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Determination of spatiotemporal variability of tree water uptake using stable isotopes (δ^{18}O, δ^2H) in an alluvial system supplied by a high-altitude watershed, Pfyn forest, Switzerland

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ABSTRACT

Sources of water use by 10 alluvial trees in various hydrogeological and ecological situations at the Pfyn forest (Wallis canton, Switzerland) were assessed by analysing ^{18}O and ^{2}H isotopes of precipitation, soil water at different depths, surface water, groundwater and xylem sap. The soil water line in a δ^{18}O versus δ^2H diagram shows evidence of kinetic fractionation related to evaporation. The tree water line is close to the soil trend; however, an additional enrichment may occur and could be related to xylem–phloem communication under water stress. At sites where the water table was at least 2 m below the ground surface, isotopic temporal variability of soils and trees was strongly linked with seasonal variation of soil water content. When soil water content was low and water table shallow, trees used both soil water and groundwater. When soil water content was high, this source was usually the dominant source for transpiration. In addition, some ecological strategies, reproduction or growth competition, could explain shifts in the utilization of different water sources, for example, from soil water to a mix of soil water and groundwater. At one site where soil water and groundwater were abundant throughout the year (next to the river course), neighbouring trees permanently used distinct water sources. This is consistent with a strategy of competition limitation, which would favour bank colonization. These results provide insight into the ecohydrological functioning of this system and will aid future management responses to both local and climate changes. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS   water uptake; deuterium; oxygen-18; trees; alluvial ecosystem; Switzerland

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INTRODUCTION

Alluvial plains are of special interest from both hydrogeological and ecological perspectives because of their high productivity for water supply and their exceptional natural value (e.g. Ward *et al*., 2002; Groundwater Directive 2006/118/EC from the European Parliament, 2006; Kløve *et al*., 2011a, 2011b; Bertrand *et al*., 2012). Additionally, they provide goods and services for human welfare such as chemical and biological purification of water (Tomlinson and Boulton, 2010). However, groundwater pumping, riverbed incisions and climatic changes may significantly affect the water balance (Kløve *et al*., 2011a, 2011b) leading to ecological changes in term of species distributions and/or productivity (Keller *et al*., 2005; Bertrand *et al*., 2012).

In the context of hydrological changes, the understanding of the mechanisms of water uptake by trees, which play a critical role for the entire ecosystem (Ewe *et al*., 1999), may help to determine the system response to water availability variability. One possible way to evaluate the spatiotemporal patterns of water uptake is to use natural tracers. Because oxygen-18 (^{18}O) and deuterium (^{2}H) fractionation does not occur during water uptake by roots and sap transfer within the xylem tissue (Zimmerman *et al*., 1967), several studies have successfully used δ^2H (e.g. Dawson and Ehleringer, 1991; Dawson and Pate, 1996), δ^{18}O (e.g. Chimner and Cooper, 2004; Asbjornsen *et al*., 2007) or both (Li *et al*., 2007; Wang *et al*., 2010) to determine the proportions of different water sources used by forest trees. Various factors can modify tree–water uptake such as season (e.g. Dawson and Pate 1996), life history stages (Feild and Dawson, 1998; Wang *et al*., 2010), life form differences (Williams and Ehleringer, 2000), functional group (Ehleringer *et al*., 1991; Dawson, 1993), tree species (Dawson and Ehleringer, 1991), plant size (Feild and Dawson, 1998; Meinzer *et al*., 1999), water availability and depth at which plants obtain their water (Chimner and Cooper, 2004), and the amount of recent rain (Xu *et al*., 2011). This highlights that there is not a simple and unique rule governing the source of water use by trees and that local conditions should be constrained to understand ecohydrological processes within a particular ecosystem. In addition, the majority of these studies were carried out in desertic, mediterranean, continental or tropical areas. However, the water uptake variability in alluvial systems supplied by high-altitude watersheds has not been investigated in detail.

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To fill this gap, the present study focused on the Pfyn alluvial forest in the Wallis Canton (Switzerland), located along the Rhône River in the Swiss Alps. In this area, the alluvial plain is governed by a glacial hydrological regime and a subcontinental climate (Schürch and Vuataz, 2000; Fette, 2005). Thus, the growth period is usually characterized by low precipitation but high river discharge leading to shallow water table conditions. In addition, this area presents contrasting ecological situations from typical alluvial stands to transitional mixed forests characterized by the presence of drought tolerant species. Because of this biodiversity, the protected Pfyn forest constitutes one of the 100 most important ecological zones at the European scale (Werner, 1985; Bendel *et al.*, 2006; OFEV, 2008).

Such an alpine system could be significantly modified by global and local changes, leading to both increases in discharge and seasonal changes to the distribution of discharge due to earlier and longer snow melt (Viviroli, and Weingartner, 2004; Beniston, 2006; IPCC, 2007). Moreover, the current third Rhône River correction (2009–2020), which aims at preventing flood damages, could locally affect the hydrological characteristics because of the lowering of the river bed. This would lead to a decrease of the recharge to the alluvial aquifer (Zwahlen, 2009).

For this study, $\delta^{18}O$ and δ^2H signatures in the various water cycle compartments were investigated. In the context of the Pfyn forest, this approach is well suited because the aquifer is mainly recharged by water coming from a high altitude (Schürch and Vuataz, 2000) and groundwater is expected to have a distinctly different isotope signature from local rain supplying soil water. The hydrological parameters were constrained by analysing isotopic signatures of rainwater, soil water and groundwater at various times of the hydrological

season and at different sites selected across the alluvial plain featured by different mean water table depths. The tree water uptakes were delineated by analysing the isotopic signatures of several trees located in these different forest stands and also characterized by distinct pedological (soil texture) and phytosociologic (species distribution, tree size) conditions.

This approach, on the basis of isotopic analysis, attempts to clarify the ecohydrological functioning of the area and could help to evaluate how changes in the water sources due to local (stream bed modification) or global (climate change) factors could affect the ecosystem.

HYDROGEOLOGICAL AND ENVIRONMENTAL SETTINGS

The Pfyn forest is located in the upper Rhone river valley, 2 km southeast of the town of Sierre, Wallis canton, Switzerland (Figure 1A), and occupies approximately 700 ha (Werner, 1985) at an altitude of 500 m a.s.l. (Bendel *et al.*, 2006). The site is surrounded by high-altitude mountains belonging to Helvetic (North of the valley) and Penninic (on the South) units. The valley is mainly composed of sandy gravel, partly overlain by rockslide deposits from the Würm period and forming small hills reaching 700 m a.s.l. (Schürch and Vuataz, 2000). With an average annual rainfall of only about 587 mm, the Pfyn forest is the driest site in Switzerland (Schürch and Vuataz, 2000). The heterogeneous Rhône alluvial sediments constitute the primary aquifer. The upper Rhône in this area is a third-order river according to Stralher's (1957) classification. Its main tributaries come from high altitudes and are supplied by snow and glacier melt in spring and summer (glacial regime) (Schürch and Vuataz,
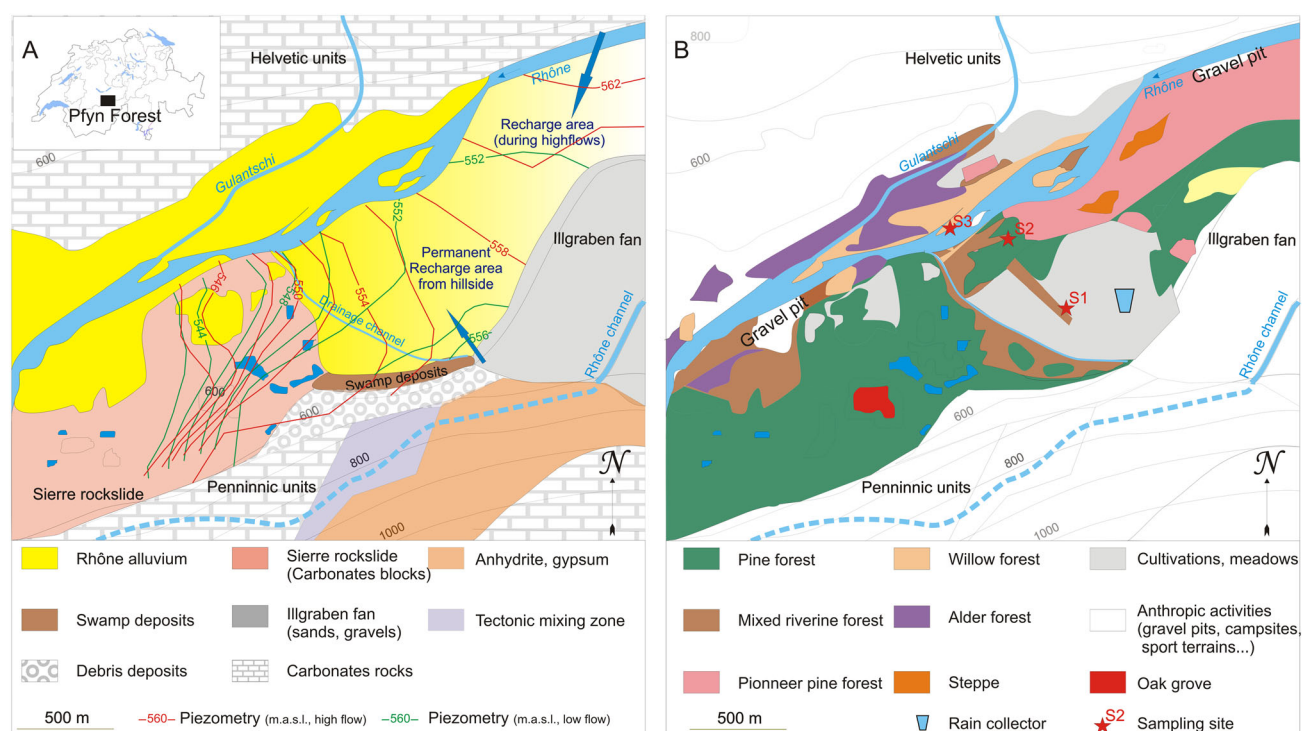

Figure 1. (A) Location and generalized geologic map of the Pfyn forest area, Canton Wallis, Switzerland (modified from Schürch and Vuataz, 2000); (B) ecological settings and location of sampling points.

2000; Fette, 2005). On the basis of a dense network of monitoring wells, Schürch and Vuataz (2000) identified two dominant recharge areas of the alluvial aquifer (symbolized by arrows on Figure 1A): the northeastern limit of the Pfyn forest where surface water moves from the Rhône river on a section of about 700 m length southward into the alluvium and the east-central part of the area where an inflow from the southern slopes of the valley supplies the Rhône alluvium along a section about 800 m wide. From a temporal point of view, the aquifer is largely supplied by the river during the high water period in summer (Figure 1A). During the low-level winter period, the local subsurface flow coming from the central-east part of the area remains almost the only source of water entering the alluvium.

The ecological value of both the riverine fringe of the Rhône and lotic systems of the Sierre rockslides are broadly recognized. From upstream to downstream (Figure 1B), phytocoenosis vary from dry environment associations (represented by *Pinus sylvestris*, *Stipa sp.*) to floodplain associations (mainly represented by *Alnus incana* and *Salix sp.* characteristic of minor riverbed and by *Populus sp.* and *Prunus avium* on stabilized alluvial terraces). Between these two end-members, a mixed transitional forest has been developed. The pedological characterization revealed that the soils consist of fluviosoils (Baize *et al.*, 2009) featured by horizontal and vertical heterogeneities of texture. Sand, loam and clay textures are sorted in layers, with presence and thickness of layers varying with location (Table I).

METHODOLOGICAL APPROACH

Sampling

The approach consisted of sampling water cycle components including rainwater, surface water, groundwater, soil water at various depths and xylem sap to identify the hydrometeorological conditions and the isotopic signatures of water. A biweekly field campaign was carried out between 22 April 2010 and 31 August 2010, and a monthly campaign between 31 August 2010 and 16 February 2011 (16 field investigations).

Three sites with various ecohydrological characteristics were selected across the plain (Figure 1B; Table I), in which the sampled trees were representative of the dominant phytocoenosis. The site S1 is located at 1 km to the south of the main river course, close to crop fields. The mean groundwater level is the deepest (annual mean depth of the water table during the study: −4 m). The sampled trees were a 15-m-high willow (*Salix alba*), a 10-m-high wild cherry (*Prunus avium*) and a 30-m-high poplar (*Populus nigra*). This latter tree is located at the boundary between the forest stand and a crop area, whereas the others were located within the forest stand. S2, where the annual mean depth of the water table during the study was −2·3 m, corresponds to the mixed riverine forest, which is featured by the cohabitation of deciduous and coniferous species. A 2-m-high willow *Salix purpurea*, a 10-m-high poplar *Populus nigra*, a 10-m-high wild cherry *Prunus avium*, a 10-m-high alder *Alnus glutinosa* and a 7-m-high Scots pine *Pinus Sylvestris* were sampled. At

S3 (the annual mean depth of the water table had not been directly measured but had been evaluated to be about −1 m), located in a gravel bar in the middle of the main Rhône river course, a 2-m-high willow and a 2-m-high alder were monitored.

Rainfall was measured with a 400 cm² pluviometer installed close to S1 (Figure 1B) and connected to a data logger (DT5, dataTaker), registering precipitation amount every 15 min. Daily temperatures were obtained from the Federal Office of Meteorology (MeteoSwiss), for the Sion weather station located 15 km to the East of the studied area (46°13′40″ N; 7°21′31″ E; 510 m a.s.l.). Hydrogeological conditions were assessed by measuring groundwater depth at sites S1 and S2, in boreholes installed by the regional centre of alpine study (CREALP, Schürch and Vuataz, 2000).

For isotopic characterization, rainwater samples were collected via the pluviometer connected to a sampling bottle by a plastic tube. To solar-induced isotopic fractionation (Clark and Fritz, 1997), paraffin was added to the sampling bottle, and the bottle was buried. Groundwater samples were collected after purging at least five well volumes from monitoring wells constructed of 10 cm diameter slotted pipe. Soil samples were taken at sites S1 and S2 at various depths (0–20, 20–40, 40–60 and 60–80 cm). Because of frequent truck traffic close to S3 (Rhône correction), soil was not regularly sampled here. Plant samples were collected by cutting stem sections from branches that appeared fully suberized. Soils and tree stems were stored in plastic bags that had been evacuated of air. Water, soils and plants were stored at 4 °C at the laboratory before analysis.

Laboratory analyses

Isotope analyses were carried out at the Center for Hydrogeology and Geothermics of the University of Neuchâtel by using off-axis integrated cavity output laser spectroscopy (DLT 100 from Los Gatos Research, Inc.). For water samples, the method of Lis *et al.* (2008) was used. This method directly injects liquid water, which is then transformed into vapour (under vacuum conditions). The absorption of specific wavelengths by the different isotopomers of H_2O (i.e. $H_2^{18}O$, $^1H^2H^{16}O$, ...) by the vapour is then evaluated, and $^{18}O/^{16}O$ and $^2H/^1H$ ratio are determined.

Soil samples were analysed according to the methodology described by Wassenaar *et al.* (2008), using a H_2O_{liquid}–H_2O_{vapour} water equilibration in freezer bags. This method is based on the fact that pore water in geologic core samples placed in a closed isothermal container will quickly reach liquid–vapour and isotopic equilibrium with the enclosed headspace. By carefully controlling the temperature and time of equilibration and by measuring the stable isotopic composition of vapour samples and a reference vapour sample equilibrated with water with a known isotopic composition, the $\delta^{18}O$ and δ^2H of the pore water can be determined. For xylem sap, because Scrimgeour (1995) demonstrated that plant samples may be used directly for equilibration with CO_2 before isotope ratio mass spectrometer analyses and provided accurate data, the method of Wassenaar *et al.* (2008) was similarly used, and

Table I. Pedology and sampled trees at S1, S2 and S3 sites.

Site	Tree species	Soil	Photo
S1	15 m willow (*Salix alba*); 10 m cherry (*Prunus avium*); 30 m poplar (*Populus nigra*)	0–1 cm: litter of the year; 1–2 cm: sandy-silty horizon with 80% of organic matter; 2–20 cm: silty-sandy horizon with 30% of organic matter; 20–45 cm: silty-sandy to sandy horizon without organic matter; 45–80 cm: silty horizon without organic matter.	
S2	2 m willow (*Salix purpurea*); 10 m wild cherry (*Prunus avium*); 10 m poplar (*Populus nigra*); 10 m alder (*Alnus incana*); 7 m Scots pine (*Pinus sylvestris*)	0–0·2 cm: litter of the year; 0·2–1 cm: sandy horizon with 95% of organic matter; 1–4 cm: sandy horizon with diffused organic matter; 4–54 cm: sandy horizon with areas of coarser material; 54–63 cm: sandy-silty horizon with organic matter; 63–80 cm: sandy horizon with organic matter. Skeleton: 90%, siliceous large pebbles (diameter until 50 cm).	
S3	2 m willow (*Salix purpurea*); 2 m alder (*Alnus incana*)	Soil bare; patchwork of sandy and pebble areas.	

H2O$_{\text{xylem-sap}}$–H2O$_{\text{vapour}}$ water equilibration was performed prior to vapour analysis

The stable isotope values were expressed relative to Vienna Standard Mean Ocean Water (V-SMOW) in ‰ (Equation 1):

$$\delta^{18}O \ \text{or} \ \delta^2 H(‰) = \left(\frac{R_{\text{sample}}}{R_{\text{SMOW}}} - 1\right) \times 1000 \quad (1)$$

where R refers to the hydrogen or oxygen stable isotopic composition (^{2}H/^{1}H or ^{18}O/^{16}O ratio) of a sample and standard, respectively.

Precision is 0·2‰ for δ^{18}O and 1‰ for δ^2H. For plants and soils, given their large ranges of signatures, few sample analyses, with weaker precision (until 0·4‰ for δ^{18}O and 2‰ for δ^2H) and which could not be done again because of a limited amount of sample, were considered acceptable.

Gravimetric soil water content was determined through weighting of samples, both prior and post sample drying. Evaporation of water from soil samples was performed

by heating the samples to 110 °C for 24 h. Results are expressed in %.

Test of reproducibility at tree scale

To evaluate if similar trees show comparable isotope trends, two neighbour trees (wild cherries at S1) with the same size (10 m) were sampled throughout eight field investigations. Statistical tests confirmed that two individuals of one species present similar signatures in same conditions (same mean and same variance, Figure 2; Table II). The presented results for the wild cherry at S1 will concern the tree analysed during the entire field campaign (16 field investigations).

Analysis of data

All statistical analyses were performed using XLSTAT 2011. Analyses of variances (ANOVAs) were used to assess the factors influencing variability of isotopic composition of soil and xylem waters. Such an approach was revealed useful to discriminate the importance of hydrometeorological, hydrodynamic and ecological factors influencing water uses (e.g. Xu *et al.*, 2011). Spatial and ecological (sites, soil layer depths, size and species of individuals) as well as temporal (precipitation height, temperature, groundwater level) factors were tested. The spatial/ecological parameters may be included all together in the calculation, whereas the chosen temporal parameters were revealed to be correlated over time (overlapping effect) and had to be analysed in distinct ANOVA tests.
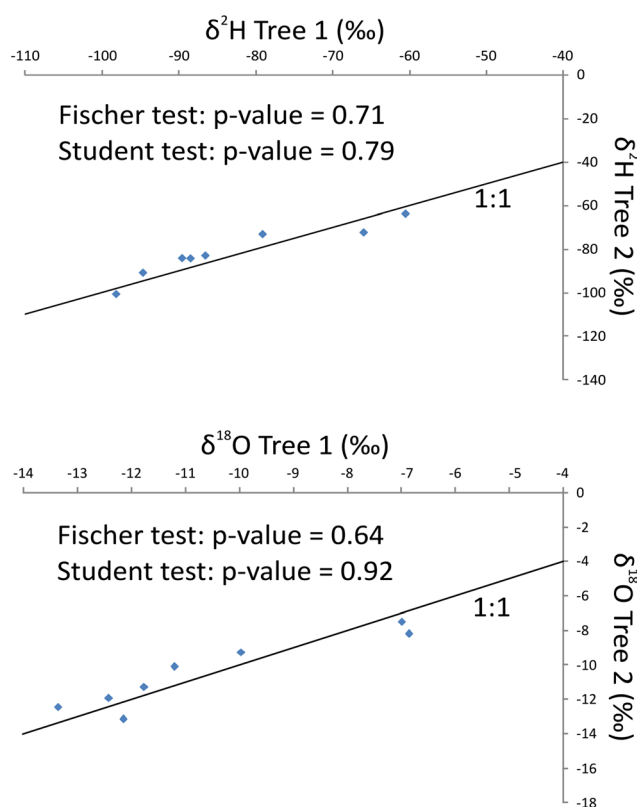
Table II. : Statistics of isotopic measurements (in ‰ vs Vienna Standard Mean Ocean Water). In bold: δ^{18}O; In normal police: δ^2H.

Rain	**−9.9 ± 3.6** −74 ± 28		
Site	S1	S2	S3
Rhône			**−15.1 ± 1** −108 ± 4
Groundwater	**−14.0 ± 0.4** −105 ± 2	**−14.9 ± 0.9** −107 ± 4	n.d. n.d.
Soil water 0–20 cm	**−10.0 ± 3.6** −71 ± 22	**−8.8 ± 4.2** −74 ± 28	n.d. n.d
Soil water 20–40 cm	**−11.4 ± 3.0** −83 ± 19	**−9.5 ± 4.2** −74 ± 28	n.d. n.d
Soil water 40–60 cm	**−13.5 ± 2.3** −96 ± 14	**−10.9 ± 2.4** −79 ± 16	n.d. n.d
Soil water 60–80 cm	**−12.4 ± 2.1** −90 ± 14	**−10.2 ± 1.7** −76 ± 13	n.d. n.d
Poplar	**−8.8 ± 2.9** −84 ± 8	**9.8 ± 2.4** −76 ± 17	
Wild cherry (16-field investigations)	**−10.5 ± 2.5** −85 ± 13	**−10.2 ± 2.4** −81 ± 15	
Wild cherry (eight-field investigations)	**−10.5 ± 2.0** −81 ± 12		
Willow	**−10.7 ± 2.4** −90 ± 7	**−10.3 ± 2.0** −83 13	**−11.7 ± 1.1** −92 8
Alder		**−11.6 ± 1.4** −90 ± 10	**−9.6 ± 3.5** −75 ± 26
Scots pine		**−8.2 ± 3.3** −70 ± 20	

The evaluation of water use proportions (soil layers, groundwater) was performed using the multisource mass balance method implemented in the IsoSource software (Available via http://www.epa.gov/wed/pages/models.htm; see Phillips and Greggs, 2003). Through this approach, the soil/groundwater (δX_1–δX_5) and xylem (δX_t) isotopic signatures at time t are used to determine the possible proportions of each soil layer (f_1–f_4) and groundwater (f_5) to the xylem water (Equations 2 and 3):

$$\delta X_t = f_1 \delta X_1 + f_2 \delta X_2 + f_3 \delta X_3 + f_4 \delta X_4 + f_5 \delta X_5 \quad (2)$$

$$f_1 + f_2 + f_3 + f_4 + f_5 = 1 \quad (3)$$

In this method, all possible combinations of each source contribution (0–100%) are examined in small increments (2%). The uncertainty level (tolerance of deviation from the exact solutions) is set between 0.1‰ and 2‰ to fit with the precision of the laboratory measurements. However, the great majority of calculations were performed with a tolerance ranging between 0.1‰ and 0.4‰. Sensitivity analyses were performed for different fractional increments and uncertainty levels. This resulted in no significant change in fractional contribution ranges from each soil depth, similar to the sensitivity tests performed by Wang *et al.* (2010).

This approach has three advantages (Asbjornsen *et al.*, 2007; Wang *et al.*, 2010): (i) it can analyse more than two water resources; (ii) it provides a means of more

δ²H Tree 1 (‰)

Fischer test: p-value = 0.71
Student test: p-value = 0.79

1:1

δ²H Tree 2 (‰)

δ¹⁸O Tree 1 (‰)

Fischer test: p-value = 0.64
Student test: p-value = 0.92

1:1

δ¹⁸O Tree 2 (‰)

Figure 2. Comparison of isotopic data over eight-field investigations between two 10-m-high wild cherries at site S1.

systematically analysing the data, thereby reducing the likelihood that observer bias will alter the interpretation; and (3) it provides a more quantitative assessment of the probable relative contributions of soil water from different depth intervals for plant water use.

RESULTS AND DISCUSSION

Isotopic variability of groundwater, rain, soil and plant water

Table II presents the statistics of the $\delta^{18}O$ and δ^2H signatures for the different water compartments analysed at S1, S2 and S3. Local meteoric water line (LMWL), soil water line, tree water line and groundwater and river isotopic signatures are plotted in a $\delta^{18}O$ versus δ^2H diagram (Figure 3).

Groundwater and river water had more negative and less variable isotopic signatures than rain, soil and plant waters (Table II). For instance, S1 groundwater ranges from $-14\cdot5$‰ to $-13\cdot4$‰ $\delta^{18}O$ (Mean: $-14\cdot0 \pm 0\cdot4$‰) and river water ranges from -18‰ to $-14\cdot4.\delta^{18}O$ (Mean: $-15\cdot1 \pm 1\cdot0$‰). The narrow range of variations of these values is in agreement with previous studies (e.g. Schürch and Vuataz, 2000) and is due to mixing of water in the aquifer leading to a buffered value. Rain, soil and tree water signatures were more variable ($-15\cdot6 < \delta^{18}O_{rain} < -5\cdot6$‰; $-116 < \delta^2H_{rain} < -35$‰; $-16\cdot8 < \delta^{18}O_{soils} < -2\cdot4$‰; $-115 < \delta^2H_{soils} < -32$‰; $-14\cdot8 < \delta^{18}O_{trees} < -1\cdot5$‰; $-111 < \delta^2H_{trees} < -37$‰). Groundwater and river signatures plot close to the calculated LMWL ($\delta^2H = 7\cdot8\delta^{18}O + 3\cdot1$), which is similar to the regional meteoric water line

($\delta^2H = 7\cdot55\delta^{18}O + 4\cdot8$; Kullin and Schmassmann, 1991). The soil water line ($\delta^2H = 6\cdot33 \ \delta^{18}O - 10\cdot7$) and the tree water line ($\delta^2H = 5\cdot49 \ \delta^{18}O - 26\cdot4$) show deviations from the LMWL, suggesting evaporation processes (Clark and Fritz, 1997). By excluding the poplar's S1 signatures, because of a possible partial influence of irrigation, the tree water line would be $\delta^2H = 5\cdot81 \ \delta^{18}O - 22\cdot4$ (not shown in Figure 3). Brooks *et al.* (2010) and Wang *et al.* (2010) found similar patterns for soils and trees suggesting evaporation, in Oregon's (USA) Mediterranean climatic area and in a warm temperate zone with a continental monsoon climate (Shanxi Province, China). These trends will be discussed in the following part focusing on the factors impacting isotopic variability in xylem.

The large isotopic variations in both soil and xylem waters indicate strong spatiotemporal changes. Hence, the understanding of water uptake by trees requires a more detailed temporal analysis of these two compartments at the three sites to determine the factors modifying them.

Factors influencing isotopic variability's within soil profiles

Figures 4 to 6 show the temporal evolutions of precipitation, temperature, soil moisture at different depths, groundwater depth in S1 and S2, and $\delta^{18}O$ of stem and soil waters. For S3, no information about groundwater level and soil water content was available, and the presented data are those of S2, for comparison. Indeed, Brooks *et al.* (2010) pointed out that differences in soil isotopic signatures are generally much greater in vertical direction than from site to site.

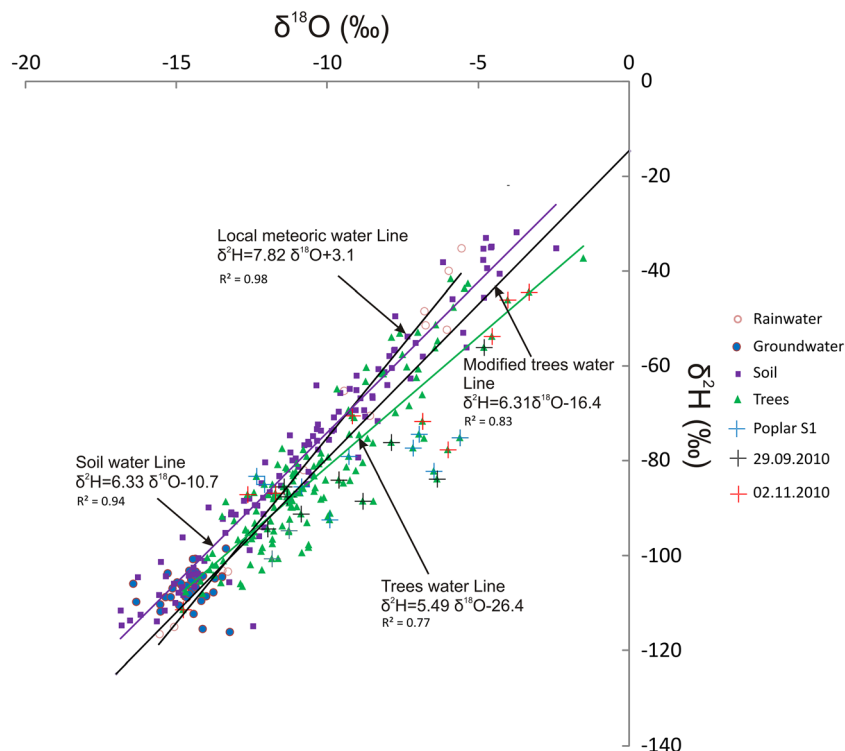
Figure 3. $\delta^{18}O$ and δ^2H of bulk soil water, xylem water, groundwater, surface water and rainwater. Local meteoric water line (from this study), soil water line, tree water line and modified tree water line (see text for details).
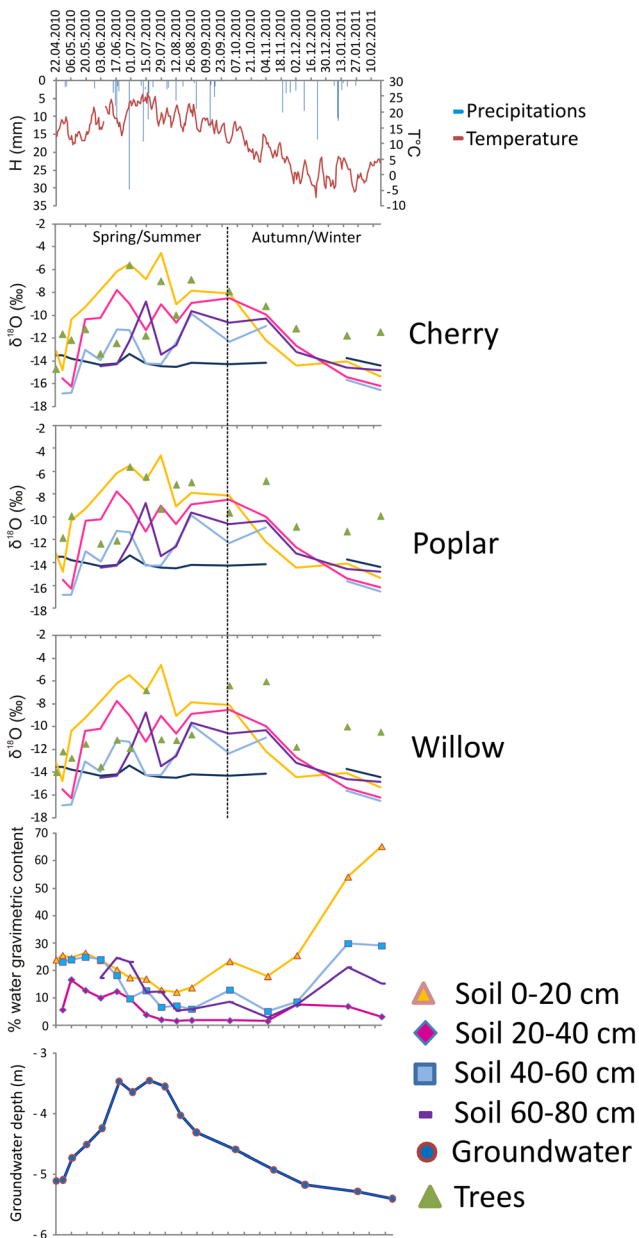
Figure 4. Temporal patterns of hydrometeorological conditions and isotopic signatures at site S1. For clarity of pictures, the symbols representing isotopic values of soils and groundwater were removed. The lines represent the trend between discrete values, which were measured at the same time as tree signatures.
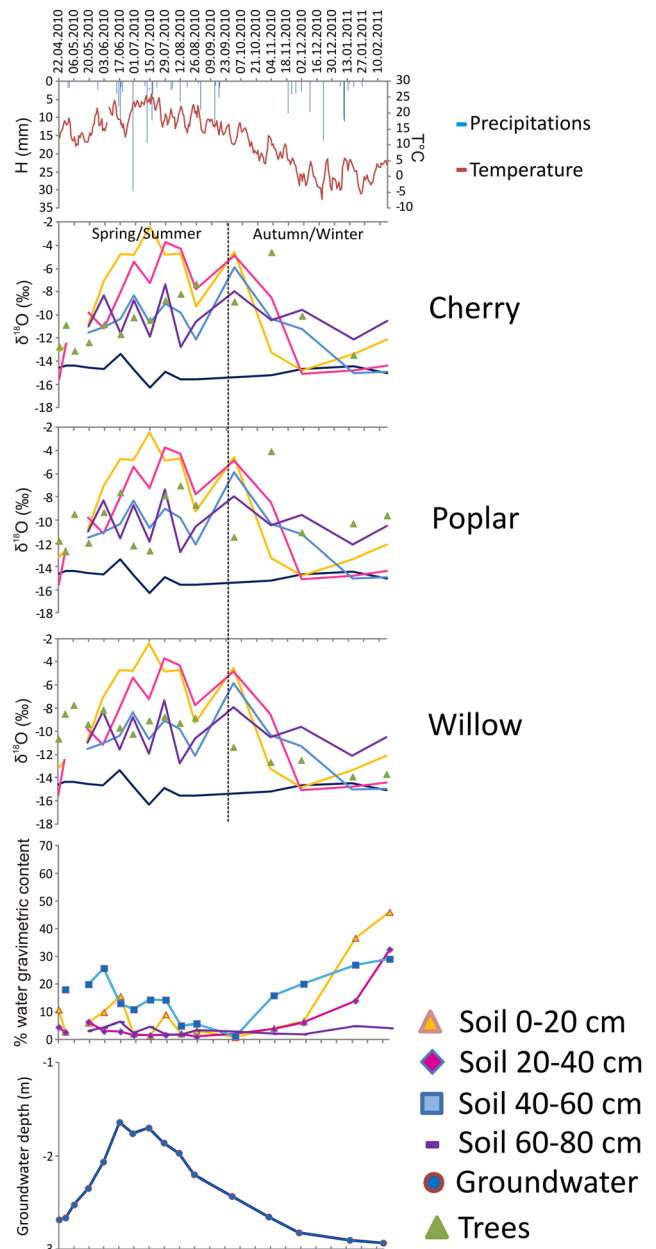

Figure 5. Temporal patterns of hydrometeorological conditions and isotopic signatures of soil and plants at site S2. For clarity of pictures, the symbols representing isotopic values of soils and groundwater were removed. The lines represent the trend between discrete values, which were measured at the same time as tree signatures.

The upper soil layers (0–20 and 20–40 cm) varied from strongly depleted isotopic signatures in the beginning of spring and winter to enriched signatures in midsummer. In contrast, 40–60 and 60–80 cm soil layers were less variable with values closer to groundwater signatures (Table II; Figures 4 to 6). This indicates that upper soil waters were recharged mainly by recent precipitation and are also directly and continuously modified by evaporative enrichment, as suggested by the simultaneous seasonal gravimetric water content variation. Consistently, the ANOVA (Table III) indicates that although soil layer, depth and site may explain significantly the isotopic variability of soil waters (Pr ≤ 0 0001), the seasonal parameters (precipitation heights, temperature and groundwater level) contribute more (the

explained sums of squares are higher) to this variability. This is in agreement with several studies pointing out the influence of hydrometeorological conditions and distance of soil layers from the surface (Xu *et al*., 2011), of kinetic evaporation processes close to the surface Li *et al*., 2007) and of the hydrodynamics properties of each soil layer on the isotopic composition of water (Stumpp *et al*., 2009).

The deepest layers however sometimes showed higher $\delta^{18}O$ and δ^2H values than the uppermost layers, especially after strong rain events (e.g. the 60–80 cm layer values for the 14 July 2010 at S1 in Figure 4). This may be explained by the activation of preferential flow paths between superficial and deeper layers, which transport enriched water downward (e.g. Boutton *et al*., 1999; Li *et al*., 2006;
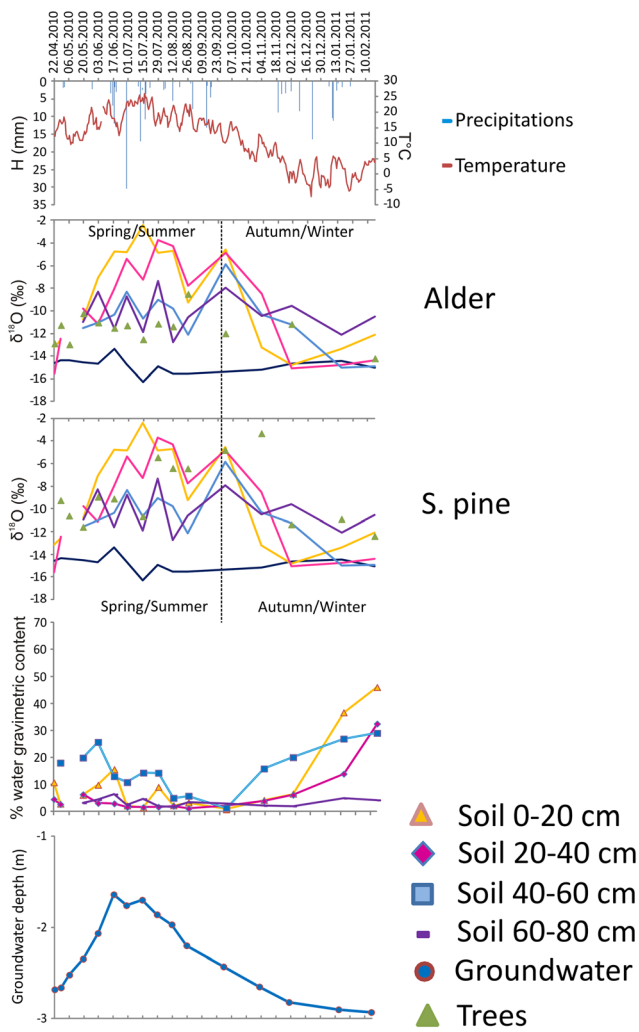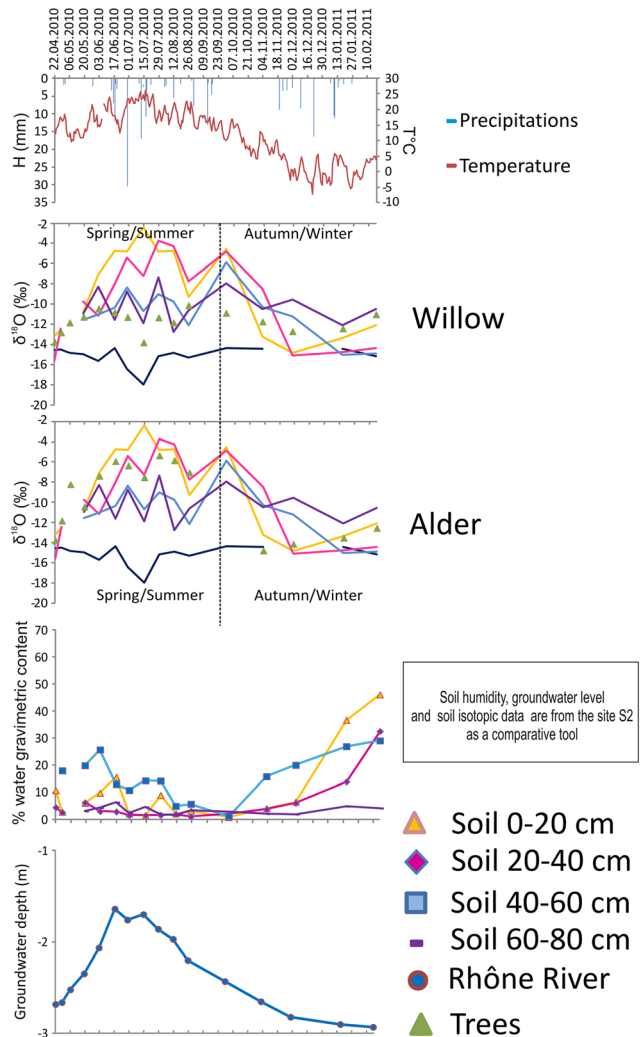
Figure 5. (Continued)

Figure 6. Temporal patterns of hydrometeorological conditions and isotopic signatures of soil and plants at site S3 (The soil data and groundwater depth are those from site S2 to provide general trend. Brooks *et al.* (2010) indicated that spatial variations of soil is generally lower than variations with depth). For clarity of pictures, the symbols representing isotopic values of soils and groundwater were removed. The lines represent the trend between discrete values, which were measured at the same time as tree signatures.

2007). Conversely, deep soil layers temporarily had depleted $\delta^{18}O$ and δ^2H, especially at S1, in the middle of summer (e.g. Figure 4, 28 July 2010 campaign, 40–60 cm: $-14\cdot3$ $\delta^{18}O‰$, 60–80 cm: $-13\cdot5$ $\delta^{18}O‰$, groundwater: $-14\cdot3$ $\delta^{18}O‰$). Such sudden isotopic depletion of soil water, when the water table is at its shallowest, suggests a possible connection between these two compartments. Upward water movement through capillary rise (e.g. Chimner and Cooper, 2004) and/or hydraulic lift in which water transits from the taproots to the lateral roots, which tend to exude water they contain (Caldwell and Richards, 1989), are possible mechanisms. Fernandez *et al.* (2008) showed that hydraulic lift may occur both in periods with very low soil water content and with high soil water availability and that this complexity makes hydraulic lift detection and quantification difficult. Thus, if the data from S1 may not exclude the hydraulic lift, then they are at least consistent with capillary rise. At site S2 (Figure 5) where the water table was closer to the soil surface, isotope data did not suggest a connection between groundwater and soil water. Pedological evaluations (Table I) suggested that S2 soil consists of coarse material (until 50 cm diameter) compared with site S1, which could reduce or prevent capillary rise.

Factors influencing isotopic variability of xylem

The poplar, cherry and willow from S1; the poplar, cherry and Scots pine from S2; and alder from S3 showed similar ranges in isotopic signatures as the upper soil layers (Table II). The alder and willow from S2 and the willow from S3 had buffered variations. As for soil, the isotopic variability of trees is strongly related to the seasonal state variables (temperature, groundwater depth, recent rainfall amount; Table IV; $p < 0\cdot0001$). From spring to summer, isotopic values of trees were generally comprised between soil layer and groundwater signatures (see, e.g. Figure 4), indicating a mix of used water sources. During autumn and winter, the isotopic values were sometimes enriched compared with the soil waters (and also to the groundwater), especially for trees of site S1, cherry, poplar and Scots pine of site S2, which are also the largest individuals. The enriched signatures in comparison with soil and groundwater after the summer suggest a reduction or a cessation of water uptake related to the decrease of

Table III. Effect of depth, site and seasonal hydrometeorological parameters (H$_{rain}$, temperature and groundwater depth) on soil isotopic signatures variability. A, B and C differ in the way that the included seasonal parameter has been changed for each analyses of variance test because of an overlapping effect (see text).

A						
Factor	Freedom	Sum of squares	Mean of squares	F	$Pr > F$	Explained sum of squares (%)
H$_{rain}$ 15 last days	14	652·5	46·6	11·2	<0·0001	70
Depth	3	172·4	57·5	13·8	<0·0001	19
Site	1	101·5	101·5	24·4	<0·0001	11
Total		926·4				100
B						
Source	Freedom	Sum of squares	Mean of squares	F	$Pr > F$	Explained sum of squares (%)
T 15 last days	14	652·1	46·6	11·2	< 0·0001	70
Depth	3	177·5	59·2	14·2	< 0·0001	19
Site	1	104·2	104·2	25·0	< 0·0001	11
Total		933·8				100
C						
Factor	Freedom	Sum of squares	Mean of squares	F	$Pr > F$	Explained sum of squares (%)
Gw prof	12	585·2	48·8	10·2	<0·0001	70
Depth	3	153·5	51·2	10·7	<0·0001	18
Site	1	97·7	97·7	20·5	<0·0001	12
Total		836·4				100

Table IV. Effect of type of tree (species), site, size and seasonal hydrometeorological parameters (H$_{rain}$, temperature and groundwater depth) on xylem isotopic signatures variability. A, B and C differ in the way that the included seasonal parameter has been changed for each analysis of variance test because of an overlapping effect (see text).

A						
Factor	Freedom	Sum of squares	Mean of squares	F	$Pr > F$	Explained sum of squares (%)
H$_{rain}$ 15 last days	14	303·9	21·7	5·3	<0·0001	69
Species	3	118·8	39·6	9·6	<0·0001	27
Site	1	17·7	17·7	4·3	0·040	4
Size	2	2·6	1·3	0·3	0·728	1
Total		443·0				100
B						
Factor	Freedom	Sum of squares	Mean of squares	F	$Pr > F$	Explained sum of squares (%)
T 15 last days	14	312·8	22·3	5·5	<0·0001	70
Species	3	116·2	38·7	9·6	<0·0001	26
Site	1	17·7	17·7	4·4	0·038	4
Size	2	2·3	1·2	0·3	0·751	1
Total		449·0				100
C						
Factor	Freedom	Sum of squares	Mean of squares	F	$Pr > F$	Explained sum of squares (%)
Gw prof	12	224·6	18·7	4·1	<0·0001	60
Species	3	131·2	43·7	9·5	<0·0001	35
Site	1	17·7	17·7	3·8	0·052	5
Size	2	3·2	1·6	0·3	0·710	1
Total		376·7				100

transpiration. Thus, the xylem water had likely kept an isotopic signature corresponding to water used previously. Ryan *et al.* (2000) explained that the restriction of transpiration is related to a decrease of water potential gradient between soil and leaves or of hydraulic conductance (water flux per unit of sapwood area) in case of water stress. This functional change would aid water supply by augmenting water storage in the conducting system to mitigate the xylem cavitations. If xylem cavitation occurred because of an important water stress, then it would also lead to water immobilization within xylem (Sperry *et al.*, 1988; Sun *et al.*, 2011). For the 29 September 2010 and 02 November 2010 field campaigns during which trees were still active, the enriched isotopic values in comparison with soil water and groundwater are consistent with physical evaporation and not only with a simple water storage within xylem tissue. Indeed, by excluding these data in the $\delta^{18}O$ versus δ^2H diagram (Figure 3), the modified tree water line ($\delta^2H = 6·31\ \delta^{18}O - 16·4$) fits better with the soil water line ($\delta^2H = 6·33\ \delta^{18}O - 10·7$). These field campaigns were preceded by warm temperatures (29 September 2010) or by a lack of precipitations (02 November 2010), and soils were dry (e.g. Figure 4). The clue of a physical evaporation suggests that the pool of immobile xylem water was subjected to re-equilibrium processes with the strongly enriched water (especially during warm periods during which water stress may occur) transferred from leaves through the phloem (which would be also exposed to evaporation). These unexpected observations argue for the possible influence of advection or diffusion of

isotopically enriched water between the phloem and the xylem proposed by Dawson and Ehleringer (1993) but still poorly documented in the literature from our knowledge.

The ANOVA also indicates the influence of species type on water use (Table IV). This is consistent with several previous studies. In a plant community, different species may have distinguished root distributions (e.g. shallow root versus deep root) to uptake water efficiently from different soil depths (Weltzin and McPherson, 1997; Schenk and Jackson, 2002; Snyder and Williams, 2003; Xu *et al.*, 2011). Although reduced, a site effect may also exist ($0.038 < p < 0.052$). An increased time resolution (e.g. daily) would probably enhance the site effect as shown by Xu *et al.* (2011) because short-term isotopic changes in xylem sap depend on both the hydrodynamics of each soil layer (which can change according to sites as in the Pfyn forest) and the priority of soil layers used by trees. Tree size does not seem to intervene significantly in water source uses ($0.71 < p < 0.751$). This is contradictory with the findings of Meinzer *et al.* (1999), who studied mainly plants between 0.25 and 1.25 m high. However, the absence of such an effect in the presented data should be considered with care because the studied trees (between 2 and 30 m) might not be in the critical size range for a water source shift (Feild and Dawson, 1998).

These observations point out the large array of factors that can modify the isotopic signatures of trees. First, as for soils, the isotopic variability is influenced by hydrometeorological processes, that is, rain amount, temperature and groundwater level (influencing potentially the soil water content through capillary rise and direct groundwater access). Second, these ANOVA highlight that the understanding of water source proportions used by trees during the growth period requires in addition the knowledge of the ecological behaviour of each specie (ecological processes).

Proportions of water sources used by trees and influence of ecological processes

In this purpose, the hydrological, soil and meteorological conditions were constrained by selecting four contrasted field campaigns during the growth season. Water source contributions were analysed through the multisource balance model implemented in IsoSource (Phillips and Greggs, 2003). The 19 May 2010 campaign was chosen because it corresponded to relatively low groundwater levels (-4.0 m at S1, -2.4 m at S2) and high soil water content (13–26% at S1; 6–20% at S2). 17 June 2010 was selected because the soil water content was still high (18–24% at S1, 6–16% at S2) and groundwater level was close to its annual maximum (-2.9 and -1.64 m). 28 July 2010 was analysed because soil water content was lower (2–13% at S1, 2–14% at S2), but the water table level was still high (-3.05 m at S1, -1.86 at S2) and temperatures were near the maximum (close to 23 °C), probably implying the maximum of transpiration. Finally, 25 August 2012 corresponded to a period during which groundwater level had significantly decreased (-3.8 m at S1, -2.2 m at S2) as well as soil water content (2–14% at S1, 1–6% at S2). For the S1 poplar, although irrigation water contamination was possible, the data were kept because

IsoSource provides a range of percentage of contributions and their frequencies in the outputs of the calculations instead of a discrete value. An example of an obtained histogram is shown in Figure 7. From these data, it is possible to delineate ranges of possible contributions as well as their weighed averages. All the results are reported numerically in Table V. They can be summarized as follows:

19 May 2010	At S1, the poplar, cherry and willow used mainly the 20–40 cm soil layer (between 18% and 74%) and groundwater resource (between 24% and 64%). At S2, the poplar, the willow and the alder preferentially used the 20–40 cm layer, whereas the Scots pine and cherry used all soil layers as well as groundwater (8–38% and 28–50%, respectively). At site S3, the alder had preferences for 20–40 and 60–80 cm (40–64% and 28–48%, respectively), and willow used mainly 60–80 cm and groundwater (86–88% and 10%)
17 June 2010	Soil waters were the most used by almost all the trees. At S1, 20–40, 40–60 and 60–80 cm layers were the most used. At S2, the poplar used mainly 0–20 cm soil layer (50–66%). The willow, alder and cherry followed the same trend. The Scots pine used additionally some groundwater (8–24%). At S3, the alder took up preferentially water from the 0–20 cm soil layer (78–88%). whereas the willow pumped mainly groundwater (56–60%)
28 July 2010	The trees of S1 were still using soils but increased their use of groundwater. At S2, two groups of trees may be delineated. At first, the poplar, the cherry and the Scots pine preferentially used soil layers. In contrast, willow and alder probably took a significant part of their water from groundwater (0–38% and 50–64%, respectively). The willow of S3 used both groundwater and soil, whereas the alder was clearly more dependent on soil
25 August 2010	At S1, the poplar likely preferred soil water (but values are weakly constrained) but used a significant proportion of groundwater (e.g. 0–20 cm: 14–72%; groundwater: 0–26%). The willow was still using groundwater (60–72%). The cherry used soil water. At S2, the cherry and the Scots pine used only the soil, whereas poplar, willow and alder showed a bimodal water uptake, using soil and a little amount of groundwater (poplar: 0–14%; willow: 20%; alder: 0–16%). At S3, the alder still mainly used soil water, whereas the willow used both soil and groundwater.

These results allow defining the general trends about the ecohydrological functioning of the area. For S1 and S2, when the soil water content was high (19 May and 17 June), the trees generally preferred this source. When the soil water content was lower and the groundwater table higher (28 July), the soil water usually remained the most important source, but
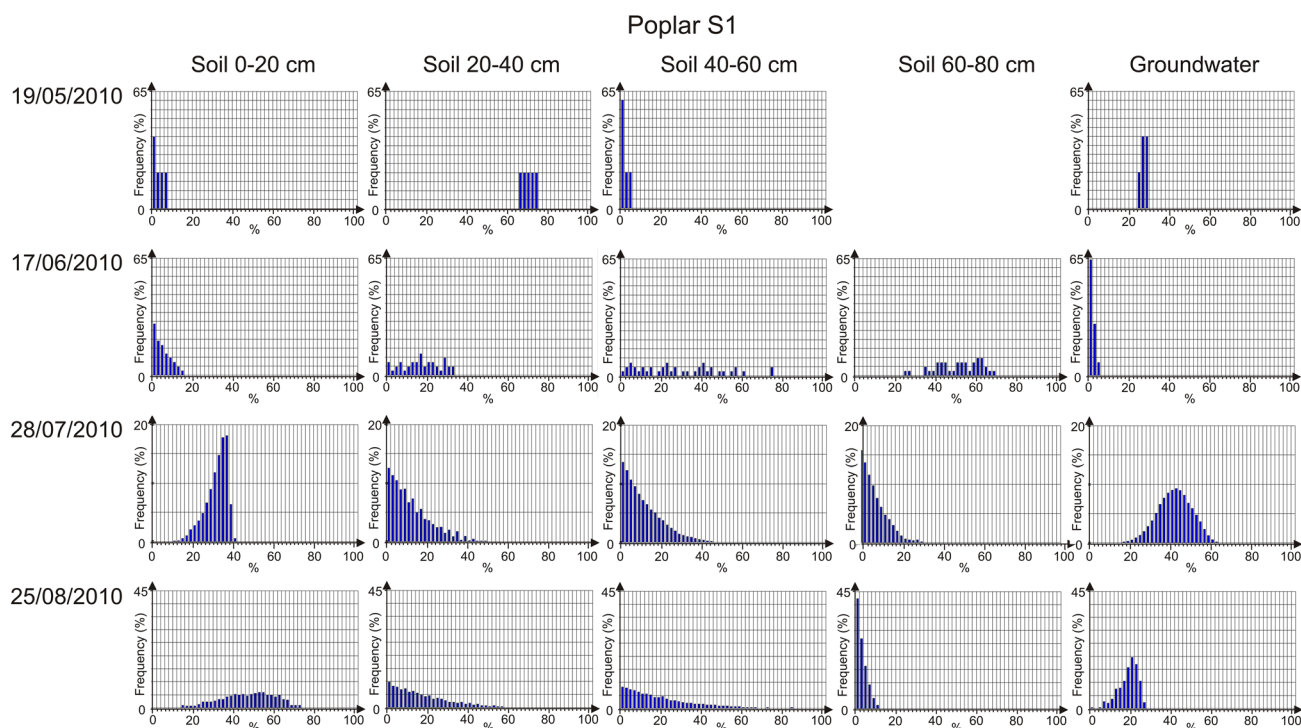
Figure 7. Examples of histograms obtained with the multisource mass balance, which show the estimated ranges of contribution of water from each soil depth and groundwater to the poplar of site S1. In some cases (e.g. 28 July 2010, groundwater), the contribution is significant and well constrained (16–62%, with a weighed mean of 41·2%). In other cases (e.g. 17 June 2010, soil 40–60 cm), the contribution is not well constrained.

the saturated zone became a more significant source of water When both the soil water content and the water table elevation were low (25 August), the contribution of groundwater diminished. Consequently, as a general rule, the soil water appears to be the preferred source of water if soil water content is high or if water table is at low elevation. Groundwater is usually an additional source for transpiration if simultaneously water table is shallow and soil water content had decreased. Ehleringer and Dawson (1992) indicated that the riparian trees tend to develop roots predominantly in the capillary fringe and saturated zone rather than throughout the soil profile if groundwater resource is reliable at long-term scales and if precipitation during the growing season is unreliable. The observed shifts at Pfyn forest rather suggest that trees had opportunistic behaviour that might be related to the hydroclimatic constraints of the area. Indeed, two extreme situations may occur in the system. At first, the ambient temperature of the watershed can be high, leading to a raise of groundwater levels due to snow/glacier melt and soil drought. In this condition, the trees should use groundwater to ensure their survival. Conversely, if temperatures were unusually low, then groundwater recharge would be reduced, whereas the soil water content would be higher. Such 'shifts in water use strategies' have been reported before (e.g. Dawson and Pate, 1996; Jolly and Walker, 1996; Meinzer et al., 1999; Ewe and Sternberg, 2002; Chimner and Cooper, 2004; Wang et al., 2010; Xu et al., 2011). The adaptations of water use revealed by this study also present some similarities with other aquatic ecosystems, for instance, hyporheic zones and springs. These ecosystems present a high degree of 'elasticity' (term used by Gibert et al. [1990]) at seasonal and

inter-annual scales because of hydrologic and nutritive variability (Cantonati et al., 2006; Boulton et al., 2010).

Specific ecological features could also impact water-use strategies. All trees from S1, as well as the Scots pine and the cherry of S2 used soil and groundwater at the beginning of the growth period (19 May). Similarly, Wang et al. (2010) found that cotton, which has a deep root distribution, used both surface and deep water during early stages of plant growth corresponding to seeding and seedling. These stages, important to ensure best reproduction or growing (Matthews et al., 1990; Goldhamer et al., 1994) coincide with the maximum rates of biomass accumulation (Fischer, 1980) and hence are more sensitive to water stress than others (Zahner, 1968; Mastrorilli et al., 1995). Accordingly, the bimodal use of soil water and groundwater at the beginning of the growth period by the trees of S1, where water resource is less reliable than in other sites (mean groundwater depth of about −4 m; Figure 1B), could be explained by an adaptation such as longer roots ensuring water availability and survival. At site S2, as water resource is likely more reliable (closer to the main stream course, mean groundwater depth: −2·3 m; Figure 1B), the distinct behaviour of wild cherry and Scots pine from the other trees (using mainly soil waters) at the beginning of the growth period should be explained by their ecological specificities. Wild cherry, which is an efficient colonizer of lowland mature forest with moist soil, needs to produce fruits attractive from a nutritive point of view (e.g. Dostalova, 2009), which requires a sufficient water supply. Scots pine, like many pioneer species, has to promote rapid growth in high light conditions (early growth season) at the expense of positive carbon balance in low light conditions (Niinemets,

Table V. Summary of results of the multisource balance approach for each tree for the different selected field campaigns. In squares shaded with dark grey are indicated the contributions that were the most significant and well-constrained values (weighed mean >10%; range of values less than 40%).

			0-20 cm (%)	20-40 cm (%)	40-60 cm (%)	60-80 cm (%)	Groundwater (%)
19/05	S1	Poplar	0-8 (2.4)	66-74 (70)	0-4 (1.2)		24-28 (26.4)
		Willow	0-18 (5.5)	18-42 (33.5)	0-10 (2.7)		52-64 (58.3)
		Cherry	0-16 (5.2)	34-56 (47.5)	0-8 (2.1)		40-50 (45.2)
	S2	Poplar	0-26 (7.4)	54-90 (73)	0-26 (7.7)	0-22 (9.6)	0-8 (2.3)
		Willow	0-12 (2.1)	48-68 (55.8)	0-14 (3.1)	26-50 (38.2)	0-6 (0.9)
		Cherry	0-40 (21)	0-36 (9.9)	0-70 (20.7)	0-26 (7.4)	28-50 (41)
		Alder	0-26 (7.4)	54-90 (73)	0-26 (7.7)	0-22 (9.6)	0-8 (2.3)
		S. pine	0-30 (8.8)	0-56 (17.2)	0-70 (20.6)	2-62 (32.4)	8-38 (21)
	S3	Willow	0-2 (0.7)	0-2 (1.3)	0-2 (0.7)	86-88 (87.3)	10-10 (10)
		Alder	0-12 (3.3)	40-64 (51)	0-18 (4.7)	28-48 (39.5)	0-6 (1.4)
17/06	S1	Poplar	0-32 (10.7)	0-38 (12.7)	0-78 (22.2)	0-72 (27.4)	0-68 (27)
		Willow	0-14 (4.1)	0-32 (16.4)	0-74 (28.4)	24-68 (50.3)	0-4 (0.9)
		Cherry	0-32 (8.6)	0-38 (14.3)	0-82 (30)	10-68 (43.2)	0-14 (3.8)
	S2	Poplar	50-66 (56.8)	0-8 (2.1)	0-50 (21.1)	0-40 (14.2)	0-24 (5.7)
		Willow	18-40 (28.6)	0-8 (1.6)	0-80 (41.7)	0-64 (22.9)	0-22 (5.3)
		Cherry	0-4 (1.3)	0-0 (0)	4-34 (19.7)	58-90 (76)	0-8 (3)
		Alder	0-2 (0.7)	0-0 (0)	46-62 (54.7)	32-50 (41.3)	2-6 (3.3)
		S. pine	0-6 (1.7)	66-80 (71.7)	0-14 (3.9)	0-20 (5.7)	8-24 (17.1)
	S3	Willow	0-2 (0.3)	34-40 (36.3)	0-8 (2.5)	0-8 (2.8)	56-60 (58.3)
		Alder	78-88 (81.8)	0-8 (2.9)	0-20 (7.1)	0-16 (4.8)	0-12 (3.4)
28/07	S1	Poplar	10-40 (30.8)	0-48 (10.9)	0-44 (10.2)	0-32 (6.9)	16-62 (41.2)
		Willow	26-28 (27.4)	0-4 (0.9)	0-6 (1.7)	0-6 (1.1)	66-72 (68.9)
		Cherry	46-66 (59.3)	0-32 (7.4)	0-30 (6.8)	0-18(4.4)	6-36 (22.1)
	S2	Poplar	8-58 (31.8)	0-14 (2.5)	18-64 (44.1)	0-74 (18.2)	0-16 (3.4)
		Willow	0-62 (15.9)	0-50 (13.8)	0-94 (27)	0-84 (21.7)	0-38 (21.7)
		Cherry	0-28 (12)	0-10 (1.8)	50-86 (70.9)	0-48 (13)	0-8 (2.3)
		Alder	0-30 (8.4)	2-32 (14)	0-34 (8.7)	0-40 (10.9)	50-64 (58)
		S. pine	0-34 (8.7)	50-82 (62.5)	0-34 (9.6)	0-40 (11.9)	0-14 (7.2)
	S3	Willow	0-18 (4.7)	0-4 (0.9)	30-62 (47)	0-22 (6.8)	36-48 (40.6)
		Alder	0-22 (7)	60-84 (69.5)	0-26 (7.3)	0-28 (8.4)	2-12 (7.8)
25/08	S1	Poplar	14-72 (46.3)	0-56 (15.3)	0-84 (18.2)	0-10 (2.2)	0-26 (18)
		Willow	0-28 (7.9)	0-32 (8.9)	0-40 (11.1)	0-26 (6.2)	6-72 (65.8)
		Cherry	72-86 (79)	2-22 (10)	0-10 (4)	0-2 (0.5)	6-8 (6.5)
	S2	Poplar	62-90 (74)	0-14 (4)	0-28 (9.3)	0-26 (6.4)	0-14 (6.4)
		Willow	78-78 (78)	0-0 (0)	2-2 (2)	0-0 (0)	20-20 (20)
		Cherry	58-80 (68.4)	20-36 (27.6)	0-6 (1.4)	0-8 (2.1)	0-2 (0.5)
		Alder	60-88 (72.7)	0-16 (3.7)	0-30 (9.7)	0-24 (6.1)	0-16 (7.8)
		S. pine	0-8 (2.3)	92-100 (96)	0-2 (0.5)	0-4 (1.2)	0-0 (0)
	S3	Willow	24-60 (42.1)	0-18 (4)	0-58 (14)	0-30 (6.7)	14-44 (33.2)
		Alder	6-40 (20.6)	60-84 (72.7)	0-10 (2.1)	0-16 (3.5)	0-4 (1)

2006; Gaudio *et al.*, 2011). Hence, for these two species, there is an important stake to rapidly reach their seeding or seedling stage to respectively ensure either the community (for wild cherry) or individual (for Scots pine) survival. The combination of adaptation to water unreliability and colonization/ growth strategies could be advantageous in a context of important hydrological changes. This assumption is supported by the fact that Scots pines are dominant in the upper part of the Pfyn forest, where the groundwater table level is deeper and more variable (Figure 1A) and the alluvial substrate coarser, and that wild cherry is well distributed at S1 where soil water content may be high but groundwater relatively deep.

In contrast to S1 and S2, the water sources for each tree varied little at S3. The alder used mostly soil water, whereas the willow was significantly dependent to groundwater throughout the growth period. This is in agreement with the concept of habitat partitioning mentioned by Casper and Jackson (1997). To decrease competition for water, especially at pioneer stages, a plant may improve water uptake by

growing a deeper root system and tapping a source of water unavailable to more shallow-rooted neighbours. As S3 stands very close to the river, these contrasted and complementary water uses are probably possible because of sufficient soil water content. Such partitioning could be associated with vertical root distributions. This should be a key factor when ensuring river bank biotope stability, especially where high energy flood events are expected to occur more frequently because of climatic changes (Ward, 1998). High soil water content could be favoured by an efficient capillary rise (shallow groundwater, local fine textures, Table I). A further analysis of water dynamics in sediments in this area would help to confirm this hypothesis.

CONCLUSION

By using hydrogen and oxygen isotopes, this study analysed the water uptake of alluvial trees of the Pfyn Forest to identify the key factors influencing the current ecohydrological processes and possible adaptations of this system to climatic or land-use changes. A conceptual scheme of these outputs is proposed in Figure 8.

This study suggests that the alluvial trees of the Pfyn forest have opportunistic strategies in their water use. Water sources used by trees may vary with season, particularly for the sites distant from the main river bed (S1 and S2). For these sites, it appeared that soil water content is the leading factor for water use and that groundwater is mainly used during the warmest periods of the year. Such a seasonal opportunistic behaviour of trees should have important consequences in a context of climate change and could maintain community resiliency under potentially increasing water stress (see, e.g. Naumburg *et al.*, 2005). In high-altitude watersheds, an increase of

temperature could deplete soil water content but conversely should increase the groundwater table level, both situations for which the trees appeared to be adapted to. However, these opportunistic shifts are likely dependent on pedological conditions. Results from this study suggest that capillary rise could partially buffer the impacts of rising temperature and be a source of soil water. For young (epiphytic) individuals needing a high amount of superficial water to grow (Feild and Dawson, 1998), this process could however be insufficient and lead to some long-term ecological changes at the community levels because of young individual water stress. In addition, the probable increase of flash floods could modify the pedological context by increasing the proportion of coarse material, which would reduce the capillary rise potentialities. Furthermore, the riverbed incision scheduled in the frame of the third Rhône river correction (Zwahlen, 2009) could counterbalance the climatic effect on groundwater level and accelerate the ecological changes. As Scots pine and cherry usually have aboveground competitive strategies (competition for light or for reproduction) influencing their groundwater use in the early growing period and at the same time look adapted to water source unreliability, these species could be advantaged in the long term. Consequently, efforts on the understanding on water pathways in fluviosoils should be done to predict the future soil water availability for trees due to climate changes.

Where the groundwater was the shallowest and the soil water content was likely and durably higher, a vertical share of water resources appeared to occur, suggesting an underground cohabitation strategy. Investigations on root distributions in this kind of environments could be a future important task (and challenge) for the scientific community and managers to evaluate if this habitats partitioning is a process potentially ensuring river bank stability, which is
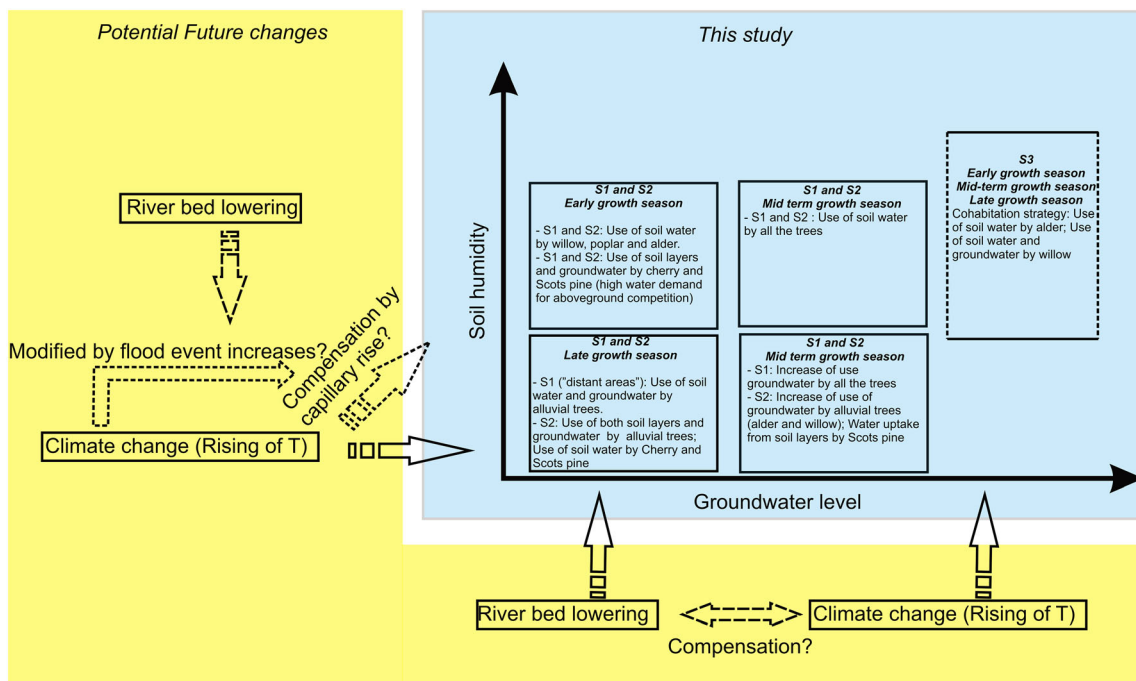

Figure 8. Conceptual scheme of the outputs of this study and of the possible effects of future local and climate changes. Dotted arrows indicate that these hypotheses should be assessed by field or modelling approaches.

of concern in case of significant hydrological changes in high-altitude watersheds (Ward, 1998).

At last, this study also unexpectedly showed that the analysis of δ^2H versus. δ^{18}O diagram could be a further potential tool assessing water stress, if xylem waters show evaporative enrichments in comparison with soils during growth periods. This approach should be evaluated, for example, by comparing such data with classical techniques outputs, for example, the leaf area index, the sap fluxes or stomatal conductances (Eamus *et al.*, 2006) and could provide an additional and quite easy systematic way to evaluate the health of an individual tree.

REFERENCES

Asbjornsen H, Mora G, Helmers MJ. 2007. Variation in water uptake dynamics among contrasting agricultural and native plant communities in the Midwestern US. *Agriculture, Ecosystems and Environment* **121**: 343–356.

Baize D, Girard MC, Jabiol B, Rossignol JP, Eimberck M, Beaudou A. 2009. *Référentiel pédologique 2008*. Editions Quae: Versailles; 480.

Bendel M, Tinner W, Ammann B. 2006. Forest dynamics in the Pfyn forest in recent centuries (Valais, Switzerland, Central Alps): interaction of pine (*Pinus sylvestris*) and oak (*Quercus sp.*) under changing land use and fire frequency. *The Holocene* **16**: 81–89.

Beniston M. 2006. Mountain weather and climate: a general overview and a focus on climatic change in the Alps. *Hydrobiologia* **562**: 3–16.

Bertrand G, Goldscheider N, Gobat JM, Hunkeler D. 2012. Review: from multi-scale conceptualization of groundwater-dependent ecosystems to a classification system for management purposes. *Hydrogeology Journal* **20**: 5–25.

Boulton AJ, Datry T, Kasahara T, Mutz M, Stanford JA. 2010. Ecology and management of the hyporheic zone: stream– groundwater interactions of running waters and their floodplains. *Journal of the North American Benthological Society* **29**:26–40

Boutton TW, Archer SR, Midwood AJ. 1999. Stable isotopes in ecosystem science: structure, function and dynamics of a subtropical savanna. *Rapid Communications in Mass Spectrometry* **13**: 1263–1277.

Brooks JR, Barnard HR, Coulombe R, McDonnel JJ. 2010. Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience* **3**: 101–104.

Caldwell MM, Richards JH. 1989. Hydraulic lift: water flux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **79**: 1–5.

Cantonati M, Gerecke R, Bertuzzi E. 2006. Springs of the Alps – sensitive ecosystems to environmental change: from biodiversity assessments to long-term studies. *Hydrobiologia* **562**: 59–96.

Casper BB, Jackson RB. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* **28**: 545–570.

Chimner RA, Cooper DJ. 2004. Using stable oxygen isotopes to quantify the water source used for transpiration by native shrubs in the San Luis Valley, Colorado, USA. *Plant and Soil* **260**: 225–236.

Clark ID, Fritz P. 1997. *Environmental Isotopes in Hydrogeology*. Lewis Publishers: New York; 328.

Dawson TE. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* **95**: 565–574.

Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use streamwater. *Nature* **350**: 335–372.

Dawson TE, Ehleringer JR. 1993. Isotopic enrichment of water in the 'woody' tissue of plants: Implication for water plant source, water uptake and other studies which use the stable isotopic composition of cellulose. *Geochimica et Cosmochimica Acta* **57**: 3487–3492.

Dawson TE, Pate JS. 1996. Seasonal water uptake and movement in root systems of Australian phreatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* **107**: 13–20.

Dostalova A. 2009. Tree seedlings: how do they establish in spontaneously developed forests? A study from a mountainous area in the Czech Republic. *Biodiversity and Conservation* **18**: 1671–1684.

Eamus D, Froend R, Loomes R, Hose G, Murray B. 2006. A functional methodology for determining the groundwater regime needed to maintain the health of groundwater-dependent vegetation. *Australian Journal of Botany* **54**:97–114.

Ehleringer JR, Dawson TE. 1992. Water uptake by plants: perspectives from stable isotopes composition. *Plant, Cell & Environment* **15**: 1073–1082.

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR. 1991. Differential utilization of summer rains by desert plants. *Oecologia* **88**: 430–434.

European Parliament. 2006. Directive 2006/118/EC on the protection of groundwater against pollution and deterioration. *Official Journal of the European Union*. Available via http://eurlex.europa.eu/LexUriServ/Lex-UriServ.do?uri=OJ:L:2006:372:0019:0019:EN:PDF [accessed 10 Feb 2012].

Ewe SML, Sternberg LSL. 2002. Water uptake patterns of an invasive exotic plant in coastal saline habitats. *Journal of Costal Research* **22**: 272–281.

Ewe SML, Sternberg LSL, Busch DE. 1999. Water-use patterns of woody species in pineland and hammock communities of South Florida. *Forest Ecology and Management* **118**: 139–148.

Feild TS, Dawson TE. 1998. Water sources used by *Didymopanax pittieri* at different life stages in a tropical cloud forest. *Ecology* **79**: 1448–1452.

Fernandez ME, Gyenge J, Licata J, Schlichter T, Bond BJ. 2008. Belowground interactions for water between trees and grasses in a temperate semiarid agroforestry system. *Agroforestry Systems* **74**: 185–197.

Fette MW. 2005. Tracer studies of river–groundwater interaction under hydropeaking conditions. PhD dissertation, Swiss federal institute of technology of Zurich; 117. Available via: http://www.rhone-thur. eawag.ch/Diss_Fette.pdf [accessed 10 Feb 2012].

Fischer RA. 1980. Influence of water stress on crop yield in semiarid regions. In *Adaptation of Plants to Water and High Temperature Stress*, Turner NC, Kramer PJ (eds). Wiley: New York; 323–339.

Gaudio N, Balandier P, Perret S, Ginisty C. 2011. Growth of understorey Scots pine (*Pinus sylvestris* L.) saplings in response to light in mixed temperate forest. *Forestry* **84**: 187–195.

Gibert J, Dole-Olivier MJ, Marmonier P, Vervier P. 1990. Surface water-groundwater ecotones. In *The Ecology and Management of Aquatic-terrestrial Ecotones*, Naiman RJ, De Camps H (eds). United Nations Educational, Scientific, and Cultural Organization, Paris and Parthenon Publishers: Carnforth, UK.

Goldhamer D, Dunai J, Ferguson L. 1994. Irrigation requirements of olive trees and responses to sustained deficit irrigation. *Acta Horticulturae* **356**: 172–176.

IPCC. 2007. *Climate Change 2007: Mitigation of Climate Change. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press: Cambridge; 7–22.

Jolly ID, Walker GR. 1996. Is the field water use of *Eucalyptus largiflorens* F. Muell. Affected by short term flooding? *Australian Journal of Ecology* **21**: 173–183.

Keller F, Goyette S, Beniston M. 2005. Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in Alpine Terrain. *Climatic Change* **72**: 299–319.

Kløve B, Ala-aho P, Bertrand G, Boukalova Z, Ertürk A, Goldscheider N, Ilmonen J, Karakaya N, Kupfersberger H, Kvoerner J, Lundberg A, Mileusnić M, Moszczynska A, Muotka T, Preda E, Rossi P, Siergieiev D, Šimek J, Wachniew P, Widerlund A. 2011a. Groundwater dependent ecosystems: part I – hydroecology, threats and status of ecosystems. *Environmental Sciences and Policies* **14**: 770–781.

Kløve B, Ala-aho P, Allan A, Bertrand G, Druzynska E, Ertürk A, Goldscheider N, Henry S, Karakaya N, Koundouri P, Kvoerner J, Lundberg A, Muotka T, Preda E, Pulido-Velázquez M, Schipper P.

2011b. Groundwater dependent ecosystems: part II – ecosystem services and management under risk of climate change and land-use management. *Environmental Sciences and Policies* **14**: 782–793.

Kullin M, Schmassmann H. 1991. Isotopic composition of modern recharge. In *Applied Isotope Hydrogeology. A Case Study in the Northern Switzerland.* Studies in Environmental Sciences, Vol. **43**, Pearson FJ, Balderer W, Loosli HH, Lehmann BE, Matter A, Peters T, Schmassmann H, Gautschi A (eds). Elsevier: Amsterdam; 65–69.

Li SG, Romero-Saltos H, Tsujimura M, Sugimoto A, Sasaki L, Davaa G, Oyunbaatar D. 2007. Plant water sources in the cold semiarid ecosystem of the upper Kherlen River catchment in Mongolia: a stable isotope approach. *Journal of Hydrology* **333**: 109–117.

Li SG, Tsujimura M, Sugimoto A, Sasaki L, Yamanaka T, Davaa G, Oyunbaatar D, Sugita M. 2006.Seasonal variation in oxygen isotope composition of waters for a montane larch forest in Mongolia. *Trees* **20**: 122–130.

Lis G, Wassenaar LI, Hendry MJ. 2008. High-precision laser spectroscopy D/H and $^{18}O/^{16}O$ measurements of microliter natural water samples. *Analytical Chemistry* **80**: 287–293.

Mastrorilli M, Katerji N, Rana G. 1995. Water efficiency and stress on grain sorghum at different reproductive stages. *Agricultural Water Management* **28**: 23–34.

Matthews RB, Reddy DM, Rani AU, Azam-Ali SN, Peacock JM. 1990. Response of four sorghum lines to mid-season drought. I. Growth, water use and yield. *Field Crops Research* **25**: 279–296.

Meinzer FC, Andrade JL, Goldstein G., Holbrook NM, Cavelier J, Wright SJ. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* **121**: 293–301.

Naumburg E, Mata-Gonzalez R, Hunter R, McLendon T, Martin DW. 2005. Phreatophytic vegetation and groundwater fluctuations: a review of current research and application of ecosystem response modelling with an emphasis on Great Basin Vegetation. *Environmental Management* **35**: 726–740.

Niinemets Ü. 2006. The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. *Journal of Ecology* **94**: 464–470.

Office Fédéral de l'Environnement (OFEV). 2008. Faune et Flore des zones alluviales. Available via http://www.auen.ch/documents_pdf/Fiche_13_f.pdf [accessed 11 feb 2012].

Phillips DL, Gregg JW. 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**: 261–269.

Ryan MG, Bond BG, Law BE, Hubbard RM, Woodruff D, Cienciala E, Kucera J. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* **124**: 553–560.

Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads and belowground/aboveground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480–494.

Schürch M, Vuataz FD. 2000 Groundwater components in the alluvial aquifer of the Alpine Rhone River valley, Bois de Finges area, Wallis Canton, Switzerland. *Hydrogeology Journal* **8**: 549–563.

Scrimgeour CM. 1995. Measurement of plant and soil water isotope composition by direct equilibration methods. *Journal of Hydrology* **172**: 261–274.

Snyder KA, Williams DG. 2003. Defoliation alters water uptake by deep and shallow roots of *Prosopis velutina* (Velvet Mesquite). *Functional Ecology* **17**: 363–374.

Sperry JS, Donnelly JR, Tyree MT. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment* **11**:35–40.

Stralher AN. 1957. Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union* **8** (6): 913–920.

Stumpp C, Maloszewski P, Stichler W, Fank J. 2009. Environmental isotope ($\delta^{18}O$) and hydrological data to assess water flow in unsaturated soils planted with different crops: case study lysimeter station 'Wagna' (Austria). *Journal of Hydrology* **369**: 198–208.

Sun SJ, Meng P, Zhang JS, Wan X. 2011. Variation in soil water uptake and its effect on plant water status in *Juglans regia* L. during dry and wet seasons. *Tree Physiology* **31**: 1378–1389.

Tomlinson M, Boulton AJ. 2010. Ecology and management of subsurface groundwater dependent ecosystems in Australia – a review. *Marine and Freshwater Research* **61**: 936–949.

Viviroli D, Weingartner R. 2004. The hydrological significance of mountains: from regional to global scale. *Hydrology and Earth System Sciences* **8**: 1016–1029.

Wang P, Song XF, Han DM, Zhang YH, Liu X. 2010. A study of root water uptake of crops indicated by hydrogen and oxygen stable isotopes: a case in Shanxi Province, China. *Agricultural Water Management* **97**: 475–482.

Ward JV. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* **83**: 269–278.

Ward JV, Tockner K, Arscott DB, Claret C. 2002. Riverine landscape diversity. *Freshwater Biology* **47**:517–539.

Wassenaar LI, Hendry MJ, Chostner VL, Lis P. 2008. High resolution pore water δ^2H and $\delta^{18}O$ measurements by H_2O(liquid)–H_2O(vapor) equilibration laser spectroscopy. *Environmental Science and Technology* **42**: 9262–9267.

Weltzin JF, McPherson GR. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* **112**: 156–164.

Werner P. 1985. La végétation des Finges et de son Rhône sauvage. *Bulletin de la Murithienne* **103**: 39–84.

Williams DG, Ehleringer JR. 2000. Intra- and interspecific variation for summer precipitation use in Pinyon–Juniper woodlands. *Ecological Monographs* **70**: 517–537.

Xu Q, Li H, Chen J, Cheng X, Liu S, An S. 2011. Water use patterns of three species in subalpine forest, Southwest China: the deuterium isotope approach. *Ecohydrology* **4**: 236–244. DOI: 10.1002/eco.179

Zahner R. 1968. Water deficits and growth of trees. In *Water Deficits and Plant Growth*, Vol. **II**, Kozlowski TT (ed). Academic Press: New York; 191–254.

Zimmerman U, Ehhalt D, Munnich KO. 1967. Soil water movement and evapotranspiration: changes in the isotopic composition of the water. In *Isotopes in Hydrology*, Proceedings of the Symposium. I.A.E.A.: Vienna: 567–584.

Zwahlen F. 2009. Analyse de la prise de position de l'Adsa relative au projet Rhône [Analysis of the Adsa position concerning the Rhône project] Technical report for Wallis canton; 8. Available via http://www.vs.ch/NavigData/DS_12/M26701/fr/rapport_zwahlen.pdf [accessed 11 February 2012].