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Key Points:
- We derived catchment-scale root water uptake (RWU) estimates from continuous streamflow records through inverse modeling
- Our RWU estimates agreed well with plot-scale studies utilizing measurements of stable isotopes in water and sap flux
- Catchment-scale transpiration fluxes of forested catchments are strongly controlled by tree rooting strategies

Supporting Information:
- Supporting Information S1
- Data Set S1

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Understanding Catchment-Scale Forest Root Water Uptake Strategies Across the Continental United States Through Inverse Ecohydrological Modeling

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Abstract
Trees influence the partitioning of water between catchment water yield and evapotranspiration through mediation of soil water via root water uptake (RWU). Recent research has estimated the depth of RWU for a variety of tree species at plot scales with measurements of stable isotopes in water and sap flux. Though informative, there are some challenges bridging the gap between plot- and catchment-scale water fluxes. We estimated catchment-scale tree RWU behavior for 139 forested catchments across the continental United States from continuous streamflow records with inverse ecohydrological modeling. Our catchment-scale RWU estimates agreed well with existing plot-scale research. Monoculture catchments dense with trees reliant on shallow soil water exhibited reduced transpiration losses compared to deep-rooted and mixed-species forests within the Budkyo framework. This research highlights the importance of representing plant characteristics that define RWU control of transpiration in land surface and earth systems models.

1. Introduction
Global forest loss has occurred at a rapid pace over the past several decades (Hansen et al., 2013), driven by industry (e.g., agriculture and timber harvesting) and wildfires (Curtis et al., 2018). The loss of forest ecosystems and growing atmospheric carbon have necessitated intergovernmental action toward forest preservation and restoration such as the Aichi Biodiversity Targets (Convention on Biological Diversity, 2019) and the UN Sustainable Development Goals (UN, 2016). Quantifying the potential economic and environmental benefits of forested landscapes, however, remains problematic for forestry practitioners (Chazdon & Brancalion, 2019; Ellison et al., 2017), particularly with respect to sustainable water resources management.

At the core of the problem is the partitioning of water by trees. Understanding how trees uptake and transpire catchment-stored water is necessary for developing reliable forecasts of future fresh water availability (Filoso et al., 2017; McDonnell et al., 2018; Zhang et al., 2017), flood hazards (Ellison et al., 2017), and riverine ecosystem stability (Poff et al., 2010) following forest cover and climate change. Trees strongly influence the availability of terrestrial freshwater and fundamentally shape forest hydrology (Brantley et al., 2017). Evaporation of canopy intercepted water, and transpiration following root water uptake (RWU) of soil water return a substantial proportion of continental precipitation to the atmosphere (Good et al., 2015), decreasing the proportion of rainfall that becomes streamflow.

There is global evidence that trees exhibit varied rooting strategies to access stored catchment waters (Barbeta & Peñuelas, 2017; Evaristo & McDonnell, 2017). In particular, signatures of stable isotopes (2H and 18O) in subsurface waters and tree-stored water have facilitated estimates of RWU depths in mixed-species forests of the tropics (Brum et al., 2019; De Deurwaerder et al., 2018; Evaristo et al., 2016), the temperate Northeast United States (Gaines et al., 2015; Knighton, Conneely, et al., 2019), Europe (Brinkmann et al., 2019; Volkman et al., 2016), the Chinese Loess Plateau (Wang et al., 2018), and urban forests (Gómez-Navarro et al., 2019) among others. Despite the broad application of stable isotopic data to estimate tree RWU strategies, several aspects of these methodologies may be limiting. First, end member mixing analysis (e.g., Evaristo & McDonnell, 2017; Knighton, Conneely, et al., 2019) necessitates assumptions about the temporal invariance of samples (De Deurwaerder et al., 2019; Penna et al., 2018; Rothfuss & Javaux, 2017) and requires that we neglect time lags induced by tree-water storage (Evaristo et al., 2019). Further, it remains

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practically difficult to collect and analyze a sufficient number of water isotopic samples to characterize the heterogeneity of soil (e.g., Oerter & Bowen, 2019) and tree-stored waters (e.g., Knighton, Conneely, et al., 2019; Knighton, Souter-Kline, et al., 2019). Finally, individual tree responses to drought conditions (Carriere et al., 2020; Nehemy et al., 2019) challenge the extrapolation of research findings from the plot to the catchment scale (e.g., Penna et al., 2018).

Advances in physically based ecohydrological modeling may provide a useful framework where tree RWU strategies and the effect on catchment hydrology can be better understood. For example, Wang et al. (2018) incorporated phreatic root groundwater uptake into the Noah-Multiparameterization Land Surface Model and showed improved transpiration estimates in an arid region of China. Kennedy et al. (2019) demonstrated that incorporating root, stem, and leaf hydraulic regulation of RWU in Community Land Model Version 5 better predicted deep soil water storage in a tropical forest. Kuppel et al. (2018) introduced an isotope-aided process-based model that allows plant growth dynamics and RWU to be refined with soil and xylem water isotopic measurements. Peaucelle et al. (2019) provided evidence that the functional leaf traits of plants emerged through inverse ecohydrological modeling fit to FLUXNET-derived gross primary production estimates, though root traits were poorly constrained. Critically though, current generation models are likely limited by our lack of a complete understanding of the physical and biological controls on tree RWU (Chang et al., 2018; Fisher et al., 2018) owing to a lack of empirical studies.

Recent research provides some evidence that catchment-scale RWU strategies could be derived from surface water observations. McLaughlin et al. (2019) observed evapotranspiration signals within wetland stage measurements. Similarly, Tashie et al. (2019) demonstrated that streamflow recessions in a headwater catchment in the southern Appalachian Mountains reflected both gravity-driven groundwater outflow to surface waters as well as forest transpiration. Using inverse modeling, they provided evidence that continuous streamflow data carries information on catchment-scale RWU. The application of inverse ecohydrological modeling could possibly obviate the methodological limitations associated with end member mixing analysis measurements of stable isotopes in water from individual trees, soils, and groundwater. Calibration to catchment discharge provides a spatially integrated measure of forest-scale behaviors, eliminating the need to “scale-up” conclusions derived isotopic or sap flux measurements of a few individuals. We sought to answer the following research questions:

1. Can RWU strategies be derived from continuous stream discharge records across the continental United States (CONUS)?
2. Do these estimates agree with previous stable water isotopic evidence of tree RWU depths?
3. Do forest rooting strategies affect the catchment-scale water and energy balance?

2. Methodology

2.1. Hydrologic Data Sets

We collected daily discharge data from U.S. Geological Survey Hydro-Climate Data Network (HCDN-2009) forested catchments across CONUS for the years 1990 through 2010. HCDN-2009 catchments are reference sites that have continuous discharge records and experienced minimal: Disturbance, human land cover alterations, or streamflow regulation from 1990 to 2010. HCDN-2009 catchments were studied where the dominant vegetation type was classified as a forest cover (Ruefenacht et al., 2008) and catchment soil properties were defined (U.S. Department of Agriculture National Resource Conservation Service (NRCS), 2019), yielding 264 catchments. Selected catchments spanned a broad range of available water capacity (Figure 1a) and catchment areas (Figure 1b).

Daily 0.25° precipitation and 0.5° daily maximum and minimum air temperature data were obtained from Xie et al. (2007) and Chen et al. (2008). Daily (1/16)° precipitation and daily maximum and minimum air temperature data were obtained from Livneh et al. (2013). The forest type for each catchment was determined from the classification of Ruefenacht et al. (2008). Catchment soil properties of available water capacity and depths to the confining layers were obtained from the Soil Survey Geographic Database (U.S. Department of Agriculture, 2019).

We reviewed plot-scale studies of tree rooting strategies compiled by Evaristo and McDonnell (2017) supplemented with several recent studies to classify tree species RWU strategies (a detailed discussion is presented
in supporting information section S1). Using these findings and Ruefenacht et al. (2008), we group the catchments into three classifications: (1) catchments with monoculture forest covers exhibiting evidence of shallow RWU (SR), (2) catchments with monocultures exhibiting evidence of deep RWU (DR), and (3) catchments of mixed tree species (MS).

2.2. RWU Parameter Estimation

We simulated daily discharge, soil moisture, snowpack water equivalent, and groundwater storage with a modified version of JoFlo, the lumped model of Archibald et al. (2014). This model has previously been applied to evaluate broad patterns of surface runoff (Knighton, Pleiss, et al., 2019) and forest cover change (Singh et al., 2019) across CONUS, as well as in catchment-scale studies of stable water isotope dynamics (Knighton et al., 2017) and nutrient transport (Georgakakos et al., 2018).

Surface runoff and infiltration partitioning was determined via a Curve Number approach that reflects variable source area hydrology (Archibald et al., 2014). Daily potential evapotranspiration (PET) was determined with the Priestley-Taylor equation as described in Archibald & Walter, 2013 Snowpack accumulation and melt dynamics were determined with the land surface energy balance of Todd Walter et al. (2005). Actual evapotranspiration (AET), shallow soil water storage, and percolation were solved with the Thornthwaite-Mather soil water budget (Archibald et al., 2014). We simulated five soil layers where the first four layers represent the upper 400 mm of soil depth in 100-mm increments and the fifth soil layer represented the remaining soil depth to the confining layer. The upper 400 mm of soil depth is within the range (5–550 mm) of soil water isotopes sampled across CONUS (Evaristo & McDonnell, 2017). Catchment confining layer depths spanned 485 to 2,286 mm (median 1,000 mm). Vertical percolation out of each layer enters the layer immediately below. Upward redistribution of soil moisture, forest loss events (e.g., forest fire), and dynamic forest growth were not simulated.

We simulated RWU demand under nonwater limited conditions (i.e., uptake demand is less than available soil water) through inclusion of a water uptake potential function (equation (1)) where RWU$_z$ is the cumulative RWU demand at depth $z$ across the rooting depth, RD, with shape parameter $B_w$. A portion of unmet RWU demand from upper layers, EPCO, may be sourced from deeper layers during periods of shallow soil water limitation (equation (2)) yielding the adjusted water uptake potential, RWU'$_z$, following the approach implemented in Neitsch et al. (2011). Through this model structure, the RD parameter describes the maximum depth of RWU. The $B_w$ parameter characterizes the depth distribution of fine root density under the assumption that all fine roots exert equal water uptake demand. The EPCO parameter describes compensation mechanisms where RWU demand increases in wetter soil layers in response to water limitations in drier layers as described in Nehemy et al. (2019). A detailed description of the model and calibration parameters is presented in the supporting information (section S2).

\[ RWU_z = \frac{PET}{1-\exp(-B_w)} \left(1-\exp\left(-\frac{B_w z}{RD}\right)\right) \quad (1) \]

\[ RWU_z' = RWU_z + EPCO \times \max(0, RWU_z - AET_z) \quad (2) \]

We calibrated JoFlo with continuous daily discharge data for the time period 1 January 2000 through 31 December 2010. A parameter sensitivity analysis demonstrated that mean absolute error (MAE) exhibited...
sensitivity to RWU parameters (RD, BW, and EPCO) (supporting information section S3). We estimated the model parameters that minimized MAE with the dynamically dimensioned search algorithm (Tolson & Shoemaker, 2007). We calibrated model parameters for each catchment within the feasible parameter ranges (Table S2) through 10,000 parameter evaluations optimizing MAE. Model calibration was carried out twice for each catchment with both 0.25° (Chen et al., 2008; Xie et al., 2007) and (1/16)° (Livneh et al., 2013) precipitation forcing data. Two model calibrations were performed to determine if differences in underlying methodologies and spatial resolutions would allow one precipitation data set to yield a significantly more appropriate representation of catchment-scale daily precipitation, improved objective function values, and more realistic parameter estimates. For each catchment, we carried forward only the calibration result that minimized MAE. We discarded all catchments where optimal calibrations produced a daily Nash-Sutcliffe Efficiency (NSE) ≤ 0.6, as well as several catchments where total precipitation was less than total catchment discharge over the 10-year calibration period. We utilized NSE given the wide use of this objective function in hydrologic model calibration and previously defined limits of acceptability (Moriasi et al., 2007).

2.3. Comparison of Tree RWU Strategies

We clustered catchments meeting the minimum NSE criteria into the three classifications defined by previous plot-scale studies (Table S1). We compared catchment-scale model parameter values between these classifications with two-sample Kolmogorov-Smirnov tests following the parameter sensitivity methodology introduced by Spear and Hornberger (1980). The null hypotheses posit that calibrated parameter values for SR and DR as well as SR and MS catchments are generated from the same underlying process. Significance was evaluated at α ≤ 0.01, 0.05, and 0.1 thresholds.

Next, we used the optimal ecohydrological model parameters for each catchment to simulate the period 1990–2010 to compare annual \( \frac{AET}{PET} \) for each forest type. We then analyzed all catchments using a parametric model of the Budyko equation (equation (3); Zhang et al., 2004), where \( P \) is gross precipitation.

\[
\frac{AET}{P} = 1 + \frac{PET}{P} - \left( 1 + \frac{PET}{P} \right)^{-\frac{1}{\omega}}
\]  

(3)

We estimated the Budyko parameter \( \omega \) for each grouping of forest types (SR, DR, and MS) to understand how rooting strategies influence catchment-scale water partitioning under varied energy availabilities. Finally, we compared the monthly distributions of \( \frac{AET}{PET} \) for each group to understand the seasonality of RWU control of catchment-scale AET.
3. Results

3.1. Ecohydrologic Parameter Estimation

Calibration of 139 catchments (out of 264) met the minimum NSE threshold of 0.6 (further details presented in supporting information section S4). SR catchments exhibited significantly shallower rooting systems than DR (Figure 2j; p value = 0.01) and higher proportions of shallow roots (Figure 2h; p value = 0.01). The calibrated parameter controlling RWU plasticity, EPCO, indicated no significant difference between SR and DR catchments (Figure 2i; p value = 0.57). Parameter values between SR and MS catchments exhibited only significant differences in rooting depths (Figure 2j; p value = 0). The initial abstraction parameter, SeMIN, suggested greater abstractions in SR than DR catchments (Figure 2c; p value = 0.12) possibly indicating increased canopy interception. Several parameters controlling baseflow recession (A1 and B1) and surface runoff (C1, Ia, and PI) suggest MS catchments generated less runoff and faster gravity driven baseflow return than SR (Figure 2), possibly indicating forest cover influences on infiltration and subsurface water transport as described in Filoso et al. (2017) and Singh et al. (2019).

The spatial distribution of RWU parameters showed a weak latitudinal gradient with higher densities of shallow roots (BW, Figure 3a) and shallower rooting depths (Figure 3c) in northern regions and deeper roots in the southeast, in agreement with the metaanalysis of rooting depth observations compiled by Fan et al. (2017). The EPCO parameter describing RWU plasticity did not exhibit a strong spatial pattern (Figure 3b). We present distributions of BW, EPCO, and RD for all catchment forest types in supporting information Figure S3. Tree species generally demonstrated consistency in the vertical distribution of rooting density, BW, and RD (Figure S3). In contrast, the EPCO parameter demonstrated substantial variance for individual tree species (Figure S3).

3.2. RWU Control of Catchment ET

AET was a substantially lower proportion of PET in SR catchments compared to both DR and MS catchments (Figure 4a). Annual AET/PET was generally consistent for catchments with the same forest cover (Figure 4a). One SR catchment (White & Chestnut oak) exhibited high annual AET/PET despite having relatively shallow rooting systems (Figure S3). Further several DR and MS catchments (Live oak, Tanoak, and California mixed conifer) had lower annual AET/PET (Figure 4a) despite deeper RWU systems (Figure S3).

Both MS and DR catchments plot along the Budyko curve with least squares fit ω values of 2.34 and 2.12, respectively, similar to the globally estimated ω = 2.5 (Zhang et al., 2004) (Figure 4b). In contrast, SR catchments plot along ω = 1.79, possibly indicating the importance of functional RWU strategies in global partitioning between AET and catchment water yield. The seasonality of RWU demonstrated that the largest AET/PET differences between SR, DR, and MS catchments occurred during the peak growing season (July–September; Figure 4c). Midsummer AET/PET in DR and MS catchments indicated slight water limitation, whereas SR catchments exhibited shortfalls in catchment transpired water relative to atmospheric demand (Figure 4c). Outside of the growing season SR, DR, and MS catchments exhibited similar AET/PET indicating the influence of RWU strategies on the catchment-scale water balance is likely constrained to the growing season.

Figure 3. Spatial distributions of (a) root distribution shape parameter (BW), (b) RWU plasticity (EPCO), and (c) maximum rooting depth (RD). (up triangle = shallow root water uptake (SR); down triangle = deep root water uptake (DR); star = mixed tree species (MS)).
4. Discussion

4.1. Catchment-Scale Estimation of RWU Strategies

Understanding forest-scale RWU strategies is critical for developing a process understanding of hydrologic responses to forest cover change. While individual- and stand-level estimates of RWU strategies facilitated by stable isotopes in water and sap flux have become ubiquitous (e.g., Brinkmann et al., 2019; De Deurwaerder et al., 2018; Knighton, Conneely, et al., 2019), uncertainties in field methods and “scaling-up” these findings to the catchment remain intractable problems (e.g., Oerter & Bowen, 2019; Penna et al., 2018). The metaanalysis of Evaristo and McDonnell (2017) reviewed 531 studies of tree RWU derived from isotopes in water, of which 354 (~67%) used less than 10 xylem samples, possibly missing infrequent locations or periods of deep RWU. RWU depth variations have been explained by elevation (Martin et al., 2018), shallow soil water limitation (Meinzer et al., 2007), and competition with nearby species (Andrews et al., 2012; Volkmann et al., 2016). Knighton, Conneely, et al. (2019) found deep RWU by Tsuga canadensis was not well explained by topographic position, shallow soil water availability, or nearby competitors for subsurface waters. Our RWU depth estimates (Figures 2h and 2j) provided corroborating evidence of plant RWU depths to those reviewed by Evaristo and McDonnell (2017) through independent, temporally continuous measurements collected across larger spatial scales.

Physically based isotopic-aided models, such as EcH2O-iso, may assist interpretations of plant xylem water measurements (Kuppel et al., 2018). Douinot et al. (2019) and Smith et al. (2019) demonstrated that some refinement of RWU patterns (i.e., the $K_{\text{ROOT}}$ parameter) could be derived from calibration of EcH2O-iso to isotopic tracer data. Similarly, Wilusz et al. (2017) demonstrated that the age distribution of transpired waters could be estimated from a chloride tracer in catchment discharge. Though plant xylem water isotope measurements are becoming more common in hydrologic research (e.g., Brinkmann et al., 2019; Brum et al., 2019; De Deurwaerder et al., 2018; Evaristo et al., 2019; Knighton, Conneely, et al., 2019; Knighton, Souter-Kline, et al., 2019; Volkmann et al., 2016), they remain uncommon relative to discharge measurements.

The calibrated EPCO values (Figure 2) possibly indicated that modulation of RWU depths in response to soil water limitations may only be identified through plot-scale studies with detailed instrumentation (e.g., Nehemy et al., 2019; Volkmann et al., 2016), and/or plant- and pore-scale studies of water dynamics in

![Figure 4](https://example.com/figure4.png)

**Figure 4.** Catchment water balance (a) the ratio of actual (AET) to potential evapotranspiration (PET) (values in parenthesis indicate number of catchments), (b) Budyko framework showing SR (open), DR (blue), and MS catchments (orange), and (c) seasonal medians of AET/PET for SR (open), DR (blue), and MS catchments (orange) where error bars represent the 10th and 90th percentiles.
the rhizosphere (e.g., Daly et al., 2017). We observed no significant difference between the cumulative distribution functions of EPCO values between SR and both DR and MS catchments. Further, we note that forest types within each grouping exhibited evidence for both temporally static and dynamic RWU depths. This variability is high among individuals of each forest type for SR and MS catchments, but lower for DR catchments (supporting information Figure S3).

4.2. RWU Control of Catchment ET

Previous efforts to understand plant regulation ET have largely defined “vegetation cover” with remotely sensed normalized difference vegetation index (e.g., Xu et al., 2016), leaf area index (e.g., Zhang et al., 2018), photosynthetically active radiation absorbed by vegetation (e.g., Zhang et al., 2016), and gross forest cover change (Zhang et al., 2017), possibly neglecting differences in RWU strategies. Yang et al. (2016) demonstrated that the rooting depth of vegetation influenced continental water balances globally, though this effect was estimated through the simplified model of Donohue et al. (2012), which lacks a mechanistic foundation. Camporese et al. (2015) reached similar conclusions with a physically based subsurface model applied to a water-limited catchment in southern Australia. Our research suggests that functional RWU strategies influence catchment transpiration (Figure 4a) particularly in northern forests (Figures 3a and 3c) during the growing season (Figure 4c), highlighting the conditional sensitivity of catchment-scale water and energy balances to forest rooting strategies.

Higher forest tree species diversity possibly increases catchment-scale transpiration and primary production through complementary RWU strategies. Andrews et al. (2012) observed divergent strategies by Douglas fir and Lodgepole pine during shallow soil water limitation in Alberta, Canada, that allowed transpiration to persist through drought conditions. Similar RWU strategies were exhibited by *Vitex negundo* in mixed species forest stands in the Chinese Loess Plateau (Wang et al., 2017). Schwendenmann et al. (2014) observed separation in RWU depths by five cooccurring tree species in Panama, increasing total mixed-stand transpiration relative to that of nearby monocultures. Brum et al. (2019) suggested the spatial distribution of tree species in a tropical forest in Brazil was determined by hydrologically complementary rooting depths, light access, and drought tolerance. In contrast, Gaines et al. (2015) observed a uniform reliance on shallow (<60 cm) soil waters among trees in a mixed temperate hardwood catchment in Pennsylvania, USA. Our derived Budyko parameters, \( \omega \), suggest that mixed species catchments (\( \omega = 2.34 \)) more closely align with the global Budyko relationship (\( \omega = 2.5; \) Zhang et al., 2004). Catchments dominated by a monoculture of deeper-rooted and shallow-rooted trees exhibited lower catchment-scale transpiration rates, \( \omega = 2.12 \) and \( \omega = 1.79 \) respectively.

How tree species diversity influences ecosystem transpiration and production remains an open question (e.g., Ammer, 2019) though some research has proposed that mixed species catchments exhibit greater resilience to water limitation (Gonzalez de Andres, 2017; Jactel et al., 2017). Hydraulic redistribution of deeper soil waters by DR trees may reduce SR uptake limitations on catchment-scale transpiration in mixed species forests (e.g., Hafner et al., 2017; Sun et al., 2018), though increased tree diversity alone may not guarantee sustained transpiration (Grossiord, 2019). Future research should disaggregate the MS classification employed in this research to investigate how complementary mixtures of tree species and RWU strategies might modulate catchment-scale hydrologic fluxes.

5. Summary and Implications

Catchment-scale RWU patterns estimated from continuous streamflow records and inverse ecohydrologic modeling produced results that were generally in agreement with previous plot-scale studies utilizing measurements of stable isotopes in subsurface- and plant-stored waters. This approach offers some advantages as we derived RWU depths without resource intensive isotopic and sap-flux measurement and avoided the need to extrapolate from plot- to catchment-scale water fluxes.

RWU strategies that control transpiration substantially affect the water and energy balances across CONUS. Within the parameterized Budyko framework of Zhang et al. (2004), catchments with mixed tree species generally plotted along the globally derived Budyko equation (\( \omega = 2.34 \)), whereas deep (\( \omega = 2.12 \)) and shallow (\( \omega = 1.79 \)) rooting monoculture forests showed evidence of reduced latent heat losses and greater catchment water yields. Our research adds to the growing evidence that monoculture forests with a dependence on shallow soil moisture may be susceptible to increases in drought frequency under climate change (e.g.,
Andrews et al., 2012; Guo et al., 2018; Link et al., 2014; Reyer et al., 2010), particularly in the absence of deeply rooted neighboring tree species. Afforestation and reforestation efforts can possibly negatively impact water availability through increased catchment transpiration (Filoso et al., 2017; Zhang et al., 2017). Identification of candidate successional tree rooting behaviors may help to comanage socio-environmental benefits and ecological function as described by Chapron and Brancalion (2019).

Recent studies provide evidence that refined RWU can improve regional representations of subsurface hydrology and transpiration (e.g., Fisher et al., 2018; Kennedy et al., 2019; Wang et al., 2018). Our research supports the broader inclusion of root uptake control of transpiration in land surface and Earth systems models.

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