Voepel et al., submitted manuscript, 2011). Therefore, the dimensionless Horton Index (ET/W) provides the ability to compare simultaneously across climates, landscapes, and vegetation types the relative fraction of precipitation that contributes to catchment wetting and potential plant available water and the use of that water by vegetation. Although the physical landscape changes slowly, both climate and vegetation can respond more quickly. For example changes in vegetation type (e.g., shrub encroachment) or physiology (response to rising CO₂) should result in

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**Figure 6.** (a) Maximum annual NDVI as predicted by precipitation for all sites and years demonstrates a rapid increase in NDVI as precipitation increases from 500 to 750 mm yr⁻¹, and reaches a plateau between 750 and 1000 mm yr⁻¹. (b) Maximum annual NDVI as a function of the Horton Index exhibits an even broader plateau followed by a sharp decline at NDVI values above 0.95.

Index at the wettest, or least water limited, sites (Figure 7). Presumably, the increase in NDVI during drier years is associated with the removal of some other limiting factor. None of these sites experience cold consistent winters and all have mean annual temperatures well above 0°C, so it is unlikely that temperature is directly limiting productivity. More likely, the ratio of available energy to water availability may explain these patterns [Milly and Dunne, 2002]. It is possible that vegetation is either directly limited by light during wetter, cloudier years [Saleska, 2007], or that nutrient availability in wet soils may limit productivity during wetter years [Schlesinger, 1997]. Any release from nutrient limitation could be due either to increased mineralization in drier soils, or through decreased solution losses of nutrients as more precipitation is partitioned to evapotranspiration and less to leaching and streamflow.

5. Implications for Ecosystem Response to Changes in Climate

[28] Our observations highlight the usefulness of multiple approaches in addressing how climate change will affect terrestrial ecosystems. The Horton Index, obtained from...
Figure 7. Plot of 86 regression lines showing the relationship between the annual Horton Index and seasonal maximum NDVI for each catchment ecosystem. Average NDVI values do not decline until the Horton index approaches 0.95, or ET approaches 95% of potentially available precipitation. This general pattern is consistent with the expectation that ecosystems maximize productivity or “greenness” for the regional climate. Greenness only decreases under extreme water limitation (as when Horton Values approach 1.0). Inset shows the slope of the individual regression equations for mean $HI$ values less than 0.95. Three $HI$ clusters were identified and are indicated in the inset as follows; $HI < 0.66$ in light gray circles, $0.66 < HI < 0.83$ in dark gray squares, and $HI > 0.83$ in black triangles. Positive slopes indicate an increase in NDVI (and presumably productivity) when the Horton Index increases and catchments become drier; a negative slope indicates that NDVI (and presumably productivity) decreases as Horton Index increases and catchments become drier.

Table 2. Characteristics of the Three Groupings of Catchment-Ecosystems Identified Through Cluster Analysis

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<th>Low $HI$</th>
<th>Moderate $HI$</th>
<th>High $HI$</th>
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<tbody>
<tr>
<td>Number of Catchments</td>
<td>11</td>
<td>55</td>
<td>20</td>
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<tr>
<td>$HI$ Values (Mean, SD)</td>
<td>0.52 (0.11)</td>
<td>0.77 (0.04)</td>
<td>0.90 (0.05)</td>
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<tr>
<td>Max NDVI (Means, SD)</td>
<td>0.86 (0.04)</td>
<td>0.82 (0.05)</td>
<td>0.70 (0.10)</td>
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<th>Vegetation Cover (%) [Homer et al., 2004]</th>
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<td>Forest</td>
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<tr>
<td>Shrub</td>
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<td>Grasslands</td>
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<tr>
<td>Agriculture</td>
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<td>Other</td>
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Dominant Ecoregions [Commission for Environmental Cooperation, 1997]

<table>
<thead>
<tr>
<th>Ozarks 70%</th>
<th>SE US Plains 51%</th>
<th>SE US Plains 45%</th>
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</thead>
<tbody>
<tr>
<td>Marine West Coast Forest 18%</td>
<td>Ozarks 39%</td>
<td>South Central Semi-arid Prairie 33%</td>
</tr>
<tr>
<td>Western Cordillera Forests 8%</td>
<td>Miss. Alluvial and Coastal Plains 4%</td>
<td>Ozarks 11%</td>
</tr>
<tr>
<td>SE US Plains 3%</td>
<td>South Central Semi-arid Prairie 4%</td>
<td>Miss. Alluvial and Coastal Plains 6%</td>
</tr>
</tbody>
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*aThe majority (75) of sites had Horton Indices greater than 0.77; 67 of these exhibited a decrease in max NDVI when Horton Index increased (the others were heavily influenced by agriculture). In general, the higher the Horton Index, the more sensitive NDVI was to dry years (indicated by an increase in $HI$ values) indicating vegetation was sensitive to changes in water availability. In contrast, maximum seasonal NDVI values increased with drying in 9 of the 11 catchments with the $HI$ values < 0.67, suggesting a decrease in water availability increased productivity. Across all sites forest cover decreased and grassland increased as $HI$ values approached 1.0.*
predictable changes in HI and the components of HI. Because landscape changes slowly relative to vegetation, comparisons of HI across catchment ecosystems with similar landscape but varying vegetation and or climate should be useful for identifying both the magnitude and direction of ecosystem response to change.

6. Summary and Conclusions

[31] We demonstrate that differences in hydrologic partitioning associated with climate and landscape control the fraction of precipitation that potentially is available to vegetation, and by accounting for the resulting differences in water availability, we show that the majority of catchment-ecosystems respond to changes in precipitation. Specifically:

[32] 1. A simple model of catchment water balance is related to interannual variability in vegetation response across a range of ecosystem types.

[33] 2. This model identifies a transition between water and energy limitation when comparing across sites. Negative relationships between interannual variability in the Horton Index and annual maximum NDVI indicated water limitation during drier years, even though P/PET ratios were greater than 1 in most sites, and highlighted the importance of hydrologic partitioning in controlling potentially available precipitation. In the wettest catchment ecosystems however, NDVI values increased as Horton Index increased indicating an increase in vegetation greenness under drier conditions and during drier years.

[34] 3. The sensitivity to drying, as described by the slope between HI and annual maximum NDVI was related to vegetation type, with grasslands more sensitive to drying than forests.

[35] We conclude, therefore, that catchment discharge data provides useful information for evaluating and scaling point or 1-D modeling or observational studies to regions. Taken together, these results provide a framework to evaluate both the magnitude and direction of vegetation response to changes in climate, and suggest that resolving the uncertainties associated with quantifying how variability in precipitation will affect ecosystem function rely on improved methods of quantifying the amount of water actually available to vegetation. Given the inherent difficulties in quantifying spatial and temporal variability in soil moisture and plant available water, our approach provides valuable, complementary information on water availability.

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References


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