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Vegetation and topographic influences on the connectivity of shallow groundwater between hillslopes and streams

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ABSTRACT

Little is known about the combined effects of vegetation and topography on hillslope water table dynamics. In forested headwater catchments, complex terrain and vegetation intersect to impose large spatial and temporal variability in the vertical and lateral redistribution of water from hillslopes to streams. Here, we demonstrate, using empirical data from the Northern Rocky Mountains, that vegetation interacts with landscape topography to influence hillslope–riparian–stream hydrologic connectivity. We compared a measured relationship between hillslope contributing area and hydrologic connectivity during the growing season to LiDAR-derived vegetation characteristics and found that two behavioural regimes emerged. Among some hillslopes, hydrologic connectivity decreased as vegetation density increased, demonstrating that growing season hydrologic connectivity is subject to the balance between evapotranspiration and lateral redistribution of soil water. Among other hillslopes, hydrologic connectivity increased as vegetation density increased. For the latter set of hillslopes, hydrologic connectivity cannot be explained by topography and vegetation alone. When we compared joint distributions of vegetation density and modelled solar irradiance between the two regimes as another indicator of evapotranspiration, we found that conditions were generally more favourable for higher transpiration on hillslopes where hydrologic connectivity decreased as vegetation density increased than on hillslopes where the opposite behaviour was observed. Our results demonstrate not only the importance of vegetation heterogeneity for hillslope–riparian–stream connectivity but also the importance of other spatially distributed variables such as energy availability when considering the influence of topography on hydrological processes. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS hillslope; hydrology; vegetation; topography; connectivity; insolation

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INTRODUCTION

Topographic and vegetation influences on the soil water balance

Understanding how topography and vegetation jointly affect hydrological processes in forested watersheds is a continuing challenge in hydrology. Topographic effects on hydrological processes have been studied intensively for several decades leading to conceptual frameworks such as the geomorphic instantaneous unit hydrograph (Shreve, 1969; Rodriguez-Iturbe and Valdes, 1979) and topographic similarity (Beven and Kirkby, 1979; Burt and Butcher, 1985). These conceptual frameworks and much empirical evidence suggest that topographic heterogeneity serves, at least in part, as a template for predicting the behaviour of a range of hydrological responses including soil water redistribution (Western *et al*., 1999), streamflow response (Jencso *et al*., 2009; Jencso and McGlynn, 2011; Nippgen *et al*., 2011) and connectivity between hillslopes and streams (Genereux *et al*., 1993; Chen and Kumar, 2001; Jencso *et al*., 2009; Jencso and McGlynn, 2011). This study provides empirical evidence demonstrating that vegetation, coupled with topography, influences the behaviour of hydrological processes within forested watersheds.

Vegetation is known to influence point, hillslope and watershed scale hydrological processes. Plants alter the soil water balance through processes that include transpiration (Rodriguez-Iturbe, 2000) and interception (Keim *et al*., 2006). These influences propagate through the subsurface and watershed network, especially during the growing season, to affect groundwater recharge (Gribovszki *et al*., 2010) and streamflow (Wondzell *et al*., 2007). Recent work using observations of stream discharge has suggested topographic and vegetative controls on watershed scale

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response times (Nippgen *et al*., 2011) and runoff dynamics (Jencso and McGlynn, 2011). However, little work to date has explored the combined influence of topography and vegetation on water redistribution at the hillslope scale and among hillslopes of differing structure.

To better understand the combined effects of topography and vegetation on hydrologic processes across forested hillslopes, we consider the soil water balance

$$nZ_r \frac{ds}{dt} = I(s,t) - ET(s,t) - L(s,t), \quad (1)$$

where n is the soil porosity, Z_r is the depth of the soil (m), s is the relative soil moisture content (−), t is time (day), $I(s,t)$ is the infiltration rate into the soil ($m\,d^{-1}$), $ET(s,t)$ is the evapotranspiration rate ($m\,d^{-1}$) and $L(s,t)$ is the leakage or deep infiltration rate ($m\,d^{-1}$) (Rodriguez-Iturbe, 2000). Leakage can be decomposed into downward groundwater recharge and lateral flow in the shallow subsurface (Scanlon *et al*., 2005). As Equation (1) demonstrates, hydrological processes associated with runoff generation depend upon soil water content, which is affected by vegetation activity (*ET*). Whenever and wherever *ET* is large relative to *L*, vegetation must be considered along with topography to understand runoff generation in forested watersheds.

Perceptual model of joint vegetation and topographic controls on runoff

Hydrologic connectivity, the continuity of a water table across the hillslope–riparian–stream interface, is an important contributor to runoff generation at the hillslope scale (Sidle *et al*., 2000; Jencso *et al*., 2009). Jencso *et al*. (2009) examined hydrologic connectivity between hillslope, riparian and stream zones (HRS connectivity) in a forested catchment and found a strong positive relationship between hillslope contributing area and frequency of annual HRS connectivity. Their work demonstrates that landscape structure, specifically topographic heterogeneity at the hillslope scale, is an important control on watershed scale hydrological processes.

We seek to extend this understanding of landscape structural controls on hillslope scale hydrological processes to include vegetation as well as topographic variability. Understanding the influence of vegetation on HRS connectivity, particularly during the growing season, is an important step toward representing the watershed as a complex, biophysical system. Here, we examine the combined influence of vegetation and topography on HRS connectivity during the growing season in a forested, mountain watershed to address the following questions: (1) Does the relationship between HRS connectivity and hillslope contributing area differ between the growing season and the entire year? (2) How do vegetation characteristics of a hillslope affect topographic controls on HRS connectivity during the growing season? and (3) Does the spatial distribution of available energy interact with the spatial distribution of vegetation to influence HRS connectivity?

SITE DESCRIPTION

Our study was conducted in the lower Tenderfoot Creek watershed (2280 ha) and in one of its subwatersheds, the Stringer Creek watershed (530 ha), both of which are located in the Tenderfoot Creek Experimental Forest (TCEF) of central Montana (46·55N, 110·54W). The study site is a forested, subalpine ecosystem dominated by lodgepole pine (*Pinus contorta*), topographically limited riparian extents (Jencso *et al*., 2010), dry meadows and isolated stands of spruce and fir (together approximately 9% of watershed) (Emanuel *et al*., 2010). The forested area has been previously described as even-aged, low diversity lodgepole forest (Mincemoyer and Birdsall, 2006). Soils in the riparian and hillslope zones are described as clayey Aquic Cryoboralfs and Typic Cryochrepts, respectively (Holdorf, 1981). The average annual precipitation is 880 mm (Farnes *et al*., 1995; McCaughey, 1996), and the mean annual temperature is 0 °C (Farnes *et al*., 1995). Approximately 70% of the precipitation occurs between November and May as snow, and snowpack accumulation peaks between late March and mid-April (Farnes *et al*., 1995). Snowmelt peaks between mid-April and late-May (Nippgen *et al*., 2011) and results in an annual hydrograph dominated by a relatively large snowmelt runoff event (Figure 2).

METHODS

We delineated 23 hillslopes along Tenderfoot Creek and Stringer Creek using a digital elevation model (DEM) derived from 1 m resolution LiDAR data provided by the National Center for Airborne Laser Mapping (Figure 1). The total upslope accumulated area (UAA) for each hillslope was determined using a triangular multiple flow direction algorithm (MD∞) (Seibert and McGlynn, 2007) applied to a 10 m DEM, which was coarsened from the 1 m bare earth DEM using bilinear interpolation. The MD∞ algorithm allows flow to be distributed among multiple downstream DEM pixels and avoids computational artefacts of single-direction (D8) flow routing (Seibert and McGlynn, 2007). Furthermore, use of the 10 m DEM reduces the confounding effects of microtopography and represents subsurface flow paths more accurately than a 1 m DEM (Jencso *et al*., 2009). The pixels within each hillslope were assigned weighting factors ranging from zero to one using the multiple flow direction weighting

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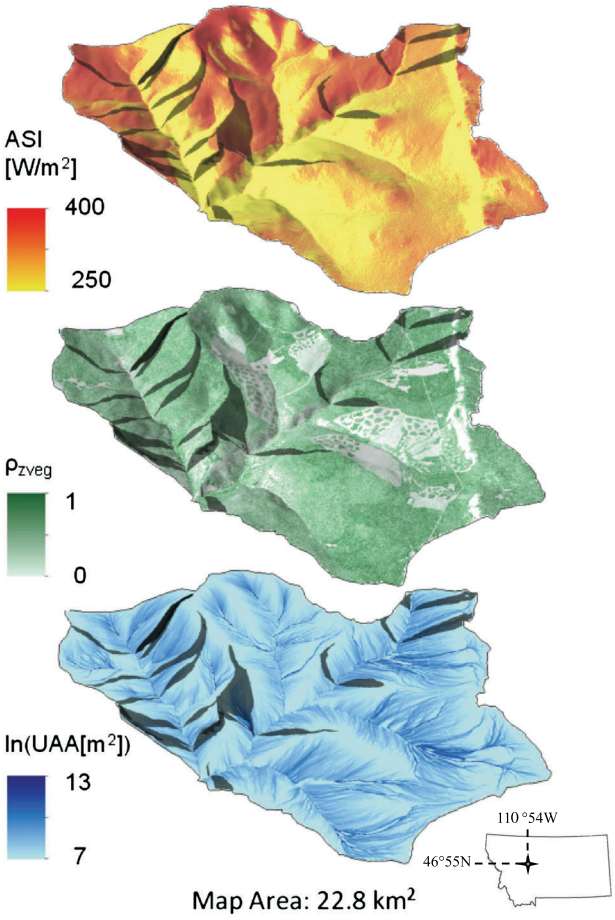

Figure 1. Average solar irradiance, vegetation density (ρ_{zveg}) and upslope accumulated area for the Lower Tenderfoot Creek watershed. The shaded regions of each map show the 23 delineated hillslopes used in this study. The inset shows the location of the field site in Montana, USA.

algorithm of Tarboton and Baker (2008), which estimates the relative proportion of each pixel that contributes to hydrological conditions at the outlet of each hillslope. The resulting weighted grid (WG) was used to assess the relative importance of each hillslope pixel to shallow subsurface runoff at the outlet of each of the 23 hillslopes (Tarboton, 2003). In other words, pixels located close to the stream or along convergent flowpaths are assigned a larger weighting factor than pixels located farther upslope or in divergent landscape positions, and the sum of WG for all pixels in a delineated hillslope equals 1. The WG was used to determine the weighted average values of vegetation and energy metrics for each hillslope, as described in the succeeding text.

We derived spatially explicit vegetation and energy metrics from the LiDAR data. Vegetation height was calculated for each 1 m pixel for the entire study site as the difference between canopy top and bare earth LiDAR returns following Emanuel *et al.* (2010). Vegetation density (ρ_{zveg}) was calculated as the fraction of 1 m pixels in a 4 m area exceeding 2 m in height (Figure 1). This metric omits herbaceous vegetation and small trees and represents the spatial variability of the forest canopy across the field site. Vegetation density provides a general understanding of the spatial variability of *ET* during the growing season because forest canopy transpiration is the dominant growing season water flux at this site (Emanuel *et al.*, 2010).

We used the System for an Automated Geographical Analysis (Böhner *et al.*, 2008) to determine the average solar irradiance (ASI; (Boehner and Antonic, 2009; Wilson and Gallant, 2000)) during the growing season from a LiDAR-derived, bare earth DEM coarsened using bilinear interpolation from 1 m to 4 m to match the resolution of ρ_{zveg} (Figure 1). The ASI provides general information about distribution of available energy across the landscape, and it can be used as a predictor of potential evapotranspiration (Xu and Singh, 2000). Rather than deriving spatially distributed potential evapotranspiration or actual evapotranspiration using available energy and other information about plant and soil conditions (e.g. Priestley and Taylor, 1972), we chose to focus on ASI and ρ_{zveg} as relatively simple environmental factors contributing directly to the spatial variability of *ET* among hillslopes. The ρ_{zveg} and ASI were each multiplied by WG, and the products were summed for each hillslope to determine the weighted average values of each variable for each of the 23 hillslopes considered in this study. Multiplying these variables by WG assumes that all landscape positions (i.e. pixels) within a hillslope may not contribute equally to shallow groundwater connectivity the hillslope base, whereas unweighted averages of ρ_{zveg} and ASI treat all landscape positions (i.e. pixels) as having equal effects on hydrologic conditions at the hillslope base. Because the variables were computed at two different resolutions (10 m for WG and 4 m for ASI and ρ_{zveg}), we used the area-weighted average of WG underlying each 4 m ρ_{zveg} or ASI pixel.

Groundwater elevations were measured by shallow wells installed at the base of each hillslope during the 2007 water year (1 October 2006 through 30 September 2007) as described by Jencso *et al.* (2009). For each of the 24 hillslopes described by Jencso *et al.* (2009), wells were installed at the lower hillslope, toe-slope and riparian landscape positions and completed at the soil–bedrock interface. Water table levels were recorded at 30-min intervals using capacitance-based water level probes (TruTrack, Ltd, Christchurch, NZ). Hillslopes were considered hydrologically connected to the stream whenever saturation was measured in both the hillslope and riparian well, above their bedrock completion depths (Figure 2). For this study, we consider HRS connectivity only during the growing season (SHRS), which extended from approximately 1 May 2007 to 31 August 2007. Annual (Seasonal) HRS connectivity was calculated as the

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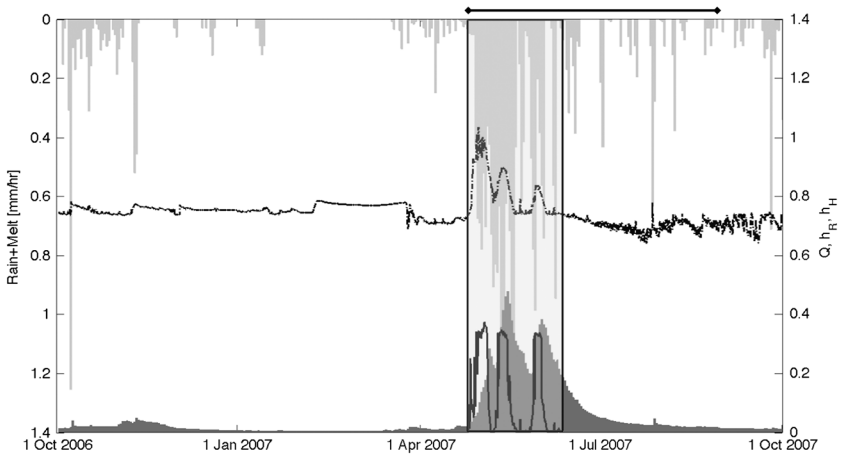

Figure 2. Time series of hydrologic variables for Stringer Creek, a 530 ha watershed in the Tenderfoot Creek Experimental Forest. Water input includes rain plus snowmelt (light grey). Runoff at outlet is shown in mm day^{-1} (Q, dark grey). Shallow groundwater levels are shown for riparian (h_R, broken black line) and hillslope (h_H, solid black line) wells of Stringer Creek Transect 2 East. Units for h_R and h_H are m. The shaded rectangle indicates time periods where hydrologic connectivity occurs, and the black overbar shows the 2007 growing season (1 May 2007–31 August 2007).

fraction of 30-min intervals during the year (growing season) in which a water table was observed in both the hillslope and riparian wells. We eliminated one of the 24 hillslopes from our analyses because of a poorly delineated contributing area and resulting unreliable estimates of hillslope-averaged terrain variables. Our analyses were conducted on the remaining 23 hillslopes.

Jencso *et al*. (2009) found UAA to be the dominant control on HRS connectivity over the entire water year. We used least squares linear regression to test the influence of UAA on SHRS. To determine how vegetation affected this relationship, we compared the residuals of the SHRS versus UAA regression (SHRS') to ρ_{zveg} using Spearman's rank correlation test. We assessed separately the behaviour of hillslopes whose regression residuals were positive (i.e. hillslopes that were hydrologically connected more often than predicted by UAA alone) and hillslopes whose regression residuals were negative (i.e. hillslopes that were hydrologically connected less often than predicted by UAA alone).

To account for uncertainty in the sign of the residuals used to assign each hillslope to a specific behavioural regime, we performed a bootstrap analysis comprising 1000 iterations of 18 hillslopes sampled randomly from 23 total hillslopes in the study (i.e. approximately 75% of hillslopes sampled per iteration). Each iteration included a regression analysis between SHRS and UAA of the 18 randomly sampled hillslopes. For each iteration, we found the average difference between the original prediction of SHRS using UAA from all 23 hillslopes and newly predicted SHRS from the subset of 18 hillslopes, and we used the 2·5% and 97·5% order statistics of the 1000 average difference values to estimate the lower and upper bounds of the 95% confidence interval for each residual of the regression between SHRS and UAA. If the 95% confidence interval of a residual surrounded zero (i.e. if its sign changed), then it was included in both behavioural regimes. We then used a two-sample Kolmogorov–Smirnov (KS) test to identify significant differences in spatially distributed variables among hillslopes where SHRS' exhibited different behaviour. We used the Wilcoxon rank-sum test to determine whether the median values of spatial variables differed significantly among these behavioural groups.

RESULTS

We compared SHRS with UAA for the 23 hillslopes in the study (Figure 3). We found a significant positive correlation between SHRS and UAA, but the relationship during the growing season was weaker ($r^2 = 0{\cdot}66$) than the annual correlation ($r^2 = 0{\cdot}91$) as observed by Jencso *et al*. (2009) at the same site. To better understand the effect of vegetation on the relationship between SHRS and UAA during the growing season, we compared SHRS' with ρ_{zveg} for the 23 hillslopes (Figure 4). Two distinct relationships emerged depending on whether hillslopes were hydrologically connected more often or less often than predicted by UAA alone (Figure 4). We observed a significant negative correlation between ρ_{zveg} and SHRS' (Spearman's $\rho = -0{\cdot}71$ and $p = 0{\cdot}003$) among hillslopes for which SHRS' was negative (i.e. hillslopes hydrologically connected less often than predicted by UAA alone). Conversely, we observed a significant positive correlation (Spearman's $\rho = 0{\cdot}71$ and $p = 0{\cdot}03$) among hillslopes where SHRS' was positive (i.e. hillslopes hydrologically connected more often than predicted by UAA alone).

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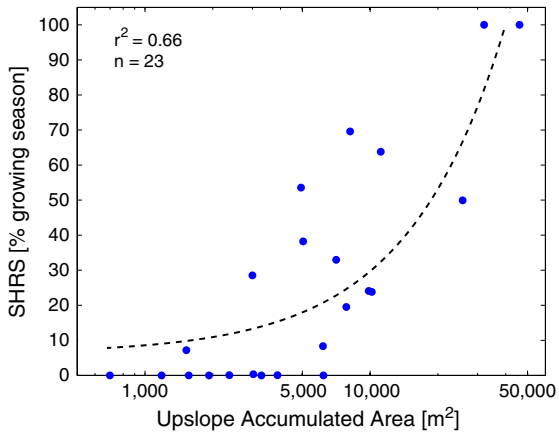

Figure 3. Percentage of the growing season in which hillslope–riparian–stream connection exists (SHRS) versus UAA for 23 hillslopes. Linear least squares regression (dashed line) shows a significant linear relationship between UAA (log axis) and SHRS ($r^2 = 0{\cdot}66$), but this relationship is weaker than the annual relationship ($r^2 = 0{\cdot}91$) observed by Jencso *et al.* (2009).

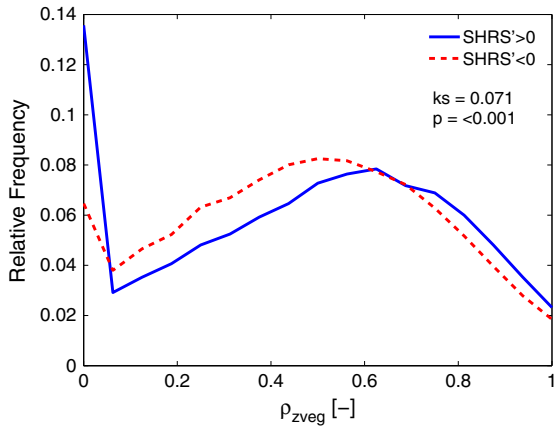

Figure 5. Frequency distribution of vegetation density (ρ_{zveg}) for hillslopes connected more often than predicted by UAA alone (SHRS' > 0, solid blue line), and hillslopes connected less often than predicted by UAA alone (SHRS' < 0, dashed red line).

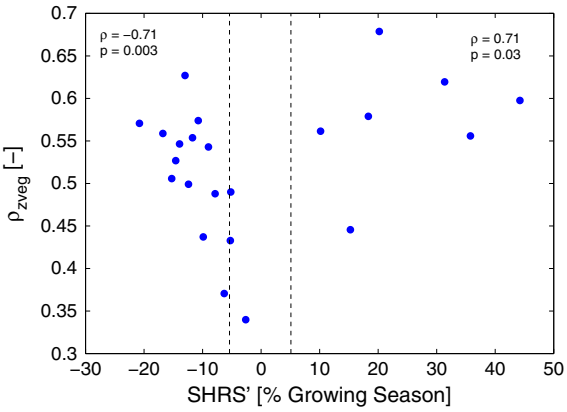

Figure 4. Regression analysis between vegetation density (ρ_{zveg}) and SHRS' showing two distinct regimes depending on the sign of SHRS. SHRS' > 0 represents hillslopes that are hydrologically connected more often than predicted by UAA alone, and SHRS' < 0 represents hillslopes that are hydrologically connected less often than predicted by UAA alone. Dashed, vertical lines show 95% confidence interval derived from bootstrapping. Points between the dashed lines are included in the analysis of both behaviours.

These relationships suggest the existence of two different regimes describing the behaviour of vegetation, topography and hydrological processes on forested hillslopes.

We also examined the vegetation characteristics of hillslopes within each of the two behavioural regimes. The frequency distribution of ρ_{zveg} pooled for all 4-m pixels on hillslopes where SHRS' < 0 is significantly different from the frequency distribution of ρ_{zveg} pooled for all 4-m pixels on hillslopes where SHRS' > 0 (KS = 0·071 and $p < 0{\cdot}001$, Figure 5). Hillslopes where SHRS' > 0 (i.e. those connected more often than predicted by UAA alone) were more likely to contain both low and high vegetation densities and less likely to contain intermediate vegetation densities than hillslopes where SHRS' < 0. Conversely, hillslopes where SHRS' < 0 (i.e. those connected less often than predicted by UAA alone) were more likely to contain intermediate vegetation densities.

When we examined frequency distributions of ASI, similarly pooled for all 4-m pixels of a common behavioural regime, we found that solar irradiance differed significantly between the two behavioural regimes (KS = 0·13 and $p < 0{\cdot}001$, Figure 6). The median value of ASI was significantly different for the two regimes ($p < 0{\cdot}001$), but the difference was slight. Hillslopes that were connected more often than predicted by UAA alone had only slightly higher median irradiance (392 W m^{-2}) than hillslopes connected less often than predicted by UAA alone (389 W m^{-2}). Although the two behavioural regimes experienced similar ASI, the joint (bivariate) frequency distributions of ρ_{zveg} and ASI (Figure 7) for each of the regimes demonstrate that hillslopes where SHRS' > 0 contain relatively few landscape positions with both high ρ_{zveg} and high ASI. In contrast, hillslopes where SHRS' < 0 contain more landscape positions where high ρ_{zveg} and high ASI intersect.

DISCUSSION

Does the relationship between HRS connectivity and UAA differ between the growing season and the entire year?

Weaker correlations between HRS connectivity and UAA during the growing season demonstrate that the strength of topographic controls on HRS connectivity varies during the year. The departure from the expected dependence of SHRS on UAA (Figure 3) was likely influenced in part by an increase in the magnitude of *ET* relative to lateral soil

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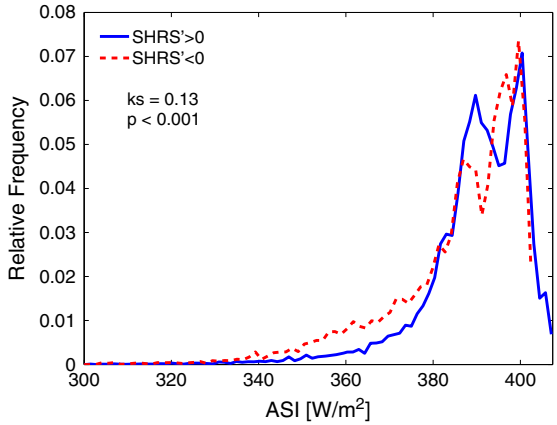

Figure 6. Frequency distribution of average solar irradiance for hillslopes connected more often than predicted by UAA alone (SHRS' > 0, solid blue line), and hillslopes connected less often than predicted by UAA alone (SHRS' < 0, dashed red line).

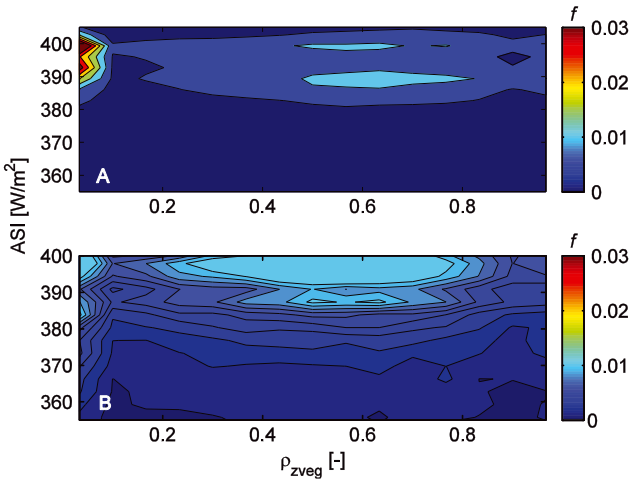

Figure 7. Bivariate distribution of average solar irradiance and vegetation density (ρ_{zveg}) for (a) SHRS' > 0 and (b) SHRS' < 0.

water redistribution. Soil moisture (not shown) and hydrologic connectivity reach an annual maximum as a result of snowmelt approximately 2 weeks into the growing season (Figure 2) and then steadily decline during the remainder of the growing season (Emanuel *et al.*, 2010). The lack of substantial soil water input after peak snowmelt amplifies the effect of *ET* during the growing season (Wondzell *et al.*, 2007; Jencso *et al.*, 2009). The weaker correlation between SHRS and UAA demonstrates the stronger influence of biological control of the hillslope water balance during the growing season. Specifically, it suggests that although topography may be the principal control on hydrologic connectivity at the annual timescale, other factors, particularly *ET*, become important during the growing season.

How do hillslope vegetation characteristics affect topographic controls on HRS connectivity during the growing season?

The effects of vegetation structure on hydrologic connectivity become apparent during the growing season. When we compared ρ_{zveg} with SHRS' across all 23 hillslopes (Figure 4), we found that two distinct regimes emerged. For hillslopes where SHRS' < 0 (i.e. those hydrologically connected less often than predicted by UAA alone), a significant negative correlation existed between vegetation density and SHRS' ($\rho = -0{\cdot}71$ and $p = 0{\cdot}003$). Among these hillslopes, growing season hydrologic connectivity decreased as the density of vegetation increased. Interpreting the effects of vegetation on hydrologic connectivity requires knowledge of the vegetation structure of each hillslope and knowledge of the behaviour of observed hydrologic connectivity with respect to the expected relationship between SHRS and UAA. One explanation for this phenomenon is that as vegetation density increases, greater leaf area is available to facilitate transpiration. According to modelling work by Emanuel *et al.* (2010), transpiration is the dominant component of *ET* during the growing season at TCEF. Therefore, hydrologic connectivity decreased during the growing season because the magnitude of *ET* became large relative to the lateral flux of soil water and shallow groundwater toward the stream. As Equation (1) dictates, in the absence of additional snowmelt or substantial precipitation inputs, soil water must be partitioned between two principal fluxes: *ET* and lateral redistribution of water downhill toward the stream. Our results suggest that for hillslopes where SHRS' < 0, hydrologic connectivity during the growing season is strongly affected by the balance between these two fluxes.

For hillslopes where SHRS' > 0 (i.e. those hydrologically connected more often than predicted by UAA alone), we observed the opposite relationship between SHRS' and ρ_{zveg}. For these hillslopes, there is a significant positive correlation between SHRS' and ρ_{zveg} ($\rho = 0{\cdot}71$ and $p = 0{\cdot}03$) (Figure 4). In other words, both vegetation density and *ET* may increase as SHRS' increases for these hillslopes. One explanation for this pattern is that both hydrologic connectivity and vegetation water use are subsidized by inputs of water other than the UAA-determined snowmelt volume. At TCEF, previous research has demonstrated that the presence of high-porosity, high-conductivity sandstone and the associated groundwater discharge influence both hydrologic connectivity (Jencso and McGlynn, 2011) and runoff response times (Nippgen *et al.*, 2011) at the watershed scale. Groundwater discharge onto these hillslopes may provide a sustained source of water during the otherwise dry growing season to facilitate hydrologic connectivity (Jencso and McGlynn, 2011; Payn *et al.*, 2012). It may be

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possible that the same water sources could increase vegetation density and subsidize growing season hydrologic connectivity (Figure 4). Research by others has established links between patterns of vegetation distribution and water availability at the watershed scale (e.g. Caylor *et al.*, 2004), and if groundwater discharge affects vegetation in this same manner at TCEF, we would expect to observe a positive correlation between ρ_{zveg} and SHRS' among the affected hillslopes. For these hillslopes, the lateral redistribution of water and *ET* may not be the exclusive fluxes dominating the hillslope water balance and controlling hydrologic connectivity at the base of the hillslope during the growing season. Further work is required to assess factors such as catchment geology that may subsidize hydrologic connectivity and vegetation response during the summer growing season.

Does the spatial distribution of available energy interact with the spatial distribution of vegetation to influence HRS connectivity?

To better understand the effect of *ET* on the predicted behaviour of growing season hydrologic connectivity and hillslope topographic contributing area (UAA), we examined the frequency distributions of both vegetation density and available energy (Figures 5 and 6), as well as the joint distribution of vegetation structure and energy availability for hillslopes within each of the two behavioural regimes (Figure 7). For hillslopes where $\mathrm{SHRS}' > 0$ (i.e. those that were hydrologically connected more often than predicted by UAA alone), high irradiance occurs primarily at landscape positions with low vegetation density. Conversely, for hillslopes where $\mathrm{SHRS}' < 0$ (i.e. those that were hydrologically connected less often than predicted by UAA alone), landscape positions with high irradiance are distributed across a wider range of vegetation densities, including intermediate and high densities. The intersection of high ρ_{zveg} and medium and high ASI on these hillslopes indicates the colocation of transpiring vegetation with energy (in the form of irradiance) needed to facilitate transpiration. This conclusion is not obvious based solely on distributions of ρ_{zveg} and ASI alone (Figures 5 and 6, i.e. the marginal distributions of Figure 7). Only by examining the intersection of these two variables, representing energy availability and vegetation structure to facilitate transpiration, can we reach this conclusion.

Hillslopes where SHRS' decreases with increased ρ_{zveg} are characterized as areas where high ρ_{zveg} and high ASI intersect (Figure 7). The occurrence of high irradiance at intermediate and high vegetation densities suggests that these hillslopes experienced more *ET* during the growing season than hillslopes where $\mathrm{SHRS}' > 0$ (Figure 7). Among these hillslopes, as vegetation density increased and raised the capacity for transpiration, energy (in the form of irradiance) was available to facilitate the process. On the other hand, among hillslopes where $\mathrm{SHRS}' > 0$, higher vegetation densities may not have resulted in as much *ET* because landscape positions with high ρ_{zveg} were less likely to be accompanied by high ASI (Figure 7). On these hillslopes, where *ET* may be small relative to the downhill flux of water during the growing season, vegetation density is less likely to play a dominant role in the duration of growing season hydrologic connectivity. These results suggest that the co-occurrence of vegetation density and available energy on hillslopes affects the variability of expected behaviour of hydrologic connectivity during the growing season.

Implications

This work has implications for management of land and water resources in forested watersheds. Our analyses show that within a given watershed, hillslopes of similar size (i.e. similar terrain) do not necessarily exhibit similar patterns of hydrologic connectivity, due in part to intersecting patterns of topography, vegetation and energy on the landscape. Vegetation disturbances, including timber management, disease and secondary ecosystem succession affect the distribution of vegetation structure within a watershed and thereby affect the intersecting characteristics of topography and vegetation on the hillslopes that form the watershed. As a result, vegetation disturbance or management activity could have a very different impact on the hydrologic response of an individual hillslope or the entire watershed depending on the topographic setting where the disturbance takes place. Our work suggests that land management decisions affecting vegetation should consider the impact of disturbance on the hillslope water balance and subsequent impacts on hydrologic connectivity between hillslopes and streams.

CONCLUSION

We examined the combined effects of vegetation and topographic characteristics on growing season hydrologic connectivity across 23 hillslopes. We determined that the relationship between HRS connectivity and UAA, which was strong at the annual time scale, became weaker during the growing season. The weakened relationship between SHRS and UAA was likely caused by increased *ET* relative to the magnitude of the downhill flux of soil water. Two behavioural regimes emerged when we compared the residuals of the expected relationship between SHRS and UAA to vegetation density. Hillslopes that were connected less often than expected followed a pattern of decreasing hydrologic connectivity with increasing vegetation density. Landscape positions with high vegetation density were accompanied by relatively high irradiance, suggesting that

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vegetation and available energy combined on these hillslopes to yield an expected increase in *ET* and decrease in hydrologic connectivity with increasing vegetation density.

Hillslopes that were connected more often than expected behaved differently. Among these hillslopes, increased vegetation density was accompanied by more frequent hydrologic connectivity. High vegetation densities on these hillslopes were not typically accompanied by high irradiance, and as a result, *ET* might not have been as high on these hillslopes as on hillslopes connected less often than expected. For these hillslopes, *ET* and the downhill flux of water would no longer be the exclusive fluxes dominating the hillslope water balance. These results not only demonstrate the importance of vegetation heterogeneity for hillslope–riparian–stream connectivity but they also suggest that vegetation interacts with other spatially distributed variables such as energy availability and geology to affect the influence of topography on hydrological processes.

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REFERENCES

Beven KJ, Kirkby MJ. 1979. A physically-based variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin* **24**(1): 43–69.

Boehner J, Antonic O. 2009. Land Surface Parameters Specific to Topo-Climatology. In Hengl T, Reuter HI [Eds.]: Geomorphometry – Concepts, Software, Applications.

Böhner J, Blaschke T, Montanarella L (Eds.) 2008. *SAGA*: *System for an Automated Geographical Analysis*, Institute of Geography, University of Hamburg: Hamburg.

Burt TP, Butcher DP. 1985. Topographic controls of soil moisture distribution, *Journal of Soil Science* **36**(3): 469–486.

Caylor KK, Scanlon TM, Rodriguez-Iturbe I. 2004. Feasible optimality of vegetation patterns in river basins, *Geophysical Research Letters* **31**: L13502, doi:10.1029/2004GL020260.

Chen J, P Kumar. 2001. Topographic influence on the seasonal and interannual variation of water and energy balance of basins in north america. *Journal of Climate* **14**: 1989–2014.

Emanuel RE, Epstein HE, McGlynn BL, Welsch DL, Muth DJ, D'Odorico P. 2010. Spatial and temporal controls on watershed ecohydrology in the northern Rocky Mountains, *Water Resources Research* **46**: W11553, doi:10.1029/2009WR008890.

Farnes, PE, Shearer RC, McCaughey WW, Hansen KJ 1995. Comparisons of Hydrology, Geology, and Physical Characteristics between Tenderfoot Creek Experimental Forest (East Side) Montana, and Coram Experimental Forest (West Side) Montana, 19 pp., USDA Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT.

Genereux DP, Hemond HF, Mulholland PJ, 1993. Spatial and temporal variability in streamflow generation on the West Fork of Walker Branch Watershed. *Journal of Hydrology* **142**: 137–166.

Gribovszki Z, Szilagyi J, Kalicz P. 2010. Diurnal fluctuations in shallow groundwater levels and streamflow rates and their interpretation – A review. *Journal of Hydrology* **385**: 371–383.

Holdorf HD. 1981. Soil Resource Inventory, Lewis and Clark National Forest: Interim in Service Report, Lewis and Clark Natl. For., For. Supervisor's Off, Great Falls, Mont.

Jencso, KG, McGlynn BL. 2011. Hierarchical controls on runoff generation: topographically driven hydrologic connectivity, geology, and vegetation. *Water Resources Research* **47**: W11527, doi:10.1029/2011WR010666.

Jencso KJ, McGlynn BL, Gooseff MN, Wondzell SM, Bencala KE, Marshall LA. 2009. Hydrologic connectivity between landscapes and streams: transferring reach-and plot-scale understanding to the catchment scale. *Water Resources Research* **45**(4): W04428. doi:10.1029/2008WR007225.

Jencso KG, McGlynn BL, Gooseff MN, Bencala KE, Wondzell SM. 2010. Hillslope hydrologic connectivity controls riparian groundwater turnover: implications of catchment structure for riparian buffering and stream water sources. *Water Resources Research* **46**(11): W10524. doi:10.1029/2009WR008818.

Keim RF, Meerveld H, McDonnell JJ. 2006. A virtual experiment on the effects of evaporation and intensity smoothing by canopy interception on subsurface stormflow generation. *Journal of Hydrology* **327**: 352–364.

McCaughey WW. 1996. Tenderfoot Creek Experimental Forest, in *Experimental Forests*, *Ranges and Watersheds in the Northern Rocky Mountains*: *A compendium of Outdoor Laboratories in Utah*, *Idaho*, *and Montana*. Edited by W. C. Schmidt and J.L. Friede, United States Department of Agriculture, Forest Service.

Mincemoyer SA, Birdsall JL. 2006. Vascular flora of the Tenderfoot Creek Experimental Forest, Little Belt Mountains, Montana. *Madrono* **53**(3): 211–222.

Nippgen F, McGlynn BL, Marshall LA, Emanuel RE. 2011. Landscape structure and climate influences on hydrologic response, *Water Resources Research* **47**: W12528. doi:10.1029/2011WR011161.

Payn RA, Gooseff MN, McGlynn BL, Bencala KE, Wondzell SM. 2012. Exploring changes in the spatial distribution of stream baseflow generation during a seasonal recession. *Water Resources Research* **48**: W04519. doi:10.1029/2011WR011552.

Priestley CHB, Taylor, RJ. 1972. On the assessment of surface heat flux and evaporation using large scale parameters. Monthly Weather Review 100, 81_/92.

Rodriguez-Iturbe I. 2000. Ecohydrology: a hydrologic perspective of climate–soil–vegetation dynamics. *Water Resources Research* **36**: 3–9.

Rodriguez-Iturbe I, Valdes JB. 1979. The geomorphic structure of the hydrologic response. *Water Resources Research* **15**(6): 1409–1420.

Scanlon TM, Kiely G, Amboldi R. 2005. Model determination of non-point source phosphorus transport pathways in a fertilized grassland catchment. *Hydrological Processes* **19**: 2801–2814.

Seibert J, McGlynn BL. 2007. A new triangular multiple flow direction algorithm for computing upslope areas from gridded digital elevation models, *Water Resources Research* **43**(4): doi:10.1029/2006WR005128.

Shreve RL. 1969. Stream lengths and basin areas in topologically random channel networks. *Journal of Geology* **77**, 397–414.

Sidle RC, Tsuboyama Y, Noguchi S, Hosoda I, Fujieda M, Shimizu T. 2000. Stormflow generation in steep forested headwaters: a linked hydrogeomorphic paradigm. *Hydrological Processes* **14**(3): 369–385. doi:10.1002/(SICI)1099-1085(20000228) 14:3<369::AID-HYP943>3.3.CO;2-P.

Tarboton DG. 2003. Terrain Analysis Using Digital Elevation Models in Hydrology. In: Conference Proceedings from the 23rd ESRI International Users Conference, San Diego, California, July 7–11.

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Tarboton DG, Baker ME. 2008. Towards an algebra for terrain-based flow analysis. in Representing, Modeling and Visualizing the Natural Environment: Innovations in GIS 13, Edited by Mount NJ, Harvey GL, Aplin P, Priestnall G, CRC Press: Florida.

Western AW, Grayson RB, Blöschl G, Willgoose GR, McMahon TA. 1999. Observed spatial organization of soil moisture and its relation to terrain indices. *Water Resources Research* **35**: 797–810. doi:10.1029/1998WR900065.

Wilson JP, Gallant, JC [Eds.] 2000. Terrain Analysis – Principles and Applications. New York: John Wiley & Sons, Inc.

Wondzell SM, Gooseff MN, McGlynn BL. 2007. Flow velocity and the hydrologic behavior of streams during baseflow. *Geophysical Research Letters* **34**: L24404. doi: 10Ð1029/2007GL031256.

Xu CY, Singh VP. 2000. Evaluation and generalization of radiation-based methods for calculating evaporation. *Hydrological Processes* **14**: 339–349.

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