# Water use patterns of three species in subalpine forest, Southwest China: the deuterium isotope approach

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## ABSTRACT

Determination of water sources of plant species in a community is critical for understanding the hydrological processes and their importance in ecosystem functions. Such partitioning of plant xylem water into specific sources (i.e. precipitation, groundwater) can be achieved by analysing deuterium isotopic composition ($\delta D$) values for source waters. A subalpine dark coniferous forest in southwestern China was selected to examine water use strategies of three key species. Our objectives are to: (1) determine contributions of rainfall and groundwater to soil and xylem water and (2) examine effects of rain, days after rain, soil depth, and species on such contributions. We found that the three species tend to have different, but complementary water use patterns. The dominant canopy tree of *Abies faxoniana* relies primarily on groundwater (i.e. 66–96% of its water sources) and does not change its dependency on groundwater between seasons. In contrast, the midstory *Betula utilis* and the understory *Bashania fangiana* depend predominantly on rainwater (i.e. 13–94% and 32–93%, respectively), and tend to use water opportunistically, switching to groundwater as the main source under stressful conditions during the dry season. The complementary and, for some species, shifting water use strategies and the lack of dependency on rainwater by the foundation species of the subalpine coniferous forest ecosystem should act together to promote species co-existence and maintain community resiliency under potentially increasing water stress caused by climate change. Copyright © 2010 John Wiley & Sons, Ltd.

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## INTRODUCTION

Water plays an important role in plant growth and function (e.g. Ehleringer *et al.*, 1991, 1999; Sala *et al.*, 1997; Snyder and Willams, 2003). The dynamics of water availability in soils and water use by plants are consequently critical to ecosystem functions, e.g. maintaining a high resistance to the changing climate (Gazis and Feng, 2004). For example, water uptake from different layers of soil can have profound implications for other soil–plant ecohydrological processes, such as hydraulic lift and redistribution (Caldwell and Richards, 1989; Brooks *et al.*, 2002, 2006). Extensive studies have been conducted to examine plant water use from soil profiles in arid and semi-arid ecosystems and Mediterranean forests where water stress is significant (Leffer *et al.*, 2005; Ryan *et al.*, 2006). Yet, little is known about water use strategies of dominant trees in montane forest ecosystems.

Determination of water sources by plant species (e.g. soil water from different depths, stream water, groundwater, etc.) should improve our understanding of the hydrological processes and their importance in ecosystem functions. Because water is the only source of hydrogen (H) for plants and there is no fractionation of water isotope during water absorption by plant roots in most cases (Dawson and Ehleringer, 1991; Mensforth *et al.*, 1994), stable H isotope ratios ($\delta D$) of water derived from plant xylem reflect the water sources that a particular plant uses (Wershaw *et al.*, 1966; Dawson and Ehleringer, 1991; Jackson *et al.*, 1999; Grieu *et al.*, 2001; Dawson *et al.*, 2002). Thus, plant water utilization from different sources can be determined by comparing H isotopic compositions in xylem water with the H isotope composition of the potential water sources (Phillips and Ehleringer, 1995; Lin *et al.*, 1996). Several studies have successfully used the natural abundance of stable H isotopes to determine the proportional use of different water sources (Williams and Ehleringer, 2000; Schwinning *et al.*, 2002, 2003; Reynolds *et al.*, 2004; Cheng *et al.*, 2006; Asbjornsen *et al.*, 2007; Ellsworth and Williams, 2007). The stable isotope method has also been used to analyse quantitatively hydrological processes and water use in different habitats (Williams and Ehleringer, 2000; Li *et al.*, 2007) and illustrate the differences in plant use of winter- and
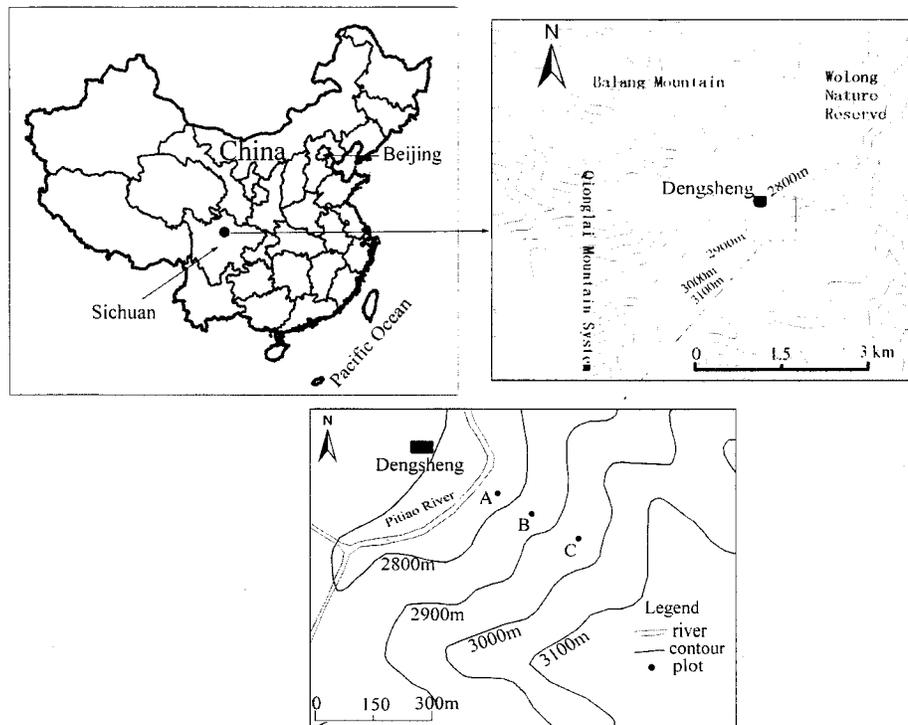
Figure 1. Location of the study site in the Wolong Nature Reserve of Sichuan, Southwest China.

summer-derived soil water in arid and semi-arid ecosystems (Burgess, 1995; Phillips and Ehleringer, 1995; Sala et al., 1997; Dodd et al., 1998).

Water use strategies of plant species in different canopy layers (e.g. overstory vs understory) within forest ecosystems have not been thoroughly investigated. Previous studies on hydrological processes of coniferous forest ecosystems in our study region were conducted with a narrow focus on individual hydrological characteristics (e.g. intensity and frequency of precipitation, canopy interception, runoff, or soil moisture) (Liu et al., 2001), with no effort made to determine water use strategies of plants in the region. Our previous studies on water fluxes at the community level have specifically indicated that the conifers play important roles in determining the interflow composition through soil profiles by regulating the downward infiltration of rainwater and the upward movement of groundwater (Xu et al., 2006). However, patterns of variability in water use among plant species remain unclear. Based at a long-term research station in southwestern China, we initiated a field study to examine the water use strategies by three key species in a subalpine dark coniferous forest: *Abies faxoniana* (overstory species), *Betula utilis* (midstory species), and *Bashania fangiana* (understory species). This forest was chosen because: (1) it is sensitive to potential climate changes (Shaw et al., 2000; Pauli et al., 2001; Xu et al., 2006), such as potential increase in drought frequency projected for the region (IPCC, 2007) and (2) it is a major forest type in western Sichuan that plays a significant role in mitigating regional flooding, protecting headwaters, and conserving water and soil in the upstream of the Yangtze River (Xu et al., 2006). We hypothesize that the three

species of interest represent different plant functional types because they extract water from different depths in the soil profile due to their different root distributions. Determining such resource niche differentiation can provide useful information for understanding the mechanisms that contribute to species co-existence (Sala et al., 1997). Specifically, our objectives were to: (1) determine the contributions of rainfall and groundwater to soil water and plant xylem water and (2) examine the effects of rain event (season or amount), number of days after rain, soil layer depth, and plant species on such contributions.

## MATERIALS AND METHODS

### Study area

Our study was conducted at the Forest Ecosystem Research Station ($30°45'-31°25'$N, $102°52'-103°24'$E) of the Wolong Nature Reserve in West Sichuan Province, China, at the eastern rim of the Tibet Plateau (Figure 1). Field sampling was conducted on a north-facing slope of Balang Mountain between 2750 and 2950 m asl. The regional climate is characterized by dry, cold winter and cool and humid, cool summers (WNRAB, 1987). Based on the climatic records from 2001 to 2003 at the reserve, the annual precipitation is about 884 mm, $81·1\%$ of which occurs between July and September. The total number of rainy days annually exceeds 200 and the mean annual relative humidity is 80%. The mean annual temperature is 4·3 °C, with averages of −5·2 °C in December and 20·4 °C in July. The annual evapotranspiration (ET) is 772 mm. Of the three species dominating the three strata of the forest, A. faxoniana is a dominant overstory

tree with a height of 25–30 m and widely distributed with a coverage of 50–70%; *B. utilis* is a midstory tree with a height of 5–15 m and a coverage of ~30%; and *B. fangiana* is an understory shrubby bamboo with a height of 0·5–7 m and a coverage of ~55%. *B. fangiana* is the main food source for the endangered giant pandas (*Ailuropoda melanoleuca*).

### Data collection

In August 2003, three replicates of 20 × 20 m plots were established in the field site. Climatic data of precipitation, air and soil temperature, and humidity were continuously recorded at a microclimatic station about 30 m away from the edge of the forest. Rainwater from two individual precipitation events, 15 mm on the 15th of August 2003 (wet season) and 5 mm on the 7th of March 2004 (dry season), was collected at the climatic station. At each plot, the following samples were taken daily for the 9 days after each rain event: (1) Three 30 × 30 cm quadrants were selected and a litter sample was taken from the litter layer and four soil samples were taken along the soil profile at four depths (0–20, 20–40, 40–60, and 60–80 cm). From each soil and litter sample, a portion was sealed in soil tins and later analysed to calculate the gravimetric water content (i.e. percentage water expressed as g water/g dry soil ×100). Water extracted from the litter and soil samples was used for hydrogen isotope analysis following the procedures described by Lin *et al.* (1996); (2) three individuals were selected for each species and a plant stem sample was taken from each individual; and (3) the groundwater sample was taken at a nearby spring about 1·5 m below the soil surface. In addition, root sampling blocks were excavated within a 30 × 30 cm quadrant for the litter layer and for the four soil depths (0–20, 20–40, 40–60, and 60–80 cm); roots were separated at laboratory into fine (≤2 mm) and coarse (>2 mm) roots and later oven-dried at 75 °C to calculate their biomass. The samples of litter, soil, groundwater, and plant xylem water before rain event were taken in the same ways on August 14 (i.e. the day before the August rain) and on March 5 (i.e. 2 days before the March rain). All field sampling was conducted between 8:00 and 10:00 am. All samples of rain, groundwater, soil, and plant stem were placed in glass bottles, sealed with parafilm, and stored at 0 to −5 °C until water extraction was conducted in the laboratory following the procedure described by Lin *et al.* (1996).

### Stable isotope analysis

Water in the soil and plant stem samples was extracted cryogenically using the approach of Ehleringer *et al.* (2000). The H isotope ratio ($\delta D$) of extracted water, rainfall, and groundwater was measured using the methods described by Dawson (1993) and Lin *et al.* (1996), with a Thermo Finnigan MAT Delta$^{Plus}$ XP isotope ratio mass spectrometer (Thermo Finnigen, San Diego, CA, USA) coupled with a high temperature conversion/elemental analyzer (TC/EA), at the Stable Isotope

Laboratory for Ecological and Environmental Research, Institute of Botany, the Chinese Academy of Sciences. The precision of $\delta D$ analysis was ±2‰, based on two internal standards calibrated against a Vienna Standard Mean Ocean Water (V-SMOW) (NIST, Washington, DC, USA). Deuterium isotopic composition can be expressed as the H isotope ratio ($\delta D$, ‰):

$$\delta D = \left[ \frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000‰ \qquad (1)$$

where $R_{sample}$ and $R_{standard}$ are the H stable isotopic compositions (i.e. the $D/H$ molar ratio) of the sample and the standard water (i.e. SMOW), respectively (Gonfiantini, 1978; Ehleringer *et al.*, 2000). Contributions to soil or plant water were determined by using a single two-end linear mixing model:

$$f_A = \frac{\delta D_t - \delta D_B}{\delta D_A - \delta D_B} \times 100\% \qquad (2)$$

where $f_A$ is the proportion of new rainwater in plant xylem (or soil), $\delta D_t$ is the $\delta D$ value of the plant (or soil) water after rain; $\delta D_A$ is the $\delta D$ value of the rainwater; $\delta D_B$ is the $\delta D$ value of the groundwater. $\delta D_A$ and $\delta D_B$ are the two extreme ends of water sources in terms of highest and lowest $\delta D$ values.

### Statistical analysis

Statistical analyses were performed with SPSS (SPSS, Inc., Chicago, IL, USA). A mixed linear analysis of variance (ANOVA) model with the Tukey's test was used to examine the effects of rain season/amount (Rain), days after rain (Day), and plant species (Species) on the $\delta D$ values of and the rain contributions to plant xylem water, while a similar analysis was performed on the $\delta D$ values of and the rain contributions to soil water by using soil layer depth (Depth) as the third factor instead of plant species. Rain was treated as a nesting factor and Day as repeated measures.

### RESULTS

Soil moisture showed clear vertical variation along the soil profile and temporal dynamics during the 9-day observation period after the two rain events (Figure 2). After each rain, soil moisture displayed a strong gradient from surface to 80 cm depth and increased slightly in the first 2 days and decreased gradually to a relative steady state. These patterns after the two rain events appeared similar, but the soil moisture content at different layers was always higher in August (wet season; Figure 2a) than that in March (dry season; Figure 2b).

The soil water $\delta D$ values were intermediate between the $\delta D$ values of rain (−82·2‰ for August and −86·3‰ for March) and groundwater (−63·2‰ and −65·3‰, respectively) (Figure 3a and b). The $\delta D$ values of groundwater remained relatively unchanged before and after the rain events. Soil depth was the predominant factor to
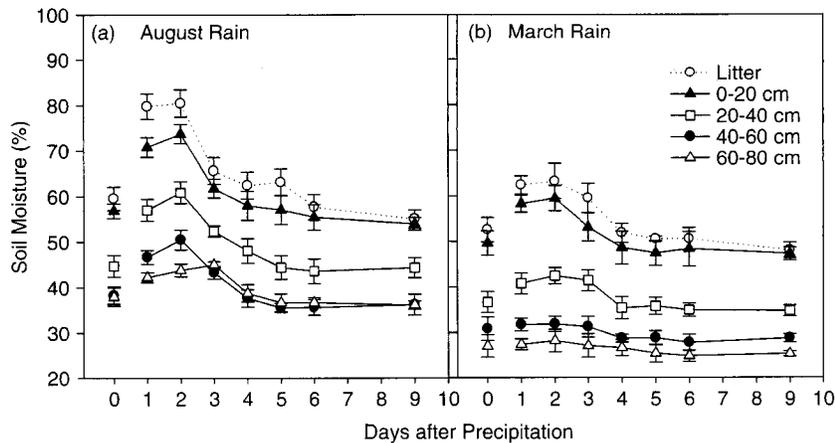
Figure 2. Soil water content (%) at different depths following two rain events, 14·8 mm on 15 August 2003 (wet season) and 5 mm on 7 March 2004 (dry season). The figure shows mean soil water content in a subalpine dark coniferous forest of Wolong in Southwest China, with the vertical bars representing ±1 standard deviation of the mean ($n = 3$).
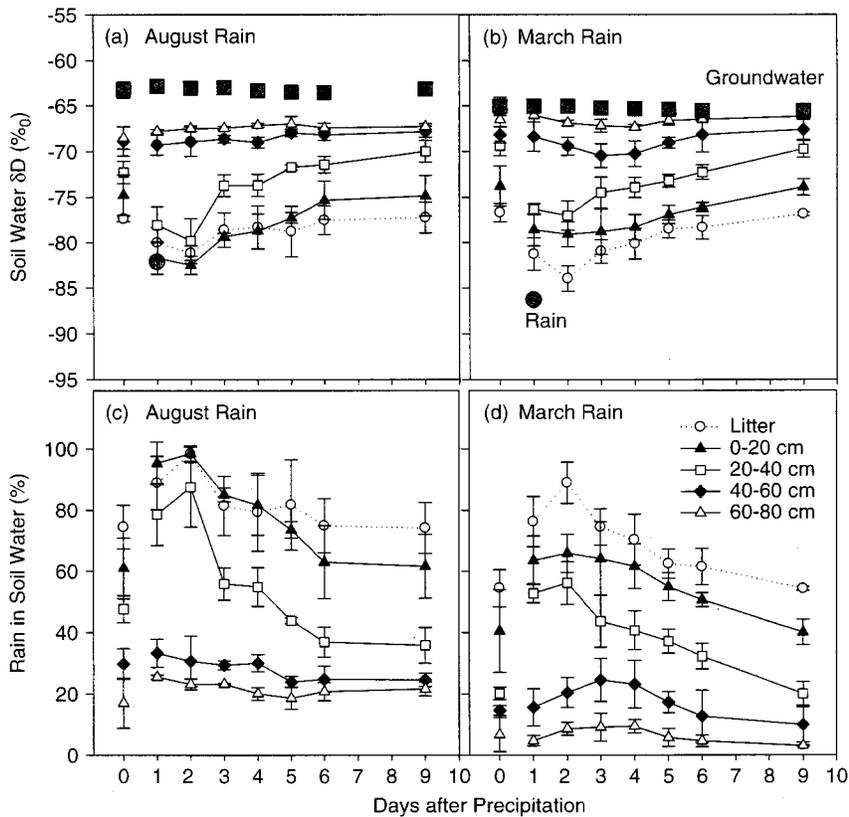


Figure 3. Temporal changes in $\delta D$ values of litter, soil, and groundwater (panels a and b), and in rain contributions to soil water (panels c and d) along the soil profile over a 9-day study period after two rain events (refer to Figure 2 for setting and data source).

soil water $\delta D$ (Table I), with the soil layer of 20–40 cm showing the most dramatic changes over time after each rain (Figure 3).

Rain contributions to soil water changed with rain amount, soil depth, and days after rain (Table I and Figure 3). In the wet season following the 15 mm rain in August, the litter layer received the highest rain contribution at 74–98% and the deep soil layer of 60–80 cm had the least at 19–26% (Figure 3c). In the dry season following 5 mm rain in March, similar pattern of rain contributions to soil was observed, but

generally with lower values (Figure 3d). The soil layer of 20–40 cm showed the most change in rain contributions (Figure3); for example, the rain contribution to soil water in this layer was reduced by 35·9–87·6% over the 9-day sampling period and decreased by more than 43% compared to the next layer of 40–60 cm (Figure 3). The mixed ANOVA model indicated that soil depth was the most important factor to explain rain contributions to soil water (Table I).

The $\delta D$ values of xylem water of the three plants resided between those of rain and groundwater (Figure 4).

Table I. Effects of rain events (Rain), soil layers (Depth), and days of rain (Day) on the stable isotopic rate ($\delta D$) of soil water and the rain contribution to soil water ($SW_{rain}$)[a].

| Factor | df | $SW_{rain}$ (%) | | $\delta D$ (‰) | |
|---|---|---|---|---|---|
| | | SSE (%) | $P$ value | SSE (%) | $P$ value |
| Rain | 1 | 7·6 | <0·0001 | 0 | 0·6663 |
| Depth | 4 | 76·2 | <0·0001 | 83 | <0·0001 |
| Day | 6 | 7·6 | <0·0001 | 7·4 | <0·0001 |
| Rain × Day | 6 | 0·5 | 0·0045 | 0·5 | <0·0001 |
| Rain × Depth | 4 | 0·5 | 0·0006 | 0·6 | 0·0008 |
| Depth × Day | 24 | 3·5 | <0·0001 | 4 | <0·0001 |
| Rain × Depth × Day | 24 | 0·6 | 0·3997 | 0·6 | 0·0010 |
| Error | 140 | 3·5 | | 3·9 | |
| Total | | 100 (164 295·4) | | 100 (6048) | |

[a] Observations were made at three sampling plots in a dark coniferous forest in the Wolong Natural Reserve, China, for two rain events (wet August vs dry March), five soil layers, and 7 days after rain. The mixed ANOVA model treated Rain as a nesting factor and Day as a repeated measure. SSE: Explained Sum of Squares.
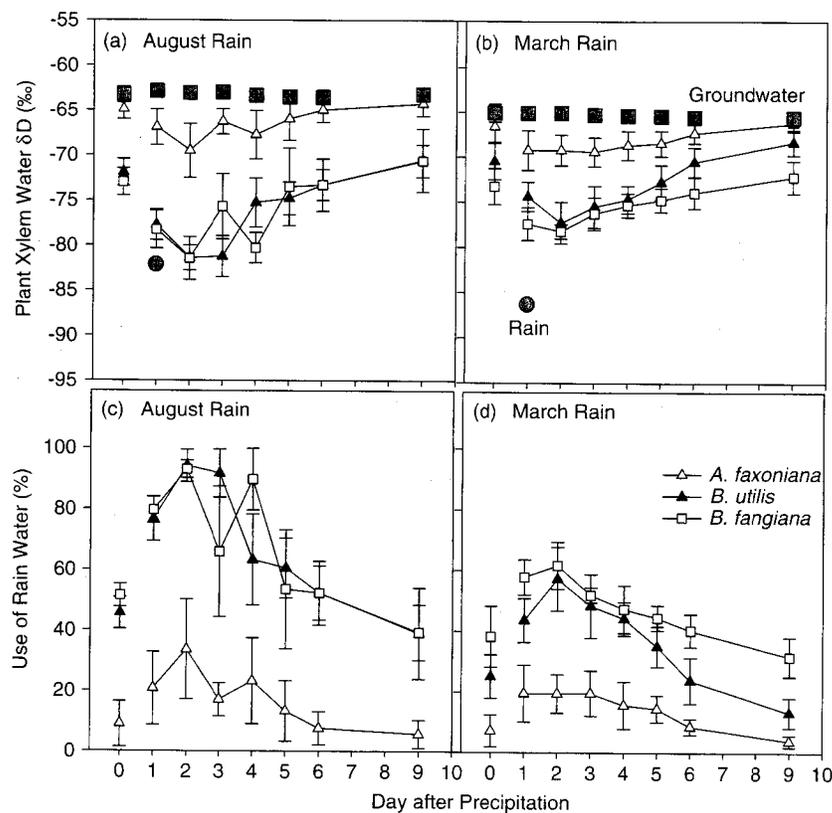


Figure 4. Temporal changes in $\delta D$ values of and in rainfall contributions to plant xylem water of three dominant species over a 9-day study period after two rain events (refer to Figure 2 for setting and data source).

*A. faxoniana* had $\delta D$ values closer to that of groundwater, while the $\delta D$ values of *B. utilis* and *B. fangiana* were relatively closer to that of rain. Variability in the xylem $\delta D$ values was also observed among the three species and with the days after rain (Figure 4).

The rainfall contributions to xylem water were also affected by plant species, days after rain, and rain event (Table II and Figure 4c and d). Species was the most important factor (Table II): while *B. utilis* and *B. fangiana* showed a similar pattern of high dependency on rainwater, *A. faxoniana* displayed a different water use strategy with a small proportion of xylem water

coming from the rain water (Figure 4c and d). During the 9-day period following each rain, the percentages of new rainwater used by the plants peaked on the second day and then decreased gradually. In addition, significant differences existed between the two rain events: the rainfall contributions to xylem water for *A. faxoniana*, *B. utilis*, and *B. fangiana* were 6–34%, 39–94%, and 39–93%, respectively, after August rain (Figure 4c) and 4–20%, 13–57%, and 32–62% after March rain (Figure 4d).

Root distributions displayed significant differences among the three plant species (Figure 5). The overstory

Table II. Effects of rain events (Rain), plant species (Species), and days of rain (Day) on the stable isotopic rate ($\delta D$) of xylem water and the rain contribution to xylem water (PW$_{rain}$)[a] .

| Factor | df | PW$_{rain}$ (%) | | $\delta D$ (‰) | |
|---|---|---|---|---|---|
| | | SSE (%) | $P$ value | SSE (%) | $P$ value |
| Rain | 1 | 10 | <·0001 | 0·4 | 0·0036 |
| Species | 2 | 47·8 | <·0001 | 53·5 | <·0001 |
| Day | 6 | 19·3 | <·0001 | 20·8 | <·0001 |
| Rain × Day | 6 | 1·1 | 0·0043 | 1·1 | 0·0009 |
| Rain × Species | 2 | 4 | <·0001 | 3·7 | <·0001 |
| Day × Species | 12 | 3·1 | <·0001 | 3·9 | <·0001 |
| Rain × Species × Day | 12 | 1·5 | 0·0127 | 1·7 | 0·0002 |
| Error | 336 | 13·2 | | 14·9 | |
| Total | | 100 (280 763·7) | | 100 (9842) | |

[a] Similar settings to Table I were used, except that three plant species (*Abies faxoniana*, *Betula utilis*, and *Bashania fangiana*) replaced the soil layers as the second factor.

species of *A. faxoniana* displayed a balanced fine root ($\leq 2$ mm) distribution in soil profiles with 50% in the lower soil layer of 40–80 cm (Figure 5a), whereas the fine roots of the midstory species of *B. utilis* and the understory species of *B. fangiana* were distributed mostly in the upper soil layers with 84 and 91% in the depth of 0–40 cm (Figure 5b and c). The total roots of the three plants showed similar vertical distributions.

## DISCUSSION

Soil water is regulated by processes such as precipitation, infiltration, interflow, and plant uptake and transpiration. Our results of rainfall infiltration showed that the rainfall contribution to soil water followed the pattern of temporal dynamics similar to that of soil moisture (Figures 2 and 3). There was a clear isotopic gradient in soil profile because of rain pulses (Asbjornsen *et al.*, 2007). However, such rain effects were short lived, lasting 4–6 days with peaks primarily on the second day (Figure 3). It is interesting to notice that, even though both the rainfall contribution to soil water and the soil moisture displayed a clear decrease between the two seasons, the change was relatively small.

The water use strategy by plants may determine the responses of ecosystems to environmental water changes (Ewe *et al.*, 1999). Consequently, tracing water sources used by major plant species in forest ecosystems is critical in understanding the hydrological regulations on ecosystem functions and services (Schimel, 1993; Gazis and Feng, 2004). Previous studies have reported that plant species uptake water from specific sources, such as precipitation, soil water, and groundwater (Flanagan and Ehleringer, 1991; Ehleringer and Dawson, 1992; Valentini *et al.*, 1992; Cheng *et al.*, 2006; Asbjornsen *et al.*, 2007). We found that the soil moisture distribution and the rainfall contributions to the soil water were clearly reflected by the patterns of rainfall contributions to xylem water of the three species (Figures 3 and 4). In addition, we found that these three species had contrasting water use patterns as indicated by the variation in the rain contributions following rain events. *A. faxoniana* appeared to

rely more on groundwater, which accounted for 66–96% of its water sources after rain, whereas *B. utilis* and *B. fangiana* seemed to be more dependent on rainwater, especially during the wet season when about 40–93% of their xylem water came from rain (Figure 4c). These results should be representative of the subalpine coniferous forest in southwestern China, at least for the wet season, because similar results were obtained for two additional rain events (one from 28 July to 6 August and the other from 30 August to 8 September 2003; Xu, 2006; Xu, unpublished data). Such differences in the water use strategies should promote species co-existence and maintain a resilient community because the differentiated resource-use niches reduce competition for water.

To meet the water needs for growth and transpiration, root systems of plants generally expand at rapid rates to spaces in the soil column where water is available for plants to uptake. In a plant community, different species may have distinguished root distributions (e.g. shallow-root vs deep-root) in order to uptake water efficiently from different soil depths (Weltzin and McPherson, 1997; Schenk and Jackson, 2002; Snyder and Williams, 2003). Our experimental data indicated that the patterns of water use by these three species displayed strong agreement with their fine root distributions in the soil profile (Figures 4 and 5). For example, *A. faxoniana* with 50% of its fine roots distributed in the 40–80 cm soil layer, where over two-thirds of soil water were groundwater. Thus, the deep-rooted *A. faxoniana* has abilities to take advantage of deep water sources derived from groundwater as reflected by the groundwater contribution to its xylem water. In contrast, *B. utilis* and *B. fangiana* were shallow rooted with 84 and 91% of their fine roots in the upper soil layers (0–40 cm and litter layer), where 40% or more of soil water comes from rain. Thus, *B. utilis* and *B. fangiana* can respond to changes in shallow water derived primarily from the rain. These findings agree with the previous studies by Kemp *et al.* (1997) and Cheng *et al.* (2006), who suggested that the root distributions in soils were likely to be responsible for the variations in the water use by different functional types of plants.
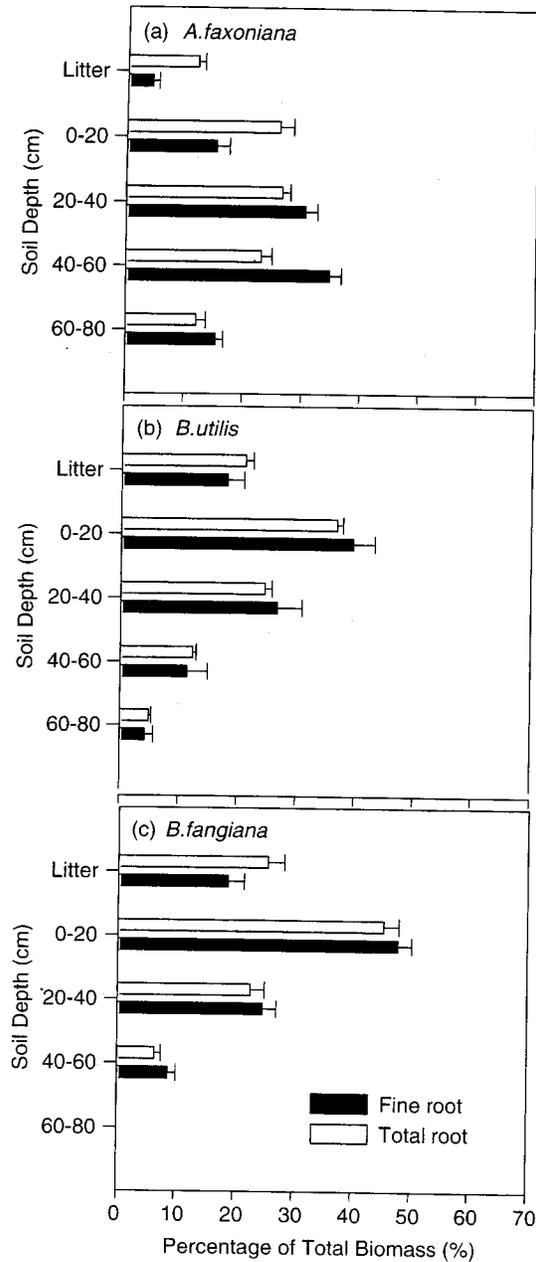
Figure 5. The distributions of root biomass of three key plant species along the soil profile in the Wolong Natural Reserve, Sichuan, China. Vertical bars represent ±1 standard error of the mean (n = 3).

The water use strategies may change as responses to changing conditions of water resources (Meinzer et al., 1999; Ewe and Sternberg, 2002; Chimner and Cooper, 2004; Wang et al., 2010). Our results showed that the three species in this subalpine coniferous forest ecosystem differed in temporal dynamics of their water use strategies. The overstory species of A. faxoniana showed a balanced reliance on both groundwater and rainfall and displayed little difference in its water use strategy between the wet season (August) and the dry season (March). In contrast, the midstory species of B. utilis and the understory species of B. fangiana were highly responsive to rainfall, especially in the wet season (Figure 4). In addition, the rain pulse effects on the soil water composition were not as pronounced

as those on the xylem water composition for B. utilis and B. fangiana (Figures 3 and 4), suggesting that these two species should have taken more water from deeper soils (thus, more groundwater) in the dry season. This result indicates that B. utilis and B. fangiana may be more opportunistic in their water use and have shifting water use strategies in different seasons. Similar results have been reported before (Donovan and Ehleringer, 1994; Meinzer et al., 1999; Ewe and Sternberg, 2002; Chimner and Cooper, 2004; Wang et al., 2010). For example, Ewe and Sternberg (2002) found that the native species in their Florida sites shifted their primary water sources from rainwater during the wet season to groundwater during the dry season. Most importantly, the lack of dependency on rain water by the dominant canopy tree of A. faxoniana, a foundation species of the subalpine coniferous forest ecosystem (Dayton, 1975), should increase the survival probability of the community as climate change intensifies with potentially more frequent droughts.

## CONCLUSIONS

Different water use strategies by plant species in a community can be fundamental to ecosystem resilience to the changing climate (Jackson et al., 1996). The three species in this subalpine dark coniferous forest ecosystem tend to have different, but complementary water use strategies: the dominant canopy tree of A. faxoniana relies primarily on groundwater (i.e. 66–96% of its water sources), whereas the midstory B. utilis and the understory B. fangiana depend predominantly on rainwater (i.e. 13–94% and 32–93%, respectively). These contrasting water use strategies of the three species are supported by their fine root distributions with A. faxoniana having 50% of its fine roots distributed in deep soils (40–80 cm) and B. utilis and B. fangiana having 84 and 91% of their fine roots in upper soils (0–40 cm)respectively. In addition, the three species differ in their temporal patterns of water use strategies. B. utilis and B. fangiana tend to use water opportunistically, switching to groundwater as the main source under stressful conditions during the dry season, whereas A. faxoniana's dependency on groundwater does not seem to change between seasons. The different and shifting, for some species, water use strategies and the lack of dependency on rainwater by the foundation species of the subalpine coniferous forest ecosystem should act together to promote species co-existence and maintain community resiliency under potentially increasing water stress caused by climate change.

In this study, our focus was on the resultant patterns of soil water redistribution because of the methodology limitations to examine the processes of soil water redistribution. Future research should focus on the full water cycle along the soil–plant–atmosphere continuum, considering the processes of soil water redistribution, runoff, plant uptake, and ET.

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