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RESEARCH LETTER

10.1002/2014GL061668

Key Points:

- Root zone storage capacity (SR) can be estimated with mass curve technique
- Ecosystems design SR to bridge droughts with 10–40 years return period
- SR was linked to aridity index, dry spell duration, seasonality, and runoff ratio

Supporting Information:

- Readme
- Figures S1–S4 and Tables S1–S3
- Data set S1

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Citation:

Gao, H., M. Hrachowitz, S. J. Schymanski, F. Fenicia, N. Sriwongsitanon, and H. H. G. Savenije (2014), Climate controls how ecosystems size the root zone storage capacity at catchment scale, *Geophys. Res. Lett.*, *41*, 7916–7923, doi:10.1002/2014GL061668.

Received 26 AUG 2014 Accepted 20 OCT 2014 Accepted article online 22 OCT 2014 Published online 28 NOV 2014

Climate controls how ecosystems size the root zone storage capacity at catchment scale

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Abstract The root zone moisture storage capacity (S_R) of terrestrial ecosystems is a buffer providing vegetation continuous access to water and a critical factor controlling land-atmospheric moisture exchange, hydrological response, and biogeochemical processes. However, it is impossible to observe directly at catchment scale. Here, using data from 300 diverse catchments, it was tested that, treating the root zone as a reservoir, the mass curve technique (MCT), an engineering method for reservoir design, can be used to estimate catchment-scale S_R from effective rainfall and plant transpiration. Supporting the initial hypothesis, it was found that MCT-derived S_R coincided with model-derived estimates. These estimates of parameter S_R can be used to constrain hydrological, climate, and land surface models. Further, the study provides evidence that ecosystems dynamically design their root systems to bridge droughts with return periods of 10–40 years, controlled by climate and linked to aridity index, inter-storm duration, seasonality, and runoff ratio.

1. Introduction

The critical influence of vegetation on the water cycle was realized early [*Bates*, 1921; *Horton*, 1933] and is by now, together with its wider implications [*Seneviratne et al.*, 2013], well acknowledged [*Jenerette et al.*, 2012; *Rodriguez-lturbe*, 2000; *Thompson et al.*, 2011]. It is also understood that water and vegetation interact in a co-evolutionary system toward establishing equilibrium conditions between vegetation and moisture availability in water-limited environments [*Donohue et al.*, 2007; *Eagleson*, 1978, 1982]. In other words, ecosystems tend to avoid water shortage [*Eagleson*, 1982; *Schenk*, 2008] and the associated negative effect on plants' carbon assimilation rates [*Porporato et al.*, 2004]. There is empirical and theoretical evidence that they do so by designing root systems that allow for the most efficient extraction of water from the substrate, thereby meeting the canopy water demand (or transpiration) while minimizing their costs in terms of carbon expenditure for root growth and maintenance [*Milly*, 1994; *Schymanski et al.*, 2008; *Troch et al.*, 2009].

In spite of a generally good understanding of how ecosystems and hydrology are interlinked, little is known about the detailed mechanisms controlling these connections, leaving many factors involved difficult to quantify. This is in particular true for the water holding capacity, or the plant available water storage capacity in the root zone (S_R), which is a key parameter for ecosystem function [*Milly and Dunne*, 1994; *Rodriguez-Iturbe et al.*, 2007; *Sayama et al.*, 2011]. It was suggested previously that changes in S_R directly affect runoff [*Donohue et al.*, 2012], transpiration rates [*Milly and Dunne*, 1994] as well as, through its influence on transpiration and thus on latent heat exchange, land surface temperatures [*De Laat and Maurellis*, 2006; *Legates et al.*, 2011; *Seneviratne et al.*, 2013] and thus the fundamental hydrological response characteristics of natural systems [*Kleidon*, 2004; *Laio et al.*, 2001; *Porporato et al.*, 2004]. In spite of the understanding that soils, and thus also S_R, are manifestations of the combined and co-evolving influences of climate, biota, and geology [*Van Breemen*, 1993; *Phillips*, 2009], S_R was in the past mostly estimated from soil characteristics or rooting depths [*Saxton and Rawls*, 2006; *Huang et al.*, 2013], disregarding the importance of climate. Thus, an approach to quantify S_R accounting for feedback among the system components will facilitate a better understanding of how much sub-surface water can be accessed by root systems and is key for efficiently constraining hydrological and ecological predictions.

2. Hypothesis

Both, ecosystems and humans, need continuous access to water, requiring a buffer to balance the high variability of hydrological fluxes in the natural system. Where humans design reservoirs to store water to do

so, ecosystems dimension their root zones. A classical engineering method for designing the size of reservoirs is the mass curve technique (MCT; Figure S1a) and refinements thereof [*Hazen*, 1914; *Klemeš*, 1997; *Rippl*, 1883]. Using this technique, the reservoir size is estimated as a function of water demand, water input, and the length of dry periods. These factors show a striking resemblance with those that have been reported to control S_R: potential evaporation, precipitation, inter-storm duration, and seasonality [*Gentine et al.*, 2012; *Milly*, 1994]. Given these similarities and treating the root zone as a reservoir, we tested the hypothesis that the MCT can be used to estimate S_R at the catchment scale, independently of point-scale root or soil observations, exclusively based on climate data (inflow and water demand) and to thereby establish a direct and quantifiable link between climate, ecosystem, and hydrology. Note that a catchment can consist of several ecosystems. Hereafter, however, S_R of an ecosystem describes the integrated value of S_R for all ecosystems in a catchment.

3. Methods

3.1. Estimation of Root Zone Storage Capacity (S_R)

3.1.1. Mass Curve Technique (MCT)

The MCT is a method to estimate the reservoir storage based on the relationship between cumulative inflow and water demand (Figure S1a). To estimate S_R (Figures S1b and S1c) first the average annual plant water demand E_{ta} is determined from $E_{ta} = P_E - Q$, with $P_E = P - E_{ii}$ where P_E is the cumulative inflow, P is precipitation, E_i is interception, and Q is runoff. Then water demand in dry seasons (E_{td}) is estimated using a linear relationship between E_{ta}/E_{td} and the ratio of annual average to dry season average Normalized Difference Vegetation Index, i.e., NDVI_a/NDVI_d, assuming that transpiration is linearly related to the vegetation index and incoming radiation while being constrained by soil moisture [*Wang et al.*, 2007]. Finally, P_E is plotted together with E_{td} . The required S_R for each year is estimated based on the periods where the rate of water demand exceeds inflow (Figure S1). In other words, the vertical distance between the tangents to the accumulated P_E , parallel to E_{tdr} at the beginning and the end of dry seasons yields the estimated S_R of that year (Figure S1b).

3.1.2. Frequency Analysis

The Gumbel distribution [*Gumbel*, 1935], frequently used for estimating hydrological extremes, was used to standardize the frequency of drought occurrence (Figures S1d and S3). Here, Gumbel uses the reduced variate *y* as a function of the return period *T* of annual S_R estimates ($y = -\ln(-\ln(1 - 1/T))$). Being a linear relationship, this allows the estimation of the S_R required to overcome droughts with certain return periods, such as droughts with return periods of 10, 20, and 40 years (S_{R10y} , S_{R20y} , and S_{R40y}).

3.2. Root Zone Storage Capacity From Hydrological Models (SuMax)

To test the MCT-derived values of S_R for plausibility, a conceptual hydrological model was used to independently estimate the root zone storage capacity. It was developed based on the FLEX framework [*Fenicia et al.*, 2008]. As for most hydrological models its core is a dynamic buffer that moderates flows and retains tension water for plant use, essentially reflecting S_R [*Fenicia et al.*, 2008; *Zhao and Liu*, 1995]. Here, the tension water storage capacity function of the Xinanjiang model [*Zhao and Liu*, 1995], controlled by parameter S_{uMax} , was adopted. The MOSCEM-UA [*Vrugt et al.*, 2003] algorithm was used for a multi-objective model calibration, based on the Kling-Gupta efficiency (KGE) [*Gupta et al.*, 2009] of flow, logarithmic flow, and the flow duration curve. All pareto-optimal parameter sets were retained as feasible and used for further analysis (in Figures 2, S1d, and S3 only the median values of S_{uMax} are shown for clarity). The description of the model is available in the Supplement (Figure S4 and Table S1). The MCT-derived S_R was then evaluated against the model-derived values of S_{uMax} .

4. Data Sets

For an initial analysis, data from six catchments in Thailand, with catchment areas between 452 and 3858 km², were used (Table S2, Dataset S1). These catchments are characterized by tropical savanna climate (Köppen-Geiger group Aw) with average annual precipitation and runoff of 1174 and 268 mm yr⁻¹. Land use is dominated by evergreen and deciduous forest (Figure 1d). Further, data from 323 in the United States catchments, with areas between 67 and 10,329 km², data records >30 years, and limited anthropogenic influence, available through the Model Parameter Estimation Experiment [*Schaake et al.*, 2006] were used.



Figure 1. Upper Ping River catchment maps: (a) context; (b) elevation; (c) average annual Normalized Difference Vegetation Index (NDVI); (d) land use. Figure 1e compares the values of mass curve technique (MCT)-derived S_R for different return periods (grey boxes) with the range of feasible calibrated values of S_{uMax} from the hydrological model (red lines indicate the medians, boxes the 25/75th, and whiskers the 5/95th quantiles).

MOPEX catchments with more than 20% of precipitation falling as snow were excluded from the analysis since neither the MCT nor the model account for snow dynamics. Likewise, catchments in very arid climates $(I_A > 2, I_A = E_P/P, E_P)$ is potential evaporation) were excluded as vegetation in such regions may favor different survival strategies such as increased water storage in the plants themselves. Catchment average precipitation was calculated with inverse distance weighting. Potential evaporation was estimated using the Hargreaves equation [*Hargreaves and Samani*, 1982]. The interception threshold E_i to estimate P_E was set to 2 mm d⁻¹. Catchment average annual and dry season mean NDVI values were obtained from the MODIS13Q1 product (2002–2012; LP DAAC) by using the average of all cells within the catchment over the required period.

5. Results and Discussions

Depending on dry season characteristics in individual years (Figure S2), the six Thai study catchments exhibited considerable fluctuations in MCT-derived S_R needed in the individual years to satisfy dry period plant water demand, with overall values across all six catchments from ~100 to ~450 mm (Figure S3). In the individual catchments the range between the minimum and the maximum values for annual S_R was on average ~200 mm. To generalize these results, the required S_R for drought return periods of 5, 10, 20, 40, 60, and 100 years were estimated using the Gumbel distribution (Figure S3).

Calibrating the hydrological model to stream flow observations for these six study catchments showed that the ranges of calibrated S_{uMax} correspond surprisingly well with the values of MCT-derived S_R (Figure 1e). In fact, values of S_R required to cover canopy water demand for droughts with return periods from 10 to 20 years coincided with the median of calibrated S_{uMax} in each catchment, with some vegetation-related variation: the results suggest that catchments with higher values of annual catchment average NDVI (P.4A, NDVI = 0.69; P.21, NDVI = 0.70) and thus higher canopy water demand develop larger S_{R20y} of 447 and 439 mm, respectively, than those with lower canopy water demand (P.14, NDVI = 0.64, S_{R20y} = 280 mm; P.24, NDVI = 0.66, and S_{R20y} = 219 mm). In other words, ecosystems in these catchments have developed root zone that allows them to overcome droughts with return periods of 10–20 years. These results suggest that plants "design" their root-accessible water storage according to a cost minimization strategy [*Milly*, 1994], i.e., to meet canopy water demand with minimal carbon allocation to roots. It could be observed in these six

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Figure 2. Relationships between S_R , S_{uMax} , and climate indices for the 329 study catchments. (a) S_{uMax} vs. S_{R20y} (storage capacity with 20 years return periods); (b) S_{uMax} vs. S_{R10y} ; (c) S_{uMax} vs. S_{R40y} ; (d) S_{R20y} vs. aridity index (I_A); (e) S_{R20y} vs. inter-storm duration (I_{ISD}); (f) S_{R20y} vs. seasonality index (I_S); (g) S_{uMax} (black circles) and ranges of S_R between 10 and 40 year return periods (S_{R10y} - S_{R40y}), sorted by increasing S_{uMax} . Colors indicate ecoregion classes, based on simplified CEC Level II ecoregions.

catchments that ecosystems develop storage capacities S_R that are mainly controlled by atmospheric moisture supply and canopy demand dynamics, which supports earlier studies that documented the importance of canopy water demand and environmental conditions for S_R [*Field et al.*, 1992; *Milly and Dunne*, 1994; *Gentine et al.*, 2012] and the hypothesis that ecosystems adapt their root zones [*Schenk*, 2006] by lateral or vertical growth [*Schenk and Jackson*, 2002a] to access the necessary soil water volume.

The hypothesis of climate and canopy water demand being dominant controls on S_R and the existence of a link between S_R and S_{uMax} were further tested by applying the same methodology as above to additional 323 very diverse catchments across the US. Based on all 329 study catchments (Thailand and US), statistically highly significant relationships between calibrated S_{uMax} and MCT-derived S_R for drought return periods of 10–40 years ($R_{10yrs}^2 = 0.61$, $R_{20yrs}^2 = 0.75$, $R_{40yrs}^2 = 0.71$; p < 0.001; Figures 2a–2c) suggest that across the contrasting environmental conditions in these catchments, ecosystems design their S_R according to similar, simple, first order principles. Figure 2g displays the full range of $S_{R10y} - S_{R40y}$, compared to S_{uMax} values for all study catchments, showing that the majority of catchments' S_{uMax} plots within the $S_{R10y} - S_{R40y}$ range.

5.1. Links Between Climate, Vegetation and ${\rm S}_{\rm R}$

The results indicate that at the catchment scale the plant available storage capacity is controlled by catchment wetness characteristics: when plotting S_{R20y} for the individual catchments against their respective aridity indices (I_A) ($R^2 = 0.28$; p < 0.001) or the mean inter-storm durations (I_{ISD}), a proxy for dry period durations ($R^2 = 0.57$; p < 0.001), it was found that the lowest S_R (<100 mm) are required in wet climates (Figure 2d) with shortest inter-storm durations (Figure 2e), while larger S_R are required in regions with higher aridity and longer dry period durations. Another determining factor for S_R was found to be the seasonality of

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Figure 3. CEC North American Level II ecoregions in the US overlain by (a) the MOPEX study catchments classified based on the simplified CEC North American Level II ecoregions and (b) the S_{R20y} for the MOPEX study catchments. The horizontal color bar applies to the background in both figures; the individual vertical color bars apply to the catchments in the respective sub-panels.

precipitation. The higher the rainfall seasonality index $(I_S = \frac{1}{P_a} \sum_{m=1}^{m=12} \left| \overline{P_m} - \overline{\frac{P_a}{12}} \right|$, where $\overline{P_m}$ is the mean rainfall of

month *m*, and $\overline{P_a}$ is the mean annual rainfall), the larger a S_R is required (R² = 0.69; *p* < 0.001; Figure 2f). Stepwise multiple linear regression further showed that combining the three predictors I_{S} , I_{A} , and I_{ISD} can explain 79% of the variance in S_{R20y} ($S_{R20y} = 218I_S + 64I_A + 5I_{ISD} - 51$; $R^2_{adi} = 0.79$; p < 0.001; variance inflation factor <4). Furthermore, the US study catchments were classified according to the CEC North American Level Il ecoregions (Table S3; Figure 3a) [Wiken et al., 2011], with the 6 tropical catchments in Thailand constituting one additional class. Note that the CEC classification was simplified for clarity of the presentation, without overall impact on the interpretation. The classification indicates that, for example, in semi-arid Prairies (Table S3; Figures 3a and 3b) dominated by seasonal short and mix-grass Prairie vegetation, S_{R20v} is around 150 - 200 mm, which is below the values of ~200 - 500 mm that would be expected for ecosystems with comparable aridity indices ($I_A \sim 1 - 2$) but dominated by evergreen plants as indicated by the regression line in Figure 2d. By going dormant during the dry season, thereby minimizing transpiration, such ecosystems only need to access sufficient moisture to reach maturity during the growing season. In contrast, the results also suggest that ecosystems in environments with marked seasonality and out of phase precipitation and energy supply, such as West-coast ecoregions (Table S3 and Figures 3a and 3b), require higher S_{B} than ecosystems with higher aridity indices in other climates (Figure 2d) to ensure sufficient access to water throughout the prolonged dry periods (Figure 2e). The here suggested concept of S_R is conceptually different from rooting depth, as it accounts for the volume of water accessible to roots and thus rather reflects the average root density in a catchment. It was, however, observed that patterns of S_R are broadly corresponding with observed rooting depths in previous studies. For example, some observations by Schenk and Jackson [2002b] include that Tropical Savanna ecosystems are characterized by, on average, deepest rooting depths, with a median value of 1.2 m. Similarly, they report elevated root depths (~0.8-2 m) in Mediterranean



Figure 4. Distributions of S_{uMax} and S_{R20y} in the seven simplified ecoregion classes of the 329 study catchments.

climates as well as low and comparable root depths in temperate forests and grasslands. Our results (Figure 4) likewise suggest that the largest S_R are required in Tropical Savanna systems (~400 mm) and, although wetter than Mediterranean climates, in the Seasonal Western Region (~100 – 200 mm), while forests and grasslands (Classes 1–3) exhibit low and comparable S_R requirements.

5.2. Implications for the Hydrological Response and Beyond

Following these results, not only a spatial pattern of S_{R20y} across the US emerges, following the precipitation and evaporative energy supply gradients (Figure 3b), but it could also be shown that the long-term annual catchment runoff coefficient ($C_R = Q/P$) exhibits a significant, negative correlation with S_{R20y} ($R^2 = 0.48$; p < 0.001; Figure 5). This suggests that flow partitioning into runoff and evaporative fluxes, as shown in the Budyko framework [*Budyko and Miller*, 1974], is strongly controlled by S_R [*Gentine et al.*, 2012]. While humid catchments are characterized by low S_R and high $C_{R'}$ vegetation in more arid catchments requires a higher S_R to store more water, resulting in lower C_R and thus in proportionally higher plant transpiration. This does not only underline the importance of S_R for understanding the hydrological response, but it also emphasizes the role of co-evolution of vegetation and hydrology. Furthermore, the positive correlation between S_{R20y} and rainfall seasonality implies a certain buffering of seasonality effects on the runoff ratio, resulting in only small deviations of catchments from the Budyko curve despite differences in climatic seasonality [*Williams et al.*, 2012].

Limitations of MCT method include its dependence on the availability of water inflow and demand data. This restricts the possibility to estimate S_R for individual ecosystems or a grid-based spatial distribution within a catchment. Further, S_R estimates are currently based on constant water demand estimates and may benefit from allowing for seasonal variations. Additional research is also required to determine at which scales the



Figure 5. Relationship between S_{R20y} and the mean annual runoff coefficient for the 329 study catchments.

method is applicable.

The root zone storage is the core of hydrological models as it controls the partitioning of available water for plant use and flow generation. The estimation of this parameter from independently observed data can reduce the number of calibration parameters and the associated parameter uncertainty in hydrological models, in particular for predictions in ungauged basins [Blöschl et al., 2013; Hrachowitz et al., 2013]. Similarly, estimates of S_R, as a controlling factor of soil moisture, are potentially useful for a range of geophysical applications: (1) in ecology, estimates of S_R may be valuable for understanding factors controlling primary production and growth as well as ecosystem development and survival strategies [Kolb et al., 1990; Briggs and Knapp, 1995; Breshears and Barnes, 1999]. (2) In land surface

schemes and climate models [*Dirmeyer et al.*, 2006; *Niu et al.*, 2011; *Seneviratne et al.*, 2013], estimates of S_R can help define land-atmosphere exchange processes of water and energy, thereby potentially improving the models' predictive ability. (3) S_R also plays a key role in biogeochemical studies. Controlling soil moisture dynamics and it establishes the physico-chemical environment for cycling of nutrients and solutes, such as nitrogen [*Pastor and Post*, 1986; *Agehara and Warncke*, 2005] or carbon [*Howard and Howard*, 1993; *Kurc and Small*, 2007]. Linking transport, plant uptake, and chemical processes, S_R estimates may improve the understanding of these processes and their representation in models. (4) Through its link to vegetation and its influence on soil saturation and overland flow generation, S_R estimates may also prove beneficial for the understanding and quantification of erosion and mass movement processes [*Seeger et al.*, 2004; *Ray and Jacobs*, 2007].

The dependency of S_R on climate and ecosystems/land cover further entails that S_R cannot be treated as static as it varies depending on changes in any of these. This potentially offers a simple way to account, to some extent, for a temporally evolving system, which is a step from Newtonian toward Darwinian modeling strategies [Harman and Troch, 2014; Harte, 2002; Hrachowitz et al., 2013; Kumar and Ruddell, 2010].

6. Conclusions

Using data for more than 300 diverse catchments in Thailand and the US, the presented results support the hypothesis that, at catchment scale, ecosystems dynamically and optimally adjust their root systems to their environment [*Milly*, 1994; *Kleidon and Heimann*, 1998] in a way that the plant available water storage capacity is controlled by the precipitation regime, canopy water demand, and land cover. It was shown that many ecosystems develop root systems that can tap sufficient water to overcome droughts with 10–40 year return periods but no more than that, as it is increasingly expensive in terms of carbon allocation to roots. It was shown that the root zone storage capacity can be calculated, independent of point-scale observations, using a simple, water-balance based method. The results strongly highlight the importance of the dynamic co-evolution of climate, ecosystems, and hydrology. With this approach we have established a climate and land cover driven technique to estimate the storage capacity of the root zone at catchment scale, a crucial parameter of the water cycle at the interface of hydrological, ecological, and atmospheric sciences.

Acknowledgments

We are grateful to the Royal Irrigation Department in Thailand and the Thai Meteorological Department for proving the hydrological and meterological data in the upper Ping River basin in Thailand. The MOPEX data set was obtained from NOAA National Weather Service (http:// www.nws.noaa.gov/oh/mopex/mo_datasets.htm). The map of CEC North Amercia ecoregions was obtained from US Environmental Procection Agency (http:// www.epa.gov/wed/pages/ecoregions/ na_eco.htm). We thank W. R. Berghuijs and D. Wang for sharing the shapefile of the MOPEX catchments. We likewise want to thank A. Anderson, M. Ertsen, M. Weiler, W. Shao, and W. R. Berghuijs for interesting discussions and critical comments. Extremely helpful and constructive comments and suggestions from an anonymous reviewer are highly appriciated.

M. Bayani Cardenas thanks two anonymous reviewers for their assistance in evaluating this manuscript.

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