

Ecohydrologic separation of water between trees and streams in a Mediterranean climate

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Water movement in upland humid watersheds from the soil surface to the stream is often described using the concept of translatory flow^{1,2}, which assumes that water entering the soil as precipitation displaces the water that was present previously, pushing it deeper into the soil and eventually into the stream². Within this framework, water at any soil depth is well mixed and plants extract the same water that eventually enters the stream. Here we present water-isotope data from various pools throughout a small watershed in the Cascade Mountains, Oregon, USA. Our data imply that a pool of tightly bound water that is retained in the soil and used by trees does not participate in translatory flow, mix with mobile water or enter the stream. Instead, water from initial rainfall events after rainless summers is locked into small pores with low matric potential until transpiration empties these pores during following dry summers. Winter rainfall does not displace this tightly bound water. As transpiration and stormflow are out of phase in the Mediterranean climate of our study site, two separate sets of water bodies with different isotopic characteristics exist in trees and streams. We conclude that complete mixing of water within the soil cannot be assumed for similar hydroclimatic regimes as has been done in the past^{3,4}.

Links between plant water-use (transpiration) and hydrology have been examined quantitatively since the paired-watershed studies in 1921 (ref. 5). These watershed-scale experiments clearly demonstrated links between vegetation and streamflow. However, the paired-watershed approach can only infer the mechanisms behind these vegetation-streamflow interactions^{6–8}. Central to these inferred mechanisms is translatory flow downslope to the stream, and mixing of water within the soil profile^{1,2}. Complete mixing of water in the subsurface is the central tenant of most watershed hydrology models today^{9,10}. These concepts influenced ecology, leading to the idea that roots take up water from the same pool that is moving to the stream. However, is this really so? Using stable isotopes, Dawson and Ehleringer¹¹ demonstrated complex interactions between plant water and hydrological pools, showing that some streamside trees used deeper groundwater instead of streamwater. Nevertheless, diel fluctuations in baseflow at watersheds around the world demonstrate clear interactions between transpiration and streamflow¹².

Here, we directly explore links between hydrology and transpiration at the small watershed scale in a seasonally dry climate. Our central questions were: to what extent do trees and streams return the same water pool to the hydrosphere and how does this vary spatially within a watershed? These questions are fundamental to testing watershed hydrology models^{3,13} and coupled ecology-biogeochemical-hydrology models, which assume complete mixing of water moving through the soil towards the stream. Little if any

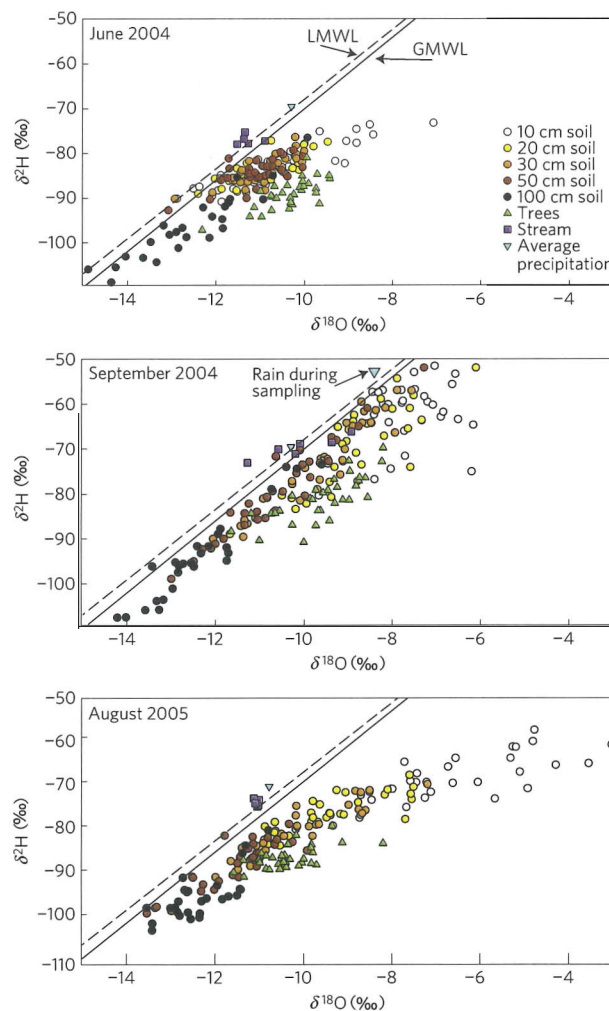


Figure 1 | Water isotopes ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) of bulk soil water, xylem water, stream and estimated annual average precipitation. Isotopes were collected on three different dates at 32 plots randomly distributed across Watershed 10. LMWL represents the local meteoric water line (dashed line, based on autumn 2006 precipitation data, $\delta^2\text{H} = 10.3 + 7.8 \delta^{18}\text{O}$) and GMWL is the global meteoric water line (solid line, $\delta^2\text{H} = 10 + 8 \delta^{18}\text{O}$).

empirical evidence exists to support or refute this assumption in humid regions. We examined $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of rainfall, streamflow and in soil and tree water collected from 32 plots throughout a 10 ha

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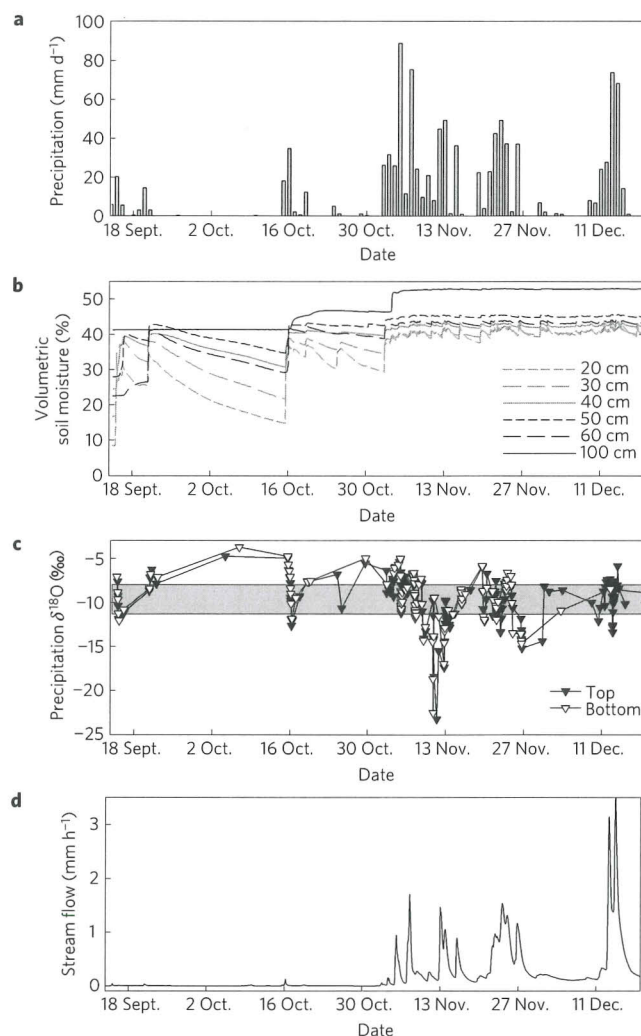


Figure 2 | Hydrologic dynamics during autumn 2006. a–d, Seasonal course of precipitation (a), soil moisture at six soil depths (b), precipitation $\delta^{18}\text{O}$ (c) and stream flow (d). The grey bar in c represents the range of isotope values measured in the stream during this timeframe. Precipitation isotopes were collected at both the top and bottom of the watershed in 5 mm increments, except in December when the bottom collector malfunctioned and collected samples integrated over a week. Precipitation and streamflow $\delta^2\text{H}$ values are not shown, but all samples fell on or very near the LMWL (Supplementary Fig. S4).

watershed at the H. J. Andrews Experimental Forest in Oregon. Our working hypothesis was that the $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of soil and tree water from plots near the stream would be more isotopically similar to streamwater than plots located further away. However, we did not find any plots where soil or tree water was isotopically similar to the stream (Fig. 1). Isotope ratios from streamwater and the average annual precipitation weighted by volume were similar (-73.0 and -72.5 ‰ for $\delta^2\text{H}$ and -10.7 and -10.8 ‰ for $\delta^{18}\text{O}$, respectively) and plotted on the local meteoric water line (LMWL), indicating that neither streamwater nor precipitation was measurably altered by evaporation. In contrast, all soil and tree water samples fell below the LMWL, indicating some evaporation. Surprisingly, vertical variation in soil-water isotopes at a single plot was much greater than spatial variation at any depth across the watershed (analysis of variance, $F = 106.6$ for depth, $F = 2.9$ for plots). Soil-water isotope ratios decreased with depth at all plots, from an average of -8.3 and -71.5 ‰ at 10 cm

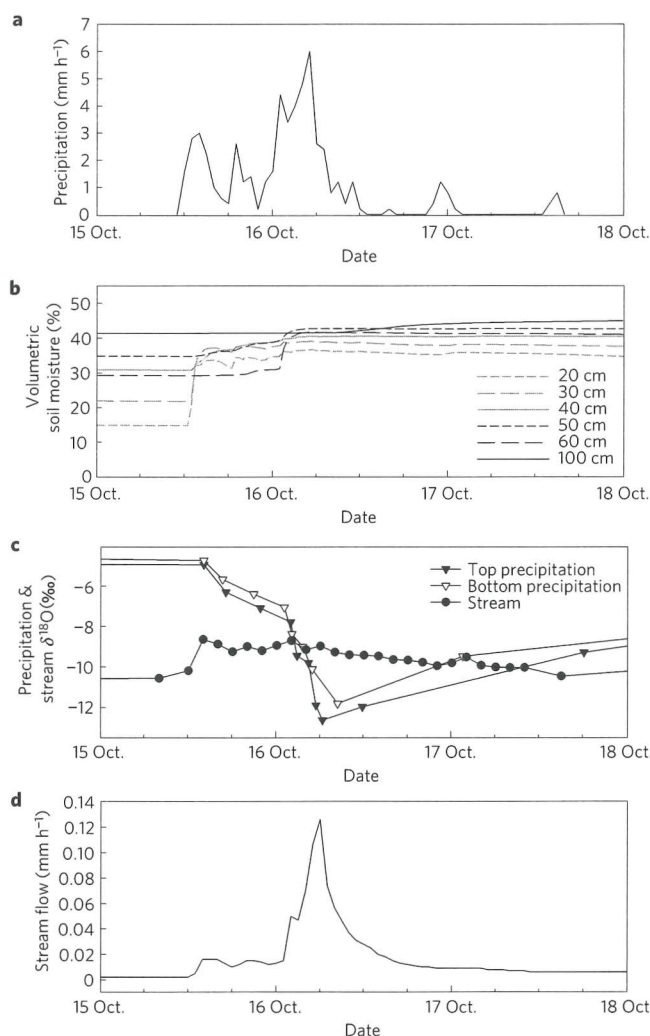


Figure 3 | Time course of the first large precipitation event in October 2006. The data are the same as shown in Fig. 2.

to -12.3 and -94.6 ‰ at 100 cm for $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively. This pattern was consistent for three different sampling times during two summers. Isotope ratios of tree water were similar to integrated values of the soil-water isotope ratios (-10.1 and -10.3 ‰ for $\delta^{18}\text{O}$ and -85.7 and -81.0 ‰ $\delta^2\text{H}$ for trees and soils, respectively). These findings suggest, paradoxically, that even in this steep, humid watershed, trees take up water from soil-water pools that do not contribute measurably to streamflow—and that streamflow shows no evidence of evaporative enrichment that is evident within the soil water during the dry summer. These two water worlds (mobile water expressed in the stream and tightly bound water represented by the plant water) are surprisingly distinct.

Although evaporation can account for the isotopic ratios falling to the right of the LMWL (Fig. 1), evaporation cannot account for variation along the line, particularly low isotope ratios found in soil water at depth: values that are lower than base-flow streamwater and the annual average precipitation isotope ratio. Furthermore, soil-water isotopic ratios collected in September 2004 were not correlated with isotopic ratios collected in August 2005 at the same depth and the same plot ($P = 0.93$, 0.73 and 0.50 for 100, 50 and 30 cm depths respectively), indicating that this tightly bound water is not the same year to year. Rainfall that occurred before sampling did not have isotopic ratios that could account for this pattern with

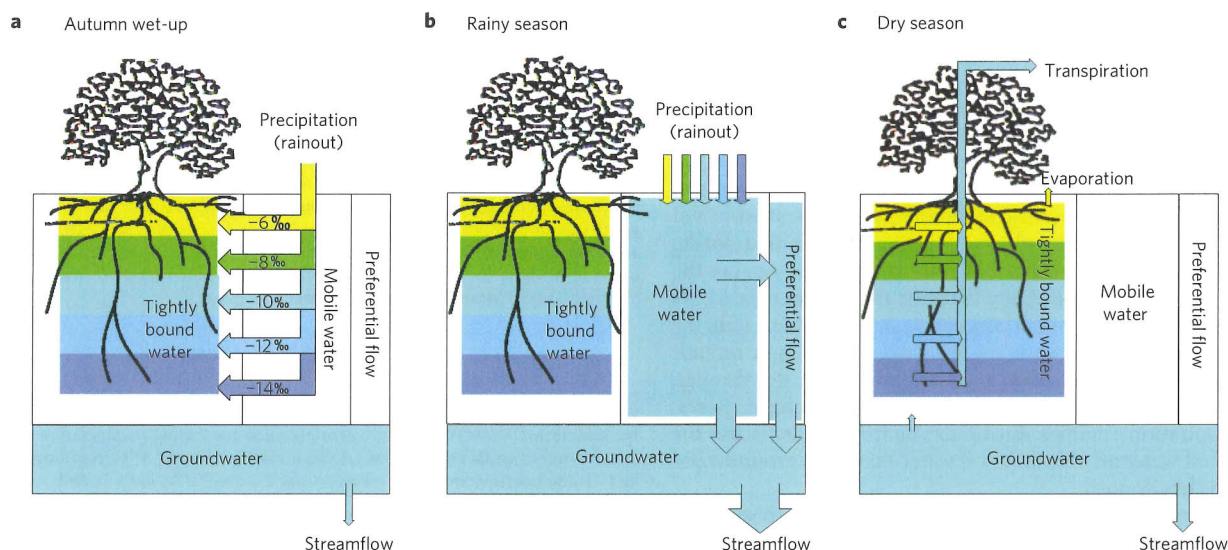


Figure 4 | Conceptual model for water resource separation in a Mediterranean climate. **a**, During autumn wet-up, pores within soil layers fill sequentially with progressively more isotopically depleted water as the wetting front moves to depth ($\delta^{18}\text{O}$ values shown) and the rainout process occurs during a large soil-wetting precipitation event. **b**, During the winter rainy season, precipitation moves through the profile through larger pores and preferential flow paths. **c**, During the dry summer, large pores drain, emptying mobile and preferential flow paths. The remaining soil water is tightly bound within small pores and used by plants for transpiration.

depth (Supplementary Fig. S1), leaving another paradox as to how these isotopic patterns were created.

We suggest that the observed depletion in heavy isotopes of water with depth is caused by soil-water recharge during the first large autumn rain event, whereby increasingly isotopically depleted precipitation through the event recharges deeper and deeper soil. We observed that precipitation isotope values (in 5mm increments) ranged from -3.7 to -23.2‰ for $\delta^{18}\text{O}$ and from -26.8 to -174.1‰ for $\delta^2\text{H}$ during 2006 early autumn rain events, spanning the range of isotopic values found in the soil. Rainfall isotope ratios became more depleted through rain events resulting from Rayleigh distillation of heavy isotopes^{14,15} (Fig. 2c), such that $\delta^{18}\text{O}$ values similar to deep soil values during summer (-14 to -12‰) were frequently observed at the end of intense rainfall. During the first storm where large rainout effects were noted, we observed the largest annual increase in soil moisture (Fig. 2b, Supplementary Fig. S2), but this event had minimal impact on stream discharge (Fig. 2d). Once soil moisture had reached a maximum, stream discharge became responsive to precipitation (Fig. 2a,d). For example, the increase in stream discharge after the first big storm on 15 October accounted for only 4% of rainfall input, whereas after soil moisture was fully recharged on 2 November, discharge accounted for 55% of precipitation input. Examining the interaction between soil-water recharge and the isotopic rainout effect during precipitation events reveals that precipitation isotopes were relatively enriched when the shallower soil-water content increased (Fig. 3). Later, when water content increased in deeper soil, the precipitation $\delta^{18}\text{O}$ values were markedly lower (approximately -12‰): the range observed at 1m depth during the summer. We hypothesize that this interaction explains the pattern of soil-water isotopes observed during the dry summers.

It is striking that these first waters that wet-up the soil are able to persist in the profile through an entire rainy season. If the observed isotopic pattern of soil water during the summer (Fig. 1) came from initial autumn rainout events, then precipitation over the remainder of the year did not mix fully with water in those small pores. We tested this by comparing the isotopic content of tightly bound soil water with mobile soil water. We measured soil water

collected in low-tension lysimeters, which represents mobile water, and bulk soil water extracted cryogenically¹⁶, which contains both mobile and matric-bound water. For each collection when lysimeter water was present, bulk soil water was always more depleted in heavy isotopes than lysimeter water collected at the same depth and location (Supplementary Fig. S3). Isotopic fractionation is not likely because all water samples fall on the LMWL, are within the range of precipitation inputs (Supplementary Fig. S4) and advection processes do not fractionate water isotopically¹⁴. This difference between pools could occur only if tightly bound water did not fully mix with water moving through the profile.

Soil in this watershed has a bimodal distribution of pore sizes, with approximately 40% of pores greater than 0.3 mm and 45% smaller than 0.03 mm in the upper soil. Below 1 m depth, this ratio shifts to 70% of pores smaller than 0.03 mm (ref. 17). As the clay content is over 30%, many of these small pores would be similar in size to clay particles, which are less than 2 μm . As a result of interactions between matric and gravitational potential, pores with the smallest body size (the largest diameter of the pore) are the first to fill, and pores with the smallest neck size (the smallest diameter of the pore) are the last to drain¹⁸. Therefore, pores with small diameters for both the body and neck fill first and drain last, thus containing water that would be relatively immobile compared with water in larger pores. As in saturated soils, hydraulic conductivity increases to the fourth power with increasing pore diameter, large pores would be the dominant pathway of water moving through the profile during the rainy season. However, during the summer once soils are below field capacity, the large pores that take the least tension to drain would be empty, and remaining soil water would be in small pores having matric potentials less than what gravity can drain. These pores have the longest water-residence time^{19,20} and probably have retained the same water that initially filled them during the autumn wet-up.

Primary forces in soils sufficient to drain smaller pores are tensions exerted by plant roots or direct soil evaporation. As evaporation from soil decreases rapidly with depth²¹, plant roots are primarily responsible for soil drying significantly below field capacity. As summer proceeds, progressively smaller pores would contain water held by lower matric potentials. We have observed

soil matric potentials in Douglas-fir stands at -300 kPa at 1 m depth to -1,200 kPa at 20 cm depth^{22,23} and Douglas-fir roots can continue to take up water at water potentials below -1,500 kPa (ref. 24). Thus, plants are able to take up tightly bound soil water when mobile water is not available during the dry summer.

Our results indicate that for this seasonally dry watershed within the Cascade Mountains of Oregon, soil water is separated into two water worlds: mobile water, which eventually enters the stream, and tightly bound water used by plants. We conceptualize that during the first autumn rains, water filling the small pores retains the isotopic signature of precipitation that first filled them (Fig. 4). As deep soils wet last (Fig. 3), small pores in deep soil would contain the most isotopically depleted water resulting from the isotopic rainout effect. Through the rainy season, water flows vertically through larger pores, and seems not to mix with water in smaller pores. Once transpiration resumes during dry summers, plants use the tightly bound water after mobile soil water that feeds groundwater and streams has drained.

This conceptual framework requires further testing to see if the underlying mechanisms are true, and if such separation of water resources holds for different climates and locations. Nevertheless, our work challenges the assumptions of translatory flow and the idea that plants and streams use the same water pools, and calls into question the assumptions of how water mixing in the subsurface operates regardless of location. Although this high degree of separation that we found would probably be observed only in other seasonally dry climates, our results imply that water with the longest residence time in soil (in small pores with low matric potential) is more likely removed by plants and not delivered to the stream. Previous estimates of streamwater-residence time in this watershed²⁵ are seriously challenged by this concept where segregation of water in small and large pore spaces result in very different residence-time distributions in the landscape. The implications of these findings are perhaps most profound for biogeochemical cycling and transport of nutrients to streams^{26,27}.

Methods

This research was conducted at the H. J. Andrews Experimental Forest in the Western Cascade Range of Oregon (44.2° N, 122.2° W). The climate is characterized by wet, mild winters and dry, cool summers. The mean monthly temperature ranges from 1°C in January to 18°C in July. Precipitation increases with elevation from about 2,300 mm at 410 m elevation to over 3,550 mm at 1,630 m, and less than 8% of precipitation falls during the summer (June–September). The study took place in Watershed 10 (WS10), a 10 ha watershed that was 100% clearcut in 1975 and is forested with ~30-yr-old Douglas-fir (*Pseudotsuga melliesii* (Mirb.) Franco). Elevation in WS 10 ranges between 425 and 700 m. Soils within this watershed are gravelly clay loams for the surface with lower layers consisting of gravelly silty clay or clay loams with textures averaging 27,35 and 38% sand, silt and clay, respectively¹⁷. Porosity is approximately 60%. Data have been collected on stream water discharge, climate, stream chemistry and vegetation since before clearcutting.

For our spatially intensive sampling, water samples for isotopic analysis were collected at 32 locations next to permanent vegetation plots randomly distributed throughout the watershed covering the range of elevation and aspect. Samples were collected at the beginning of the dry season, 28 June 2004, and once at the end of the dry season, 14 September 2004, and again on 28 August 2005. At each site, tree water samples were collected from suberized xylem of three trees, which reflects soil water from where the trees are withdrawing water, as trees do not fractionate water during uptake²⁸. Soil samples were collected from 5 depths (10, 20, 30, 50 cm and 1 m, if possible) and were divided into two parts, one for isotopic analysis and another for gravimetric soil moisture measurement. In addition several stream samples were collected at the weir during the day.

For our temporally intensive sampling in the autumn of 2006, water samples for isotopic analysis were collected weekly from five of the permanent vegetation plots: two in the upper watershed, north and south aspects, two in the lower watershed, north and south aspect, and a further mid-watershed, south aspect location. Xylem samples and soil samples were collected as outlined above, except that soil sampling was limited to 10, 20 and 50 cm depths. In addition, water was collected from low-tension (max 60 kPa of tension was applied) porous-cup lysimeters, (Soil Moisture Equipment Corp.) at 20, 50 and 1 m depth when water was present. Precipitation was collected in 5 mm increments at both the upper and lower parts of the watershed using passive sequential samplers²⁹. Stream water was collected hourly during storms and every 4–8 h between storms. Soil

volumetric water content was quantified using multi-sensor, frequency domain capacitance probes (EnviroSCAN, Sentek Pty) at 20, 30, 40, 50, 60 and 100 cm depth at 30 min intervals.

Samples for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ analysis in plant and soil water were collected in glass vials with polyseal cone inserts in the cap and sealed to prevent evaporation. Water was extracted from the plant and soil samples using cryogenic vacuum distillation¹⁶. Water samples were analysed for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ on an isotope ratio mass spectrometer (Delta plus, Finnigan) interfaced with a high-temperature conversion/elemental analyser (ThermoQuest Finnigan) or a laser absorption water-vapour isotope spectrometer (Model 908-0004, Los Gatos Research) located at the Integrated Stable Isotope Research Facility at the Western Ecology Division of the EPA, Corvallis, Oregon. All $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values are expressed relative to Vienna Standard Mean Ocean Water (VSMOW) in ‰

$$\delta^2\text{H} \text{ or } \delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000$$

where R is the ratio of deuterium to hydrogen atoms or ^{18}O to ^{16}O atoms of the sample and VSMOW. Measurement precision for the high-temperature conversion/elemental analyser was 1.5 and 0.2‰ for $\delta^2\text{H}$ and $\delta^{18}\text{O}$, respectively, and for the laser spectrometer, precision was 0.5 and 0.2‰ for $\delta^2\text{H}$ and $\delta^{18}\text{O}$, respectively.

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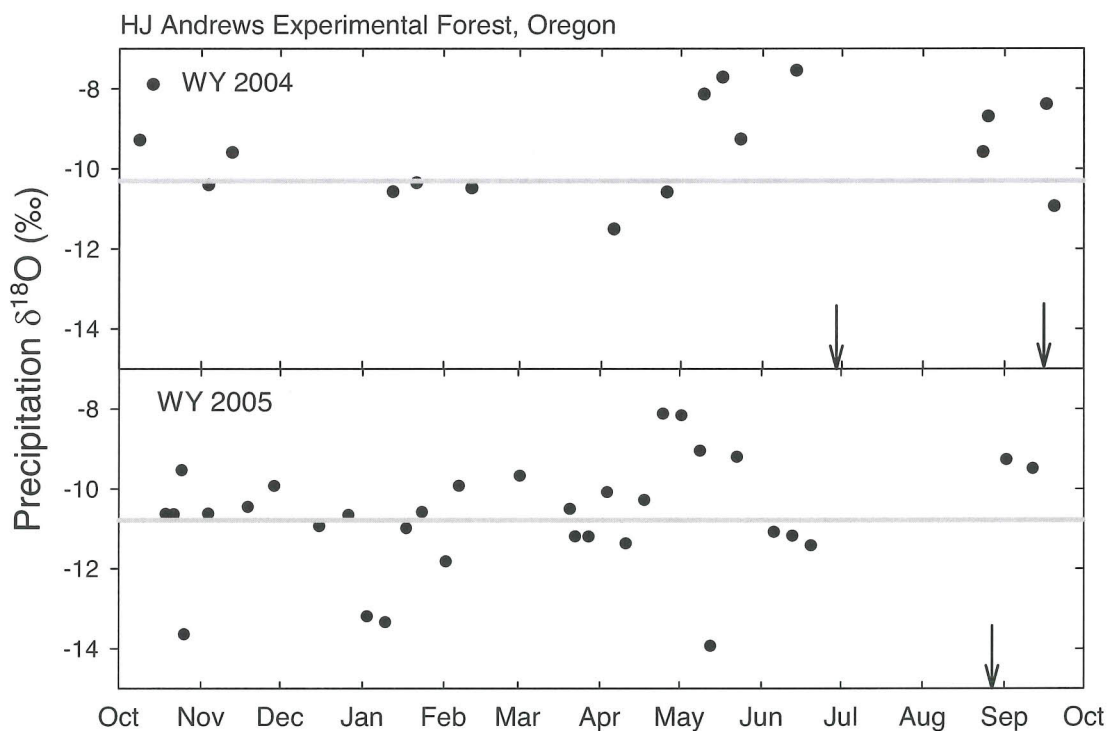
Author contributions

J.R.B. designed the research plan, obtained financial support, analysed and interpreted the data and wrote the paper. H.B. participated in data collection, analysis and interpretation, and contributed to the writing of the paper. R.C. coordinated sample collection efforts, led field crews and ensured the data quality of all field collections. J.M. advised throughout, assisted with interpretation of the results and contributed to the writing of the paper.

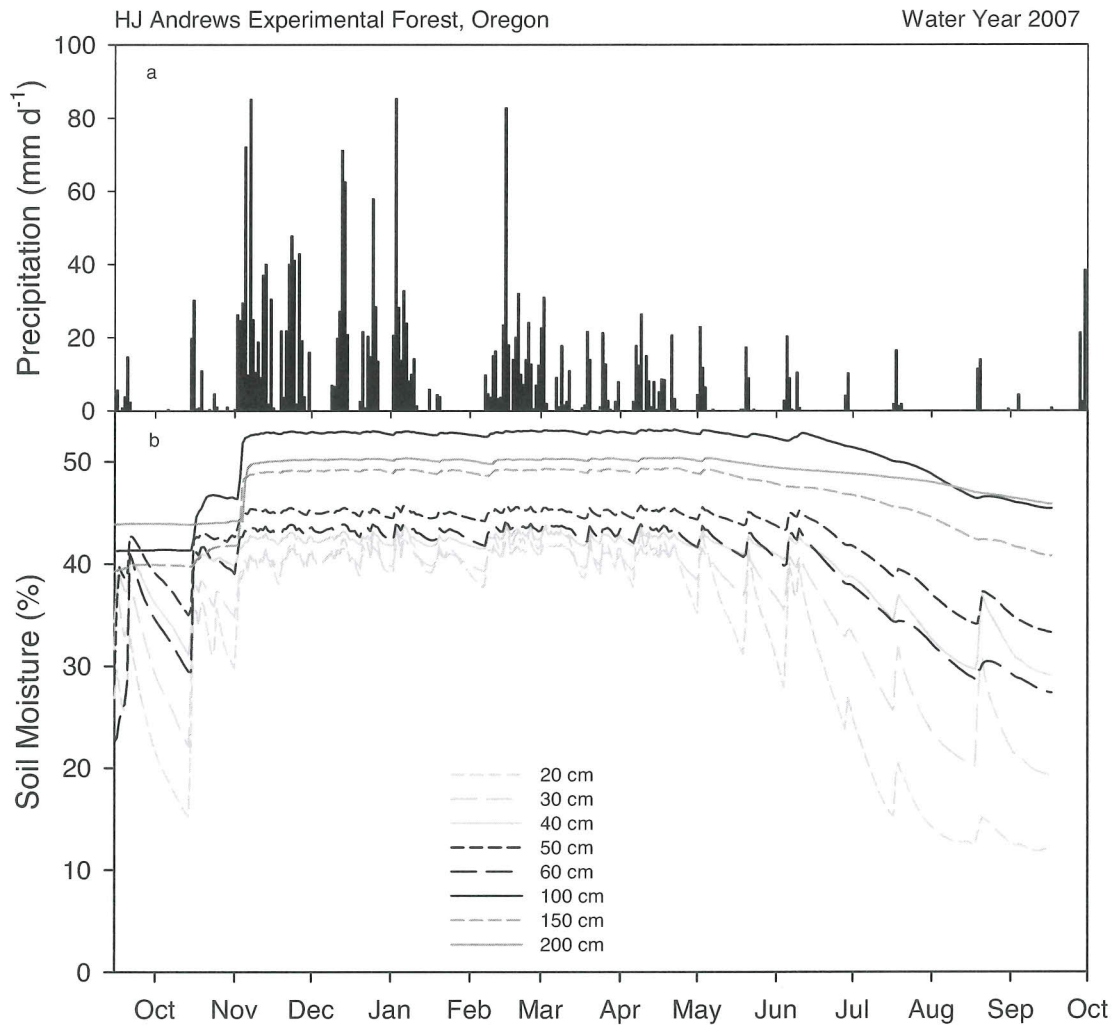
Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at <http://ngg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to J.R.B.

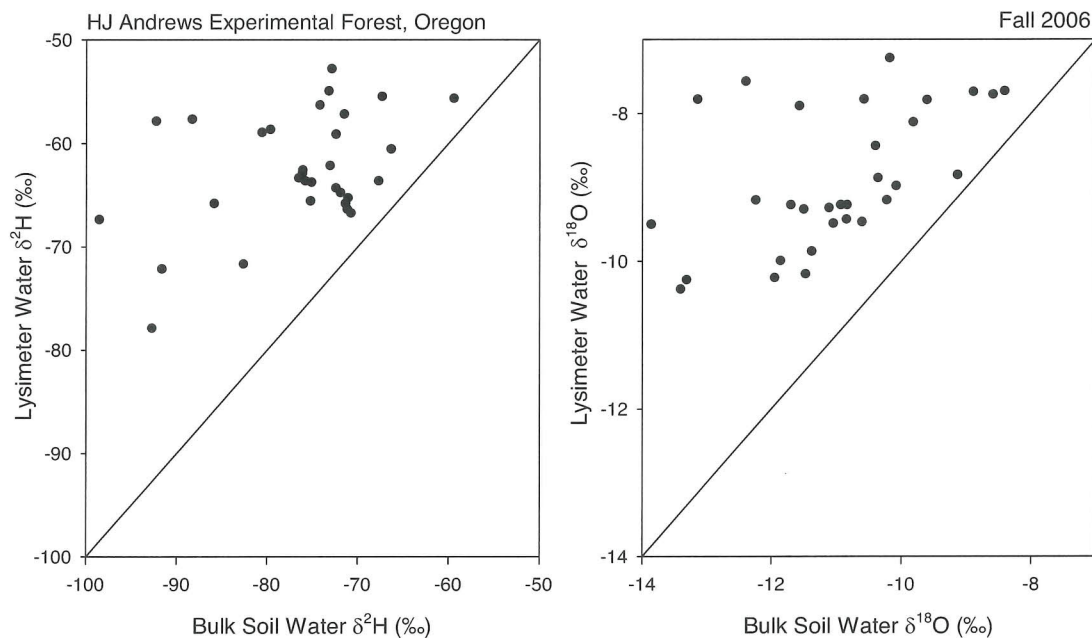
Figure Legends for Supplementary Information



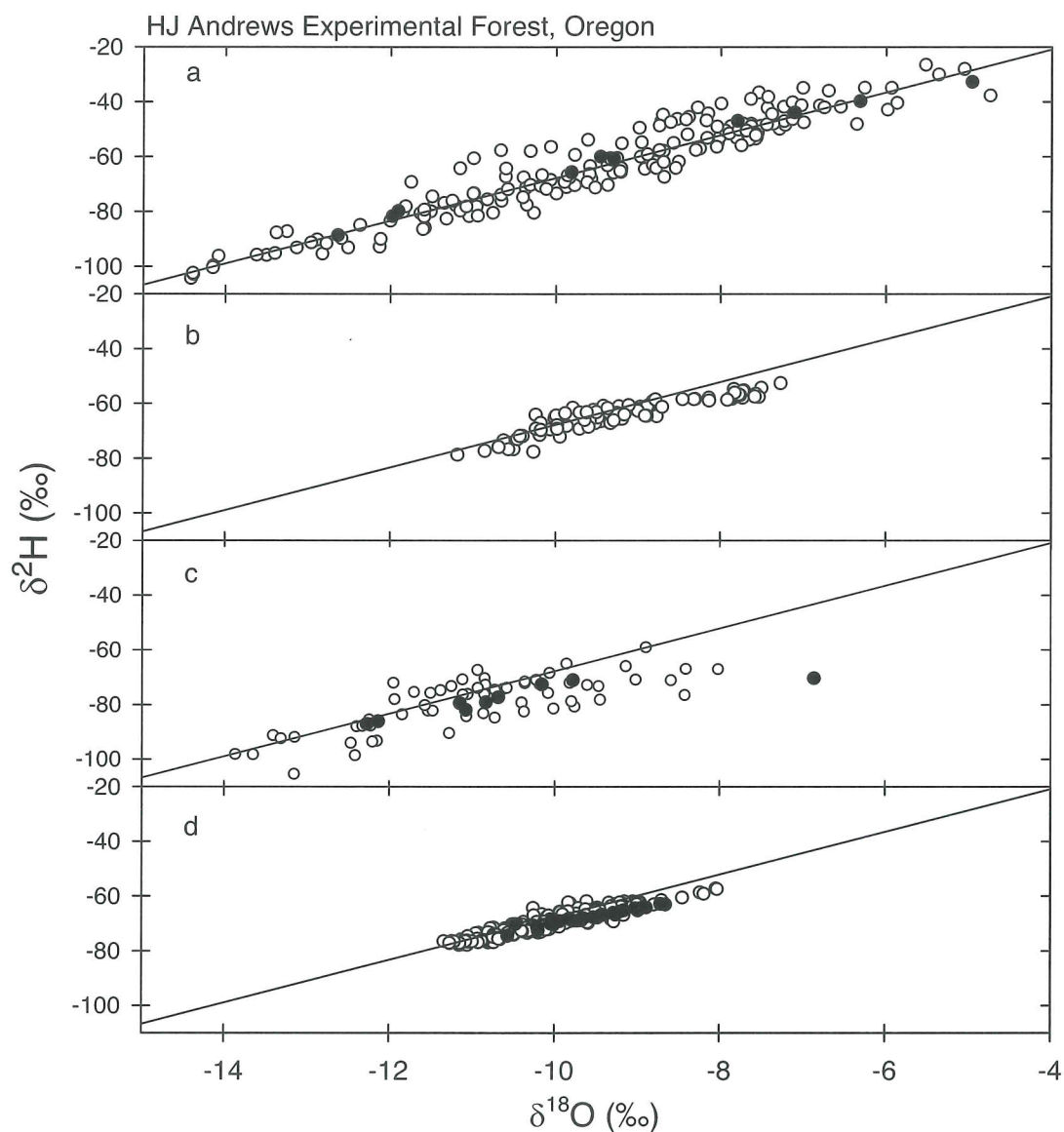
Supplemental Figure 1. Estimated weekly precipitation $\delta^{18}\text{O}$ values for water years 2004 and 2005. Arrows correspond to the sampling dates in Figure 1. Weekly $\delta^{18}\text{O}$ values for HJA precipitation were estimated from precipitation isotopes collected weekly in Corvallis, Oregon using the following equation: $\delta^{18}\text{O}_{\text{HJA}} = -4.778 + 0.658 (\delta^{18}\text{O}_{\text{Corvallis}})$, $N=40$, $R^2_{\text{adj}}=0.65$. Gray lines represent the volume-weighted annual precipitation $\delta^{18}\text{O}$ estimates.



Supplemental Figure 2: Precipitation from HJ Andrews Primet Climate Station (a) and volumetric soil moisture at WS-10 (b) from Sept 15, 2006 to Sept 25, 2007. Soil moisture stays saturated during the wet winters and only drops notably in June when plant transpiration increases and precipitation events decrease significantly. Soil water depletion attributed to plant transpiration during the summer months totaled ~300 mm averaging 2.2 mm per day.



Supplemental Figure 3: A comparison of lysimeter water isotopes to bulk water isotopes for samples collected at the same depth and time. Samples were paired based on the same time when the hand held vacuum was applied to the lysimeter and bulk soil water was collected. Lysimeter samples were collected a week later. However, pairing based on collection dates produced the same result.



Supplemental Figure 4: Water isotopes ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) of (a) precipitation, (b) lysimeter water, (c) bulk soil water, and (d) stream water collected during Fall 2006. The line is the LMWL (see Figure 1). Filled symbols are samples collected during the first large precipitation event in October (Figure 3).