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Commentary: What ecohydrologic separation is and where we can go with it

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Key points:

- Isotope ratios of plant water should differ from water flowing in soils to streams and so we need to move beyond confirming this difference.
- To move beyond identifying ecohydrologic separation towards understanding it, we provide a framework for assessing soil water flow processes.
- By focusing on dynamics of how water infiltrates into the subsurface and becomes available to plants we can better interpret past findings.

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Abstract

The "Ecohydrologic separation" hypothesis challenged assumptions of translatory flow through the rooting zone. However, studies claiming to test ecohydrologic separation have largely diverged from testing how water infiltrates and recharges the rooting zone, towards identifying isotopic differences between stream water and plant water. We suggest that differences should exist among the isotopic compositions of water in plants, streams, and other subsurface pools in most scenarios and that ecohydrologic separation is not solely about observing fractionated isotope ratios in plant water. The discussion of ecohydrologic separation should refocus on how heterogeneous infiltration and root uptake processes lead to such differences. More generally, we propose that research objectives should involve interpreting isotope data in the context of processes, rather than settling on describing data patterns that have confounded interpretations (i.e., that plant and stream water isotopically differ). Consequently, we outline areas where plant and soil water stable isotope data can progress us towards improved understanding and representation of soil-water transport and plant-water recharge.

From ecohydrologic separation to two water worlds and back again

Ecohydrologic separation is a consequence of preferential flows through soils that result in soil-water heterogeneity. In 1864, Schumacher noted that "the permeability of a soil during infiltration is mainly controlled by big pores, in which the water is not held under the influence of capillary forces" (*quoted in* Beven & Germann, 1982). Over the century that followed, countless studies have described how water flows heterogeneously through soils: transport through soils is dominated by flow through macropores such that it may interact little with the water stored in smaller pores. Notable progress was made when Brooks et al. (2010) used stable isotopes of water (^{2}H and ^{18}O) to demonstrate a severe dichotomy between fast moving water and the slow moving storage that was presumably composed of smaller pore spaces (that consequently hold the water that is taken up by plants in the dry season). Roots took up water that fell as precipitation more than six months before the growing season, and there was little evidence that the tree-available water was displaced or diluted by the subsequent meters of precipitation that must have passed through those trees' root zones. Such temporal separation between the time of water input and its use by plants would not occur if water flow through the rooting zone is translatory (Figure 1a) or well-mixed (Figure 1b). Instead these data imply that preferential flows dominate: after plant-available pore spaces are refilled at the beginning of a wet season, precipitation mostly bypasses these storages (Figure 1c). In this commentary, we argue that evaluating the occurrence of this temporal *ecohydrologic separation*, as described by Brooks et al., is important because such patterns indicate which flow processes dominate infiltration (*sensu* Figure 1) and influence the interplay between root distribution and plant water availability. Using stable isotope data to classify the relative expression of translatory, well-mixed, and preferential flow would constitute progress towards conceptualizing relationships between soil properties and soil-water transport; it would also support building upon simply considering plant uptake from shallow versus deep zones, towards also considering uptake across pores with faster and slower flow.

Focusing on ecohydrologic separation, in the context of soil water flow mechanisms, contrasts with the objectives of many recent ecohydrology studies that use soil-, plant- and stream-water isotopic differences in dual-isotope space (δ^2H vs. δ^{18}O) to confirm the *two-water-worlds* hypothesis. While often used interchangeably, we distinguish '*ecohydrologic separation"* (defined above) from the '*two-water worlds"* which McDonnell (2014) introduced as a hypothesis of 'vegetation and streams returning different pools of water to the hydrosphere'. As stated by Pfister & Kirchner, 2017, the two-water worlds hypothesis is a test of a "homogeneity assumption" that would require the entire pool of waters contributing to streamflow and ET being well mixed. Indeed decades of theory and all recent isotope studies suggest that stream water and plant water should differ in δ^2H, δ^{18}O, or lc-excess (Figure 1d); accordingly, we consider that assumption of homogeneity to be reasonably invalidated (regardless of whether or not corresponding representations are still useful). However, diverse processes cause stream water to differ isotopically from xylem water, and consequently inferences drawn from stream-xylem differences are generally confounded.

We propose revisiting the original conceptualization of ecohydrologic separation (Brooks et al., 2010). This requires diagnosing the expression of different potential transport pathways, especially preferential flow, through examining how soil-water isotope compositions respond to new inputs (as abstractly represented in Figure 1a,b,c). If we accept flow (and thus isotopic) heterogeneity as a given, we can move towards more precise interpretations of stable isotope data (and thus more precise understanding of how water infiltrates into soils and recharges plant-available water). Towards that objective, we offer four observation-driven statements that we believe should be considered when investigating ecohydrologic separation.

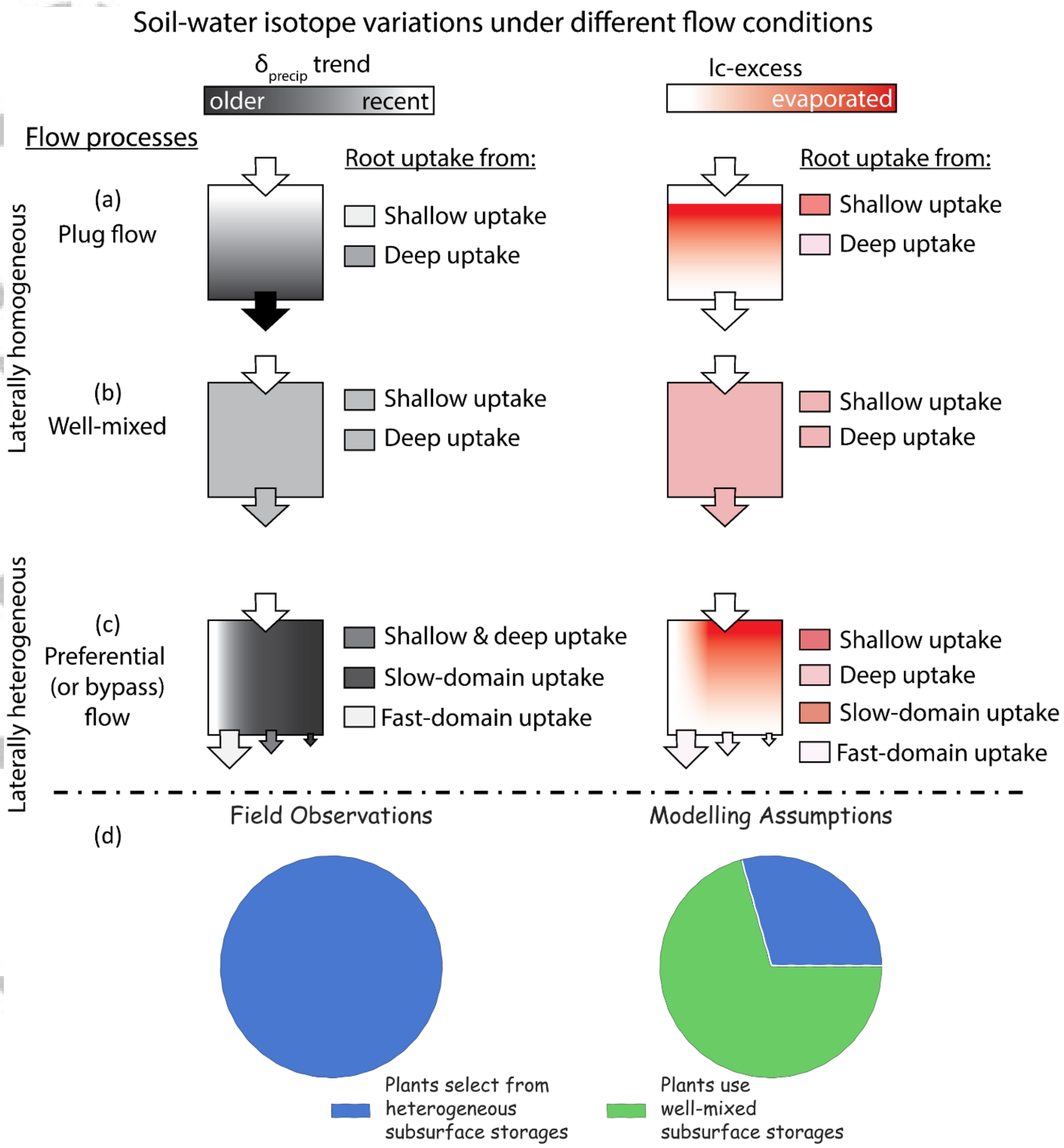

*Figure 1: (a-c) Stable isotope ratios of soil water, as a function of different idealized transport conditions manifest where isotopic variations reflect water-age variations (left column) or evaporation effects on lc-excess as defined by Landwehr & Coplen (2006) (right column). Color codes represent the age of water (left; from white to black representing young to old), assuming that the age series reflects distinct isotopic variations, and values of lc-excess from undergoing evaporative fractionation (right; from white to red representing non-fractionated to kinetically fractionated). (d) Models often assume laterally homogeneous conditions, yielding assumed profiles that match the first two rows on the figure; however, observations demonstrate that laterally heterogeneous processes affect the isotope depth profiles, and thus also which water is used by plants. The 51 modeling studies published since 2010 used for this diagram as listed in the supplementary material. Line-conditioined excess is used instead of deuterium excess because it is defined relative to local meteoric water lines, lc-excess = δ2H – a * δ18O – b, with a and b being the slope and intercept of the local meteoric water line, Landehr & Coplen, 2006).*

Soil waters seem to almost never be isotopically homogeneous, but it would be useful to identify under what conditions they are.

In few scenarios do soil and plant waters have identical isotope ratios, let alone plant- and stream-waters. We have reviewed and synthesized dozens of soil-and-plant water isotope studies in previous works (Sprenger et al., 2016; Sprenger et al., 2019b); none revealed isotopic uniformity across the critical zone and no study found complete mixing of new precipitation with previously stored water, to contribute to both streams and transpiration. Even in the absence of the evaporation effects on isotope variations, streamwater isotopes ratios should not equal those of soil water or plant water because water flows heterogeneously into and through the critical zone. Even in the improbable hypothetical scenario where isotopically varying precipitation percolates uniformly (i.e. translatory flow), we would still expect stream-isotope variations to differ from those of plants because most flow paths to roots are shorter than to the streams, resulting in higher variation in stem water than in streamwater.

Thus, we argue that isotopic homogenization is a very interesting case, because it indicates efficient mixing and mobilization of subsurface water by newly infiltrating water. Sprenger et al. (2019a) showed that even rising water tables briefly saturate soils but do not flush older waters and isotopically homogenize the soil-water pools. We can hypothesize that there are some conditions where stream, soil, and plant isotope ratios would be similar: e.g., with plant uptake from saturated zones with near-complete mixing of waters supplying streams and plants in riparian zones, if soils are coarse enough that near-stream groundwaters are indistinguishable from stream waters. Another cause could be a lack of isotopic variation in the input; however, precipitation isotope ratios vary systematically in most places on earth (Allen et al., 2019a). Regardless, for quantifying and conceptualizing the transport of carbon, nitrogen, or other solutes or pollutants, it is imperative to identify instances when inputs (either vertical or lateral) do seem to completely replace, displace, or mix with the previously stored soil waters. Thus, we should not consider a lack of ecohydrologic separation to be an unimportant null finding (unless it is due to a lack of input signal variation and lack of ability to detect separation), but actually one that contrasts with expectations.

Trees do not prefer water under high tensions, but they might root in less conductive pores

The finding that plant water is isotopically similar to bulk soil water (from cryogenic vacuum distillation) but not to suction-lysimeter water often spurs comments on how mysterious (or impossible) it is that plants ‘preferentially’ take up so-called “bound waters” that are under high tensions (Berry et al., 2017). We believe that confusion underlies this discussion. Indeed, cryogenic vacuum distillation of soil water can extract waters under higher tensions than can suction lysimeters, but this does not mean bulk soil waters are always reflecting a higher tension pool. A fully saturated soil sample will experience high water tensions during vacuum extraction and only small amounts of water remain in the soil; however, this does not mean that it was under high tension in the field when plants were potentially accessing it. Perhaps more significant is that suction lysimeters pull water; larger pores are more conductive and thus will transport water to lysimeters more quickly (Weihermüller et al., 2005). Thus, we posit that the difference between lysimeter and bulk soil water isotope ratios may often reflect the pore sizes sampled more so than their relative tensions.

We can see that tension does not always explain isotopic variations because they occur when tension is less relevant (e.g., in saturated conditions): in addition to the aforementioned Sprenger et al. (2019a) study that showed lysimeter water and bulk soil water isotopically differed even after saturation, soils in the Brooks et al. (2010) study were extremely wet throughout the winter when bypass flow occurred. For another example, Morales (2019) submerged in-tact soil monoliths into buckets of water and found that the water in these clayey soils did not homogenize even after one month. These examples highlight that mixing and equilibration across pores can take a very long time even without the influence of tension (due to saturation). Thus, isotopic heterogeneities in soils are not necessarily a product of tension variations, but also of contrasts in how water flows through different pores.

Accordingly, when plant water matches bulk soil water but not suction lysimeter water, this does not imply a preference for higher tension water. Instead, such differences imply that roots are located in less-conductive pores where water tends to travel more slowly and can reside for longer times, potentially across seasons. These variations in conductivity are not only reflections of roots occupying smaller pores, which occurs partially because roots grow towards water due to the so-called hydropatterning mechanism (Bao et al., 2014), but also that plants reduce conductivity around roots through compaction and mucilage production (York et al 2016). It has been long observed that soil surrounding roots has lower porosity (Dexter, 1987; Young, 1998). Furthermore, given that fungal hyphae can have much smaller diameters than roots (Smith et al., 2010), hypothetically, mycorrhiza associations may further facilitate access to slower moving pools. Importantly, these pools are not dead storage as these waters can move at various velocities, inconsistent with the common problematic description of these subsurface waters as “immobile” or “bound”. We therefore advocate for referring to this as bulk soil water, which can include water in finer pores and is less likely to include water in the coarsest pores (that already drained).

We note that hydrologists often ignore the role of nutrients in determining root distributions (see recent exception by Muñoz-Villers et al., 2020), despite extensive research showing root uptake patterns track nutrients (e.g., Caldwell et al., 1991; Kroon & Mommer, 2006; Kulmatiski et al., 2017), even at short timescales (Jackson et al., 1990). Given that pore-scale variations in water retention affect nitrogen dynamics as well (Hall et al., 2016), questions on how roots differentially access pores of different filling / draining dynamics may also be central to investigating how factors other than water availability further control rooting habits.

Concepts of plant-water availability should account for lateral heterogeneities

For decades, root-water uptake studies have primarily focused on identifying the depth of water uptake, by matching plant-water isotope ratios to isotope depth-profiles. However, such practices are challenged by the findings of Brooks et al. (2010) that demonstrate the additional need to also focus on the difference between faster and slower flowing waters in soils (e.g., Figures 1c). Isotope variations reflect only depth (and thus support inferring depth of root water uptake) in conditions controlled by evaporation or by translatory flow (Figure 1a). In reality, soil structure is three dimensional and not only do vertical flow rates vary laterally (as conceptualized in Figure 1c), but water also flows laterally at different rates. Both may yield lateral isotopic variations that can be as large as the vertical variations (Yang et al., 2016; Goldsmith et al., 2019; Penna & van Meerveld, 2019), which further complicates identifying depths of root water uptake. Theoretically, where preferential flow and heterogeneous transport dominate, depth of uptake may not be inferable from isotope variations unless a strong evaporation signal is present (Figure 1c). Instead, if preferential flows dominate, stable isotopes are better suited for identification of different pore sizes containing water of different ages, because these pores will be filled and drained at different time scales (e.g., Gerke & van Genuchten, 1993). For example, Allen et al. (2019b) showed that broadleaf trees used isotopically different water than collocated conifers despite having similarly shallow root distributions, suggesting uptake from different pore domains. Hypothetically, this may result from the broadleaf trees – which isotope ratios matches winter precipitation – having smaller-diameter fine roots and thus occupying smaller pores than conifers, as has been described of mixed broadleaf-conifer systems elsewhere (Bauhus & Messier, 1999; Comas & Eissenstat, 2004). Such findings challenge common assumptions that isotopic differences among tree xylem waters exclusively reflect rooting depth differences (vertical variability), rather than access to different soil pores that contain waters percolating at different velocities (horizontal variability).

Considering lateral variations in plant-water sources, rather than solely focusing on vertical variations (root depth) as in most concepts and model representations, supports testing of new hypotheses. For example, we posit that tree roots often do not use the most-recently infiltrated water (e.g., Brooks et al., 2010; McCutcheon et al., 2017; Hervé-Fernández et al., 2016; Evaristo et al., 2019; Allen et al., 2019b; Knighton et al., 2019) because they root in fine pores (with slower moving waters) where water is more reliably held, consistent with the needs of a long-lived organism to endure varying conditions (including droughts). Alternatively, we hypothesize that plants with more ephemeral life-histories (e.g., opportunistic or weedy species) dramatically reduce transpiration when water is unavailable and may use more quickly moving waters when they are transiently availably. This dichotomy has been evaluated in hot desert summers, where cacti and herbaceous plants tend to use recent precipitation whereas co-occurring woody plants rely more on precipitation from past seasons that is stored in deep soil layers (Ehleringer et al., 1991). Isotope measurements have previously been used to test ecological niche partitioning theories with respect to depth (see review by Silvertown et al., 2015), but the evidence of plants selecting older water prompts questions on how niches separate by pore size. We are not the first to ask how roots occupy different sized pores (e.g., Stewart et al., 1999). Nonetheless, using stable isotope data to ask how plants associate with different pore or soil structures could lead to better understanding which and how much infiltrating water becomes available to plants, ultimately allowing for framing niche partitioning findings in an ecohydrologic separation context.

Preferential flows should be represented to accurately model soil-water transport and plant uptake

Although soil-water isotope data are laterally heterogeneous (Figure 1d), indicating preferential flows (Figure 1c), most hydrological modelling studies use soil storage conceptualizations that neglect the processes that can create this heterogeneity; this affects our ability to model how infiltrating water reaches roots and enters the transpiration stream (Figure 1d). Recently, many studies have shown improved model representation of soil-water stable isotope dynamics through parameterizing preferential flow fractions (e.g., Stumpp & Maloszewski, 2010; Sprenger et al., 2018; Knighton et al., 2019), regardless of how those flowpaths are oriented within soils' 3-dimensional structure. At catchment scales, modelling studies show the need to represent heterogeneous incomplete mixing to match stream-water isotope observations (Fenicia et al., 2010; McMillan et al., 2012; van der Velde et al., 2015; Knighton et al., 2017). However, such practices remain an exception in tracer-aided models representing soil-water transport: about 2/3 of their applications over the last ten years assumed that evapotranspiration is supplied by a well-mixed soil-water pool (Figure 1d). Thus, if isotope-enabled models do not consider subsurface heterogeneous flow, they may be misrepresenting soil water transport processes given that they are calibrated to tracer data that mostly show evidence of heterogeneous, preferential flow through soils (see e.g., model comparisons in Stumpp et al., 2010, Mueller et al., 2014, and Sprenger et al., 2018). While various decades-old soil physical models account for heterogeneous solute/tracer transport (e.g., Gerke & van Genuchten, 1993; Hutson and Wagenet, 1995), dual-porosity or multi-region simulation of subsurface isotope tracer dynamics remain under used (considering the current state of observations). Although the role of vapor-phase exchange across the pore space in dual-porosity modeling approaches may diminish the heterogeneities (Sprenger et al., 2018), we admittedly only have limited evidence to guide representation of those processes.

A consequence of neglecting preferential flows includes underestimating the tail of soil-water residence time distributions and overestimating the amount of young water in soils. If all else is equal, greater contrasts between the ages of waters stored in soils versus those percolating through the profile occur when water flows more preferentially (Berghuijs & Allen, 2019). If preferential flows are not considered in simulations of soil-water systems, an inaccurately large fraction of precipitation contributes towards the displacement of previously stored soil water. Thus, if a model that does not represent preferential flow is fitted to data reflecting preferential flow, the turnover-time of water in the matric would be underestimated and the rate of flushing of stored solutes would be overestimated.

Another consequence of neglecting preferential flows is poorly estimated evapotranspiration flux isotope ratios, which may diminish the value of constraining earth-system models with isotope values. The parameterization of evapotranspiration in tracer-aided hydrology models is mostly through optimizing the tracer signal in catchment runoff, and not explicitly calibrated to the soil-transport processes that are explicitly represented. Improving our ability to simulate soil and plant isotope variations is key to interpreting isotope ratios in the atmosphere (Aemisegger et al., 2014; Good et al., 2015; Dee et al., 2015; Risi et al., 2016) or in plant waters (e.g., Kuppel et al., 2018; Knighton et al., 2019) to estimate the relative importance of evaporation and transpiration fluxes. Moving towards these larger scale applications in a non-speculative way requires an accurate representation of processes at the soil-profile scale.

Conclusion

Many recent studies demonstrate isotopic differences between soil or saprolite, plant, and stream waters, but it is often unclear how these observations differ from expectations. Underlying these differences is more than the unsurprising observation that plants use evaporatively fractionated soil water. While those observations are often invoked as evidence of ecohydrologic separation, ecohydrologic separation should be seen as a manifestation of diverse flow heterogeneities in the critical zone. We need to move beyond simply identifying “ecohydrologic separation” or “two-water worlds” behavior and dig deeper into the questions that originally prompted those hypotheses. Regardless, future work should be grounded in seeking to understand the physical and biological processes that underlie the tracer observations caused by the interplay of roots and the heterogeneous subsurface. Accordingly, we discuss several of such opportunities to advance the topic of ecohydrologic separation in isotope ecohydrology.

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