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## Higher plasticity of water uptake in spruce than larch in an alpine habitat of North-Central China

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### ABSTRACT

Understanding interspecific differences in tree water use will aid in the assessment of both tree-level ecophysiological adaptation to climate change and forecasts of forest dynamics. We investigated the seasonal variation of water sources between two co-occurring trees species with contrasting leaf phenology and rooting traits: the deciduous *Larix principis-rupprechtii* Mayr. and the evergreen *Picea meyeri* Rehd. et Wils. At weekly/biweekly intervals from September 2013 to October 2014 in the Luya Mountains in North-Central China, we collected and analyzed a total of approximately 2400 samples of  $\delta D$  and  $\delta^{18}O$  in tree xylem water, potential water sources for all study trees, and the contribution of water at different soil depths. Concurrently, we monitored leaf phenology by direct observation and wood phenology with the microcore method. Microcoring allowed us to trace intra-annual dynamics of wood formation (i.e., onset, end, and maximum growth rate). These results, including a seasonal origin index, indicated that winter snowmelt water is sourced for growth initiation for both larch and spruce, although larch relies on it more than spruce. Larch and spruce mainly absorbed water from the same soil layer of 10–20 cm during the growing season (circa 38.9% and 37.5% of total water uptake, respectively). However, this potential inter-specific water competition did not increase until growth rates reached the maximum for the year; larch used more water from deeper soil layers while spruce used water generally equally from each soil layer. Unlike deeper-rooting larch, the more shallow-rooted spruce showed a greater ability to shift water uptake among various soil layers. This plasticity in water uptake was accompanied by tighter stomatal regulation, suggesting spruce growth is generally more tightly coupled to water availability. Such diverging species-specific water use strategies improve our knowledge on tree-level ecophysiological mechanisms, with implications for understanding ecosystem-level forest dynamics and potential resilience to environmental stress.

### 1. Introduction

Forests in many regions have been affected by water deficits due to increased temperatures and decreased precipitation over the last three decades (Allen et al., 2015). At high elevations and high latitudes, rates of warming are greater than the global mean (Pepin et al., 2015), leading to a declining snowpack (Campbell, 2019). Global warming has made tree growth in northern high latitudes more water limited than in the past (Babst et al., 2019; Driscoll et al., 2005; Wu et al., 2019). Thus,

understanding the response of high-altitude trees to inter-seasonal fluctuations in water sources during a period of rapid warming is critical to more accurately model how water availability can limit tree growth. Such an understanding will aid in estimating future forest composition, structure, and development (Grossiord et al., 2019).

Water stable isotope signatures ( $\delta D$  and  $\delta^{18}O$ ) have been used as tracers to demonstrate that trees growth responses to water availability are complex and trees may vary water sources throughout the growing season (Allen et al., 2019a; De Micco et al., 2016; Zhang et al., 2019d).

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In some regions, earlywood growth depends on the previous year's snowpack and soil moisture (Castagneri et al., 2018), while much of the variation in latewood growth often depends on current year soil moisture availability (Shamir et al., 2020). Beside externally uptaking water through tree roots, some have reported that internal stem water storage in trees may act as a direct, internal water source that buffers water stress during periods of reduced soil moisture (Čermák et al., 2007; Hu et al., 2018). In addition, Edwards et al. (1985) found the correlation of tree ring and source-water isotopic values ( $\delta^{18}\text{O}$ ) differ with relative humidity. Under early spring drought, the formation of wood might partially use assimilates from the previous year, leading to tree ring isotopic signals that are a combination of the previous year's precipitation and growth rate (Buhay and Edwards, 1995). To interpret the variation in plant water uptake, it is necessary to combine the analysis of water sources and tree growth. While most case studies have reported tree water use mostly focused at an inter-annual scale by using tree ring widths or isotopic signals (Jiao et al., 2019a; Liu et al., 2019), the seasonal origins of water use by trees at an intra-annual scale have not been systematically explored (Sohel et al., 2019). Some experiments support intra-annual variation of tree water sources and indicate that plant growth can be driven by seasonal rainfall, a finding which is not evident when we consider rainfall at an annual scale (Hovenden et al., 2014). Analyzing seasonal variations of potential water sources throughout the year can aid in determining specific water sources for trees. Such work would also help in understanding the timing and magnitude of previous year's water and/or stored water as an important water-source for trees.

Co-occurring tree species with differing leaf phenologies or physiologies may express different growth responses to water availability, enabling detailed analysis of the relationships between water sources and tree growth (Singer et al., 2013). These different water acquisition strategies among species can be explained by the hydrological niche segregation hypothesis (Kukowski et al., 2013), which proposes that within a community, plants may differ in hydraulic traits to tolerate or avoid drought to reduce competition (Silvertown et al., 2015). These traits include differences in water uptake capability (e.g. different leaf water uptake capability or rooting depths), stomatal control (e.g. anisohydric or isohydric behaviour) and xylem vulnerability to embolism (Brum et al., 2019; Choat et al., 2012; McDowell et al., 2008; Schreel and Steppe, 2019). Recent findings indicate that co-occurring species with different hydraulic traits may reduce species-specific sensitivity to drought and enhance forest resilience to climate change (Drobyshev et al., 2013). Thus, investigating co-occurring species with varying tree-level responses to water availability can improve understanding of community-level resilience to climate change and particularly to water stress.

*Larix principis-rupprechtii* Mayr. and *Picea meyeri* Rehd. et Wils. are two dominant species in the cold-temperature coniferous forests (1800–2800 m a.s.l.) of North-Central China. Each species has its own set of leaf phenological and physiological traits (Fang et al., 2011). Hereafter, *Larix principis-rupprechtii* is referred to as 'larch' while *Picea meyeri* is referred to as 'spruce'. Larch is a pioneer species and is more commonly found in high radiation habitats, while spruce can grow in shady habitats (Oberhuber et al., 2014). Unlike spruce, whose long-lived needles enable a longer photosynthetic season; larch is deciduous and rebuilds its foliar canopy annually. Larch also develops deeper root systems than spruce, and can seemingly access deeper, more reliable soil water (Schmid and Kazda, 2002). It is thought that this trait allows larch to keep their stomata open and maintain high photosynthetic activity under water stress (Bischetti et al., 2009). However, this strategy has a potential cost: increased water loss through high transpiration (Eilmann and Rigling, 2012). On inner alpine dry valleys in Austria, for example, Leo et al. (2014) predicted that *Larix decidua* Mill. may encounter higher risk of hydraulic failure due to lower stomatal regulation in comparison with co-occurring *Picea abies* [L.] Karst. However, Lévesque et al. (2013) anticipated that both *Larix decidua* and *Picea abies* had high vulnerability to drought and would undergo significant growth reductions either at a

xeric site in the dry inner-Alps or at a mesic site in the Swiss lowlands. In contrast, Peters et al. (2019) reported *Larix decidua* showed a more efficient water use compared to *Picea abies* in the Swiss Alps. These contrasting results indicate that the capacity to cope with water stress for co-occurring larch and spruce are not constant over space and may vary under different local environmental conditions.

Larch and spruce are the third and fifth most dominant tree species of natural forests in China, covering over 7.67 and 3.85 million hectares, respectively (National Forestry and Grassland Administration, 2019). They play an important role for soil and water resource conservation in mountainous areas (Zhang et al., 2012). We know of two studies investigating the water use relations of coexisting larch and spruce; both were conducted in alpine or boreal forests (King et al., 2013; Pappas et al., 2018). Conducting similar research in different ecological and climatological settings within a monsoonal region can give insight as to whether previous findings are universal or, perhaps, representative of local settings and conditions. To determine the potential universality of the relations found in prior work, we monitored tree wood phenology, leaf phenology, and water source of co-occurring *Larix principis-rupprechtii* and *Picea meyeri* in a temperate alpine habitat, the Luya Mountains, in monsoonal China. These two species have overlapping geographical distributions, giving our investigation greater equitability or a fairer comparison of species. Notably, our study site is located at the center of each species' distributional range making the comparisons appropriate to study the ecology of potential water stress.

To better understand species' vulnerability and adaptability to water availability throughout the growing season, our objectives were: (1) to explore the timing and magnitude of trees' variation in water sources throughout the year, including previous years' water and/or stored water in stems for initial growth in the spring; (2) to quantify trees' water uptake from various soil layers to observe whether species' water niches were separated; and (3) to compare co-occurring larch and spruce water-use strategies in response to summer precipitation. Considering the leaf phenology and physiological traits of both species, we hypothesize that: compared to evergreen spruce, (H1) deciduous larch will more likely to use water from the previous year or stored water for earlier growth initiation; and (H2) larch will shift water sources less often than spruce under decreased water availability. This information combined with an analysis of the relationships between growth and ecophysiological traits, and water source and seasonal timing of water uptake will help to assess the adaptation potential of different tree species to climate change.

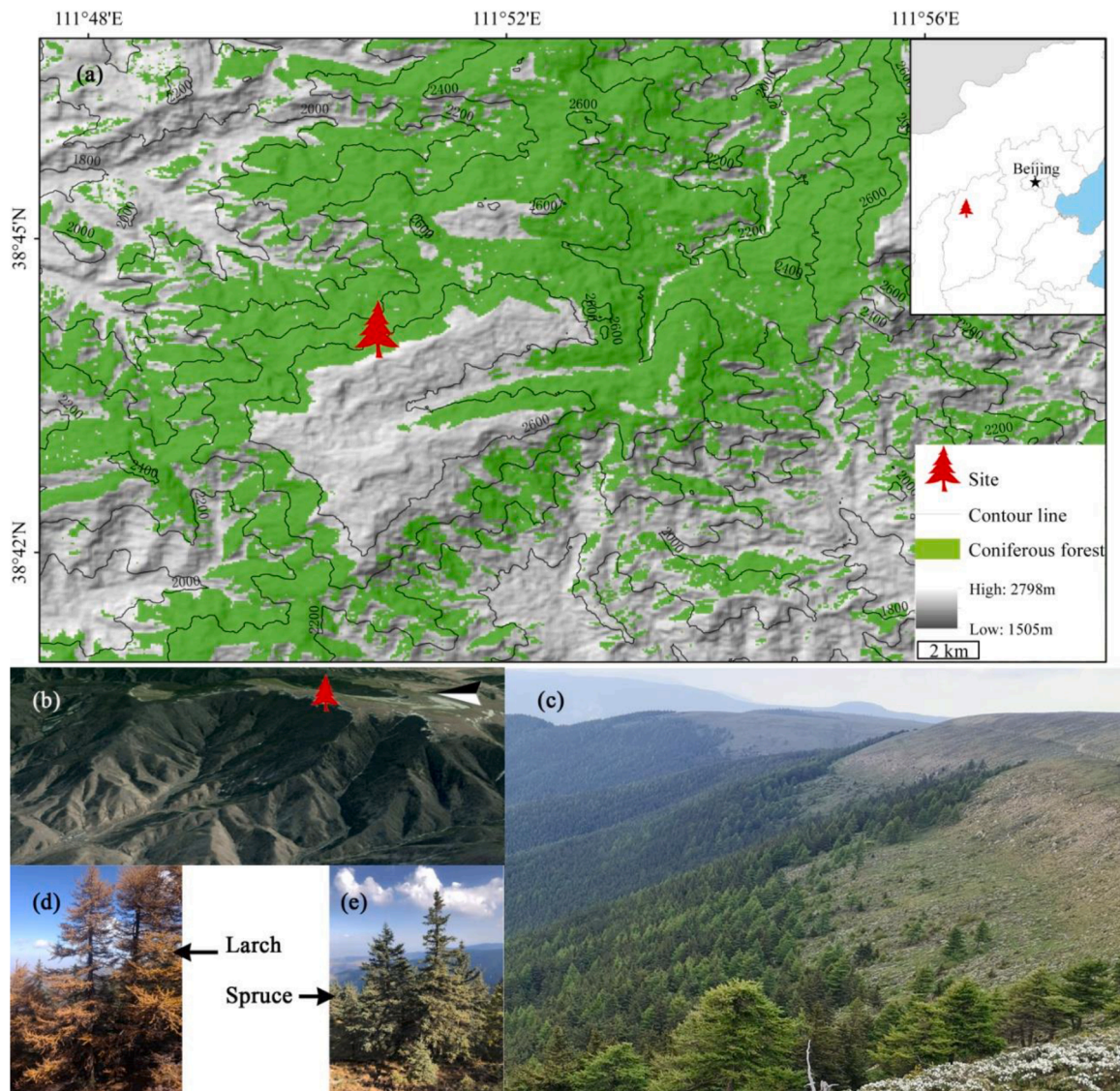
## 2. Materials and methods

### 2.1. Study site and species description

The study site is situated near the summit of Luya Mountains in North-Central China (38°40' N–38°50' N, 111°50' E–112°00' E, 2740 m a.s.l., Fig. 1a). The site is on a north-exposed slope with 18°–20°. The climate type is semi-humid temperate with monsoon rainfall during summer. Meteorological data from Wuzhai (38°55' N, 111°49' E, 1401 m a.s.l.) records the mean annual temperature and total precipitation are 5.2 °C and 473 mm, approximately 60% of which falls during the growing season (May–September) (Fig. 2). Climatic records in the Wuzhai region showed an increasing trend in annual mean temperatures and a large increase in annual precipitation and annual maximum daily vapor pressure deficit (VPD) since the 1990s (Fig. S1).

To better understand the microclimatic conditions at the study site, we set up an automatic weather station to monitor meteorological factors, including precipitation, air temperature, soil temperature, and soil volumetric water content. Soil water content was observed at depths of 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm. A detailed description of meteorological instrumentation can be found in Zhang et al. (2018b).

The soil in the study area is mountainous brown forest soil, which is well-drained sandy loam with 12–18% clay and 50–60% fine sand



**Fig. 1.** Location of study site in North-Central China (a), the study area landscape from google earth (b) and photo (c), and the photos of two tree species *Larix principis-rupprechtii*(d)and *Picea meyeri* (e). Photo C was taken by Feng Xue.

(National Soil Survey Office, 1995). The soils are generally not more than 50 cm deep, overlying the fractured parent material. The pH of the topsoil ranges between 6.4 and 7.3 (Jiang et al., 2014).

*Larix principis-rupprechtii* and *Picea meyeri* are two dominant species at our study site. As the study site is near the upper treeline at 2740 m a. s.l., these stands are sparse and the trees are isolated (Fig. 1b, c). The study site is also in the transition zone from cold coniferous forest (1850–2700 m a.s.l.) to subalpine meadow (2450–2780 m a.s.l.) (Ma, 2001). The fine root distribution (< 2 mm) of larch and spruce were investigated in September 2014. To avoid root interference from other trees, five isolated trees per species were selected. For each tree, six soil cores were taken by hand auger from both the north and south (Zhang et al., 2018b). A total of 480 soil samples for fine root biomass were collected.

## 2.2. Plant, soil, and water isotopic sampling

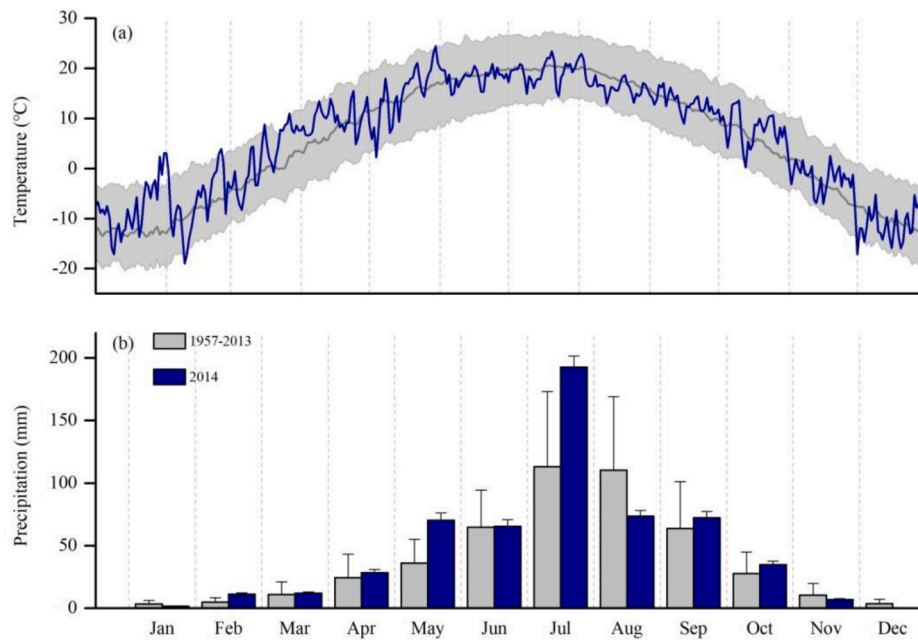
Sampling for the water source of trees was conducted over 10 months from September to October of 2013 and from April to October of 2014. We sampled monthly in 2013 and increased to on average weekly (at midday) sampling in April 2014. To determine the onset of the growing

season accurately, sampling occurred at intervals of 3–5 days from mid-April to early July. From July to September, sampling was set at 7 to 10-day intervals. October is typically the end of the growing season; therefore, we decreased sampling frequency to biweekly (González-González et al., 2013).

Five trees per species were selected, with similar ages, diameters, and heights (Table 1). For each tree, three 5 cm-long lignified twigs from the sun-exposed crown at heights above 2 m were obtained. For each twig, the phloem tissue was removed to avoid contamination by isotopic-enriched water. Samples were put into glass vials, sealed with parafilm (BEMIS Company Inc., USA), and stored in a freezer (−10 °C) until water extraction.

Soil samples were collected on the same days that tree twigs were collected. Using a hand auger, four soil profiles were dug near the selected trees. Two replicates were collected in each profile for depth class (0–10 cm, 10–20 cm, 20–30 cm and 30–40 cm). It was impractical to obtain soil samples from a depth greater than 40 cm because of the underlying rock at most sampling sites. A total of 1344 soil samples were obtained, sealed in glass bottles, and kept frozen until isotopic analysis.

Precipitation samples were obtained 32 times during each sampling periods using a rain collector with five replicates from April to October,



**Fig. 2.** Comparison of (a) the mean daily air temperatures and (b) the monthly sums of precipitation for the monitoring year of 2014 (blue) and the 1957–2013 average (light grey). Grey shading in (a) indicates the mean minimum and maximum temperatures averaged over the 1957–2013 period. The data in (b) represents mean  $\pm$ SD. Data were obtained from the nearest state meteorological station in Wuzhai (38°55' N, 111°49' E, 1401 m a.s. l., linear distance approximately 20 km north of the study site).

**Table 1**  
Characteristics of the sample trees ( $N = 5$ ).

Species	Age (year)	Diameter (cm)	Height (m)	Crown Breadth (m $\times$ m)
<i>Larix principis-rupprechtii</i>	57 (6)	21.1 (2.9)	7.8 (1.8)	3 $\times$ 3
<i>Picea meyeri</i>	58 (9)	21.5 (4.6)	8.5 (1.5)	4 $\times$ 3

Age and diameter recorded at breast height. Mean (standard deviation).

2014 (Liu et al., 2014). Snow in spring is often a primary water source for trees (Sugimoto et al., 2002). Therefore, observations of snow cover were conducted from early April to May 23, 2014, until the snow completely disappeared. Entire layers of snow cover were taken, transferred into plastic bags to reduce evaporation, and kept in a warm room for thawing. A total of 165 snow samples were collected. There is no groundwater in this study because the site is located at the summit of Mt. Luya.

### 2.3. Isotopic analysis

Plant xylem and soil water were extracted using the cryogenic vacuum distillation method (West et al., 2006). Generally, this required 0.5–1.5 h, depending on the water content of samples (Meißner et al., 2014). All water isotopic compositions (hydrogen and oxygen,  $\delta D$  and  $\delta^{18}O$ ) were analyzed using an isotopic ratio infrared spectroscopy system (Model DLT-100, Los Gatos Research, Mountain View, CA, USA) at the State Key Laboratory of Earth Surface Process and Resource Ecology, Beijing Normal University, China. The precision of the liquid water isotope analyzer was typically better than  $\pm 1.2\text{‰}$  for  $\delta D$  and  $\pm 0.3\text{‰}$  for  $\delta^{18}O$ . Due to the presence of organic contaminants (methanol and ethanol) in cryogenically extracted water samples from plant tissues, the  $\delta D$  and  $\delta^{18}O$  of xylem water were corrected following the procedure of Schultz et al. (2011) and Wu et al. (2016).

Monthly weighted means of  $\delta D$  and  $\delta^{18}O$  for precipitation were calculated as:

$$\delta p = \frac{\sum_{i=1}^n \delta_i \times P_i}{\sum_{i=1}^n P_i}$$

where  $\delta_i$  is the  $\delta D$  and  $\delta^{18}O$  of the  $i$ th precipitation, and  $P_i$  is the amount

of the  $i$ th precipitation.

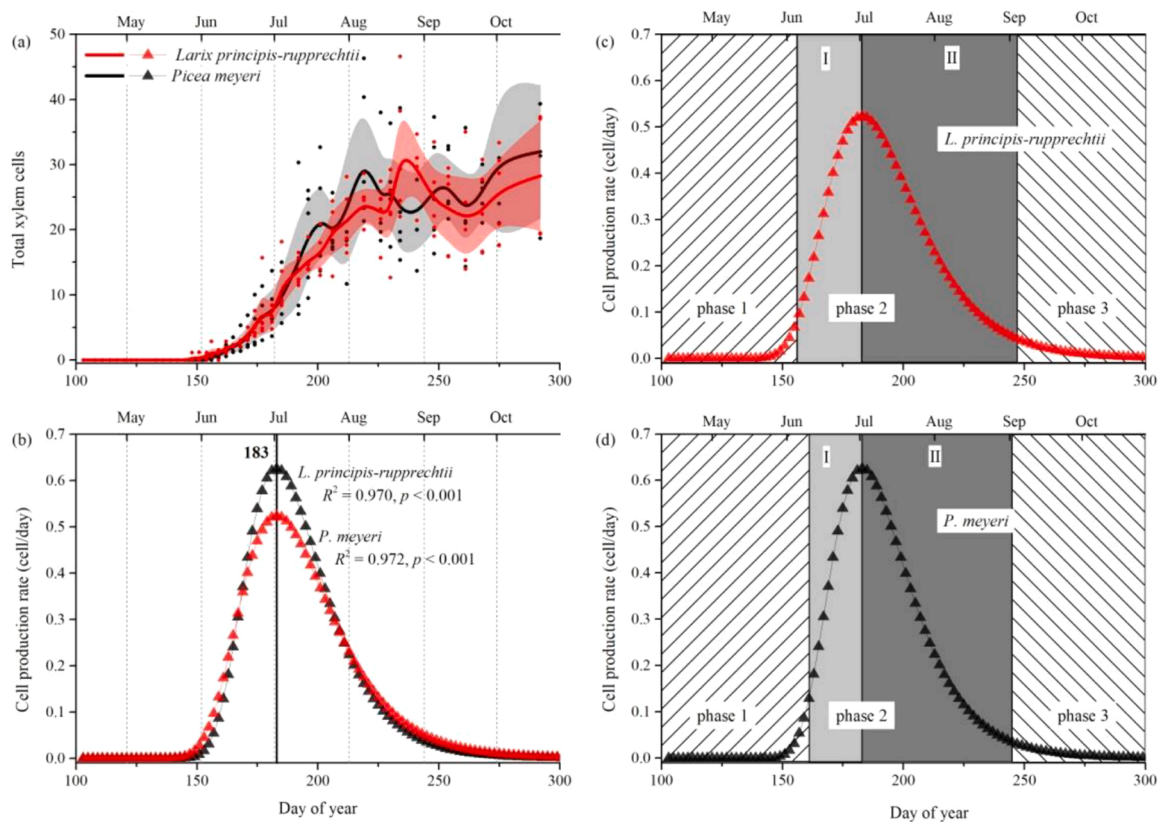
### 2.4. Wood and needle phenology observations

Wood phenology was determined by monitoring intra-annual stem cambial activity and xylem formation using the microcore method (Rossi et al., 2013). This widely-used microcore method is an effective technique to monitor growth at high temporal resolution (Camarero et al., 2010). Wood phenology was monitored on the same dates and in the same trees where the tree xylem water was sampled, either on a weekly or biweekly basis depending on the season. In spring, the first appearance of an enlarging cell signifies the onset of the wood growth (Deslauriers et al., 2017). In late summer/autumn, the last-formed tracheid finishing cell wall thickening, and lignification with the empty lumen and red cell walls (stained with safranin) indicate the end of the wood growth (Rossi et al., 2006).

Based on weekly micro-core sampling, the onset and end of wood growth were determined from early June to early September. Because no significant differences were observed between larch and spruce (Table S1, Fig. 3), the observation period was divided into three phases: before the growing season (April–May), the growing season (June–August), and after the growing season (September–October). Moreover, Gompertz models fitted to xylem cell production predicted that maximum growth rates occurred around July 2 (DOY 183) for both species (Table S3, Fig. 3b). From this result, the growing season was subdivided into two stages: the accelerating growth stage

(June 4 to July 3 and June 9 to July 3 for larch and spruce, respectively; the difference in timing between larch and spruce is related to the onset of wood growth, larch beginning five days earlier than spruce), and the decelerating growth stage (July 4 to September 4 and July 4 to September 2 for larch and spruce, respectively). Additionally, the growth initiation stage was fixed from late May to early June (May 29 to June 4 and June 2 to June 9 and for larch and spruce, respectively; these differences are, again, due to growth phenology).

The development of needle phenological stages were monitored for the same trees by recording the times of budburst, needle unfolding, needle full elongation, and leaf defoliation (Zhang et al., 2019c). Needle phenological observations were carried out weekly (3–5 days shorter intervals after budburst). Larch trees began bud burst on May 5 and soon started to unfold needles on May 16. Spruce began bud burst on May 25



**Fig. 3.** Division of growing and non-growing season based on the dynamics of wood growth. (a) Dynamics of wood growth (total xylem cells). For each species, the line represents the mean cell number of the five monitored trees, and the shadowed area represents 90% confidence intervals. (b) Daily cell production rates are modeled by applying the Gompertz function. (c) and (d) Division of the observed periods for *Larix principis-rupprechtii* and *Picea meyeri*. Phase 1, phase 2, phase 3 represent before, during, and after the growing season, respectively; I and II represent the accelerating growth stage and the decelerating growth stages, respectively. Dates are displayed as days of the year (DOY).

(Table S2).

### 2.5. Contribution of summer and winter precipitation to trees

To quantify the relative contributions of summer (current year) and winter (previous year) precipitation used by trees, we used a seasonal origin index (SOI) to infer (Allen et al., 2018):

$$SOI = \begin{cases} \frac{\delta_x - \delta_{annP}}{\delta_{summerP} - \delta_{annP}}, & \text{if } \delta_x > \delta_{annP} \\ \frac{\delta_x - \delta_{annP}}{\delta_{annP} - \delta_{winterP}}, & \text{if } \delta_x < \delta_{annP} \end{cases}$$

where  $\delta_x$  is the fractionation-compensated  $\delta D$  isotopic signature of xylem water or soil water, and  $\delta_{summerP}$ ,  $\delta_{winterP}$ , and  $\delta_{annP}$  are the  $\delta D$  isotopic signatures of typical summer, typical winter, and volume-weighted annual precipitation at study site. The SOI will be near  $-1.0$  for plant and soil water samples derived entirely from previous year's precipitation (winter precipitation) and near  $1.0$  for samples derived entirely from current year's precipitation (summer precipitation). The fractionation-compensated xylem and soil water isotopic values were calculated using the Craig–Gordon model as implemented by Benettin et al. (2018). The values of  $\delta_{summerP}$  and  $\delta_{winterP}$  were modeled using a sinusoid isoscape approach (Allen et al., 2019b). The  $\delta_{annP}$  was used the volume-weighted mean precipitation during 10-month field sampling (September 2013–October 2014).

### 2.6. Quantification of water sources

The water uptake from different soil layers to trees were analyzed

using SIAR (Stable Isotope Analysis in R, version 4.2). SIAR is a Bayesian stable isotope mixing model that can incorporate the uncertainty of multiple sources, the variability in isotope signatures, and isotope fractionation (Parnell et al., 2010). The Bayesian mixing model is shown to have better performance in source water estimates and is more useful than the simple mass balance approach (i.e., IsoSource model) (Evaristo et al., 2017; Rothfuss and Javaux, 2017).

To rule out the possible effect of hydrogen fractionation on the assessment of water use, we selected  $\delta^{18}O$  to calculate tree water sources (Lin and Sternberg, 1993). The input data for SIAR included  $\delta^{18}O$  data of xylem water and  $\delta^{18}O$  data of soil water with 10 cm intervals (0–10 cm, 10–20 cm, 20–30 cm and 30–40 cm). The fractionation value was set to zero because there was no isotopic fractionation of  $\delta^{18}O$  during plant water uptake in the growing season. Model predictions were presented as the 50th, 75th, and 95th confidence percentile values, and were combined into three source endpoints (0–10 cm, 10–20 cm, and 20–40 cm) (Moore and Semmens, 2008).

### 2.7. Data and statistical analysis

After testing for the normality of residuals and homogeneity of variances, the temporal pattern of differences in  $\delta^{18}O$  of precipitation and xylem water across the three phases (before, during, and after growing season) were assessed with a one-way analysis of variance (ANOVA). Then, post hoc multiple comparisons were conducted by using the Fisher's Least Significant Difference (LSD) test.

Soil water content and  $\delta^{18}O$  values differences across soil depths and sampling phases were evaluated with Kruskal-Wallis non-parametric rank test due to lack of homoscedasticity of these data (Minderlein and Blodau, 2010). Subsequently, a multiple comparisons test was

performed by using the Mann-Whitney U test. Comparisons of xylem water between larch and spruce on each sampling date were determined using independent-samples *t*-test. Relationship between xylem water with environmental variables was investigated using general linear models. All statistical analyses were performed in SPSS 20.0 (SPSS Inc., Chicago, USA).

### 3. Results

#### 3.1. Meteorological conditions and variations in the precipitation and soil water

The study year, 2014, was relatively wet. Annual precipitation was 20.4% higher than the 1957–2013 average (Fig. 2). However, this surplus precipitation mainly fell in July, which is 70.4% more than the mean value of that month. Precipitation events of 5 mm or less accounted for 70.4% of the total precipitation. Average snow depth was approximately 20 cm during springtime. The period of snow melt was from May 5 to May 23, during which the soil temperature reached 0 °C (Fig. 4).

Soil volumetric water content (SWC) exhibited significant changes with both soil depth and month. Maximum SWC occurred at the depth of 10–20 cm during the sampling period, except for in late May when there was an infiltration of snowmelt water at the 0–10 cm depth (Fig. 4). Thus, SWC<sub>10</sub> (0–10 cm) and SWC<sub>20</sub> (10–20 cm) reached its yearly maximum value of 38.2% on May 24 and 46.0% on June 7, respectively. The infiltration after spring snowmelt can be traced down to 20 cm. The contribution of snowmelt to 0–10 cm soil water is estimated about 9–15%. In addition, there was a trend of decreasing SWC around the time of a drier period in mid-August. Precipitation was < 33.1% of the long-term mean for that month.

#### 3.2. Isotopic values of potential water sources

A strong linear relationship between  $\delta D$  and  $\delta^{18}O$  was observed in both local precipitation and soil water. The slopes of  $\delta D$ - $\delta^{18}O$  for the local meteoric water line and soil water line were 7.95 and 7.06, respectively, indicating that the soil water, but not rainfall, had undergone slight evaporative enrichment (Fig. S2). The  $\delta^{18}O$  of precipitation was significantly depleted after the growing season ( $p < 0.05$ , Table 2). Snow depth was approximately 20 cm and  $\delta D$  and  $\delta^{18}O$  of snowmelt were -96.52‰ and -14.00‰, respectively.

The  $\delta^{18}O$  values of soil water changed significantly with both soil depth and growth phase ( $p < 0.05$ , Table 2). Soil  $\delta^{18}O$  profiles were

characterized by less negative values in shallow soil layers relative to deeper soil layers except for after early September. Soil  $\delta^{18}O$  at 0–10 cm below the surface was most variable and strongly reflected the seasonal variation of  $\delta^{18}O$  in precipitation ( $r = 0.663$ ,  $p < 0.01$ ,  $N = 28$ ). Among soil layers, soil  $\delta^{18}O$  at 0–10 cm was significantly different than at 20–40 cm ( $p = 0.015$ ). However, soil  $\delta^{18}O$  at 10–20 cm did not differ significantly from either the  $\delta^{18}O$  at 0–10 cm or at 20–40 cm ( $p = 0.076$  and  $p = 0.352$ , respectively); this indicates that precipitation may reside or mix with storage in the 10–20 cm layer. Values of soil  $\delta^{18}O$  differed significantly between the growing and non-growing seasons for both the 10–20 cm and the 20–40 cm layer, but not for the 0–10 cm layer.

Variations in soil seasonal origin index (SOI) convey the seasonal contributions of winter and summer precipitation to soil water. Strong infiltration of winter precipitation (snowmelt water) to top soil layers can be observed during snowmelt period, then more summer rainfall during growing season (Fig. 5a). Mean seasonal origin index in 0–10 cm soil layer was reduced to -0.56 during snowmelt period and then increased to 0.21 during growing season. Summer precipitation signatures were common in soil water from June to August; seasonal origin index of soil water was >0 for 76% at 0–10 cm, 72% at 10–20 cm, and 68% at 20–40 cm.

#### 3.3. Isotopic composition in plant xylem water

Xylem water  $\delta^{18}O$  showed pronounced seasonal trends (Table 2, Fig. 6). Before the growing season, particularly before larch needle unfolding (May 16), xylem  $\delta^{18}O$  was much higher than the highest soil  $\delta^{18}O$  values. During the growing season, xylem  $\delta^{18}O$  of both species followed the seasonal patterns of soil  $\delta^{18}O$  at 10–20 cm (Fig. 6, larch: slope = 0.447, intercept = -5.844,  $r = 0.521$ ,  $p < 0.05$ ,  $N = 20$ ; spruce: slope = 0.420, intercept = -5.649,  $r = 0.485$ ,  $p < 0.05$ ,  $N = 18$ ). Potential linkage between xylem  $\delta^{18}O$  and soil  $\delta^{18}O$  at 10–20 cm disappeared both during the entire year and after the growing season. Moreover, the seasonal patterns of  $\delta^{18}O$  in precipitation did not match xylem  $\delta^{18}O$  either at any single phase or through the entire year.

Larch had more enriched xylem  $\delta^{18}O$  values relative to spruce, ranging from -4.16‰ to -12.98‰ versus -6.41‰ to -13.31‰, respectively. Before the growing season, xylem  $\delta^{18}O$  of larch trees were significantly higher than spruce ( $p < 0.001$ , Table 2), but, during the entire year, xylem  $\delta^{18}O$  did not differ significantly between the two species ( $p = 0.241$ ). In fact, there was a strong positive correlation of xylem  $\delta^{18}O$  between the two species ( $r = 0.485$ ,  $p < 0.01$ ,  $N = 42$ ). While this association strengthened during the growing season ( $r = 0.846$ ,  $p < 0.001$ ,  $N = 20$ ), it was absent before and after the growing season.

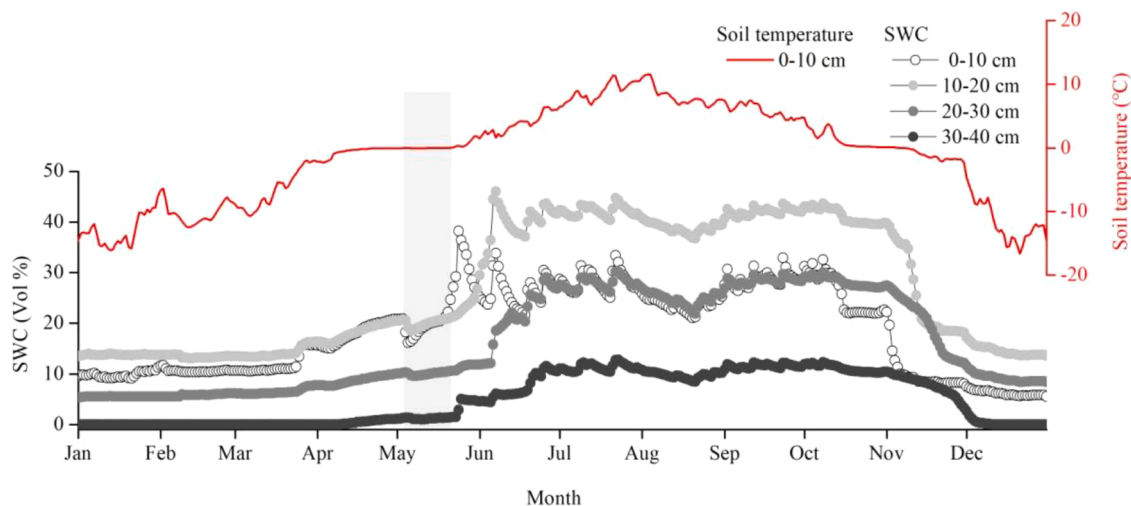
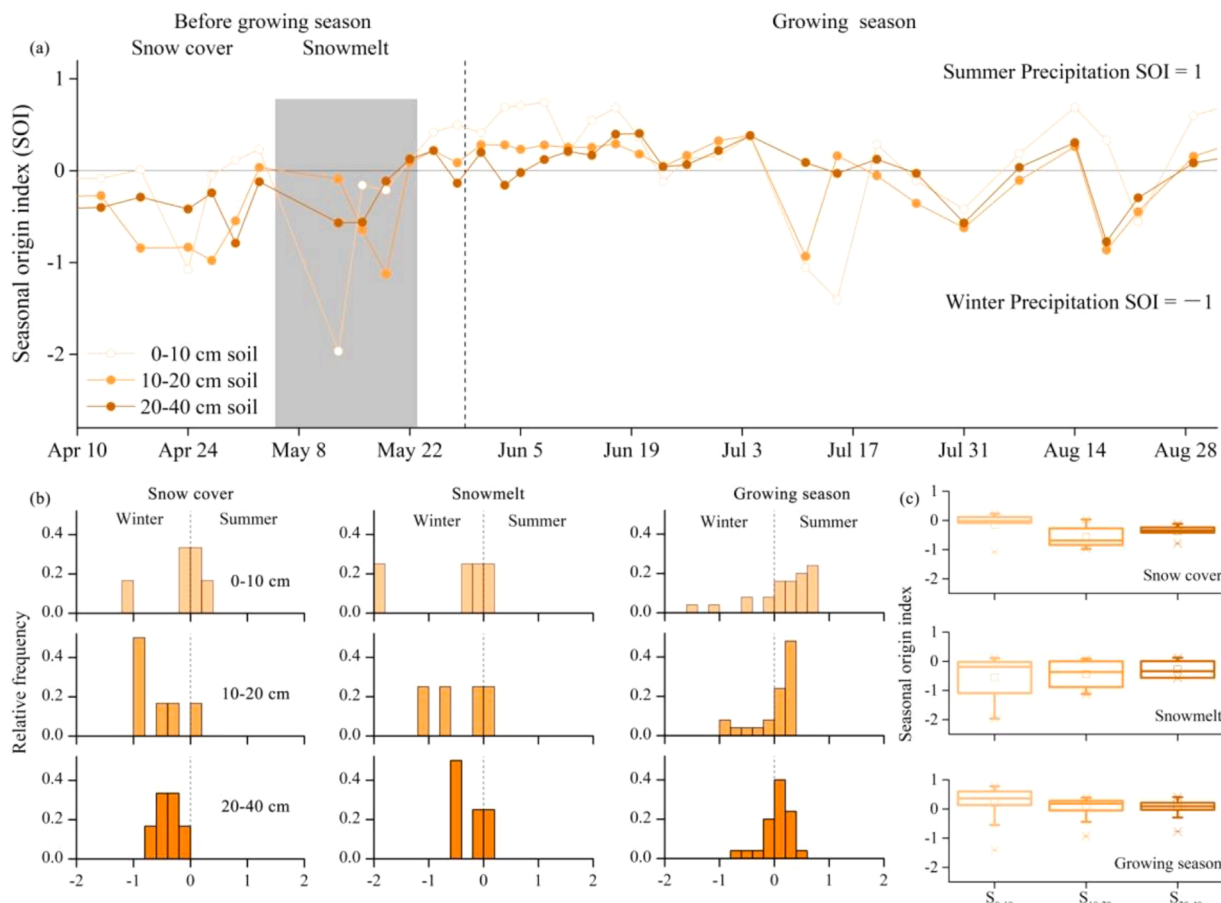


Fig. 4. Daily mean soil temperature and soil water content (SWC) in 2014. Grey shading represents the period of snow melting.

**Table 2**  
Mean  $\delta^{18}\text{O}$  of precipitation, soil water and xylem during different phases during different phases of the growing season from September 2013 to October 2014.

Source	2013 phase3	2014 phase1		Phase2/(june-july-August)		phase3	
Precipitation	NA	-10.58 <sup>a</sup>	-10.62 <sup>a</sup>	(-10.17	-11.69	-8.10)	-14.76 <sup>b</sup>
Snow	NA	-14.00 ± 0.20		NA		NA	
0–10 cm Soil	-11.07 ± 2.05	-10.61 ± 1.83 <sup>ab</sup>	-9.20 ± 2.34 <sup>a</sup>	(-8.31 ± 1.38	-10.63 ± 1.84	-8.54 ± 1.64)	-14.08 ± 5.48 <sup>b</sup>
10–20 cm Soil	-12.08 ± 1.82	-11.26 ± 1.48 <sup>a</sup>	-10.18 ± 1.53 <sup>b</sup>	(-9.50 ± 0.73	-10.60 ± 1.03	-10.62 ± 1.00)	-11.58 ± 2.46 <sup>a</sup>
20–40 cm Soil	-12.26 ± 1.71	-11.25 ± 1.04 <sup>a</sup>	-10.11 ± 1.47 <sup>b</sup>	(-10.02 ± 0.72	-10.28 ± 0.81	-10.64 ± 1.04)	-11.14 ± 2.07 <sup>a</sup>
<i>Larix principis-rupprechtii</i> xylem	-10.77 ± 1.54	-7.03 ± 1.51 <sup>aA</sup>	-10.37 ± 1.13 <sup>bA</sup>	(-9.86 ± 0.80	-10.58 ± 1.31	-11.13 ± 0.88)	-10.05 ± 0.56 <sup>bA</sup>
<i>Picea meyeri</i> xylem	-11.22 ± 0.82	-9.05 ± 1.23 <sup>ab</sup>	-9.80 ± 1.26 <sup>bA</sup>	(-8.98 ± 0.84	-10.60 ± 1.15	-10.53 ± 0.98)	-9.63 ± 1.03 <sup>aA</sup>

phase 1 = before growing season (April–May), phase 2 = growing season (June–August), phase 3 = after growing season (September–October);  $\delta^{18}\text{O}$  values of precipitation was weighted by volumetric precipitation; the lowercase (a, b) and uppercase (A, B) indicate significant differences among three phases or two species, respectively, which were based on LSD Test or Mann–Whitney rank-sum Test ( $p < 0.05$ ).



**Fig. 5.** (a) Temporal variations of seasonal origin index (SOI) values in soil water at different layers, (b) distributions and (c) boxplots of SOI values for soil water in different phases. Boxplots show the maximum, 75th percentile, average (square), median (horizontal line), 25th percentile, and minimum. Grey shading represents the period of snow melting.

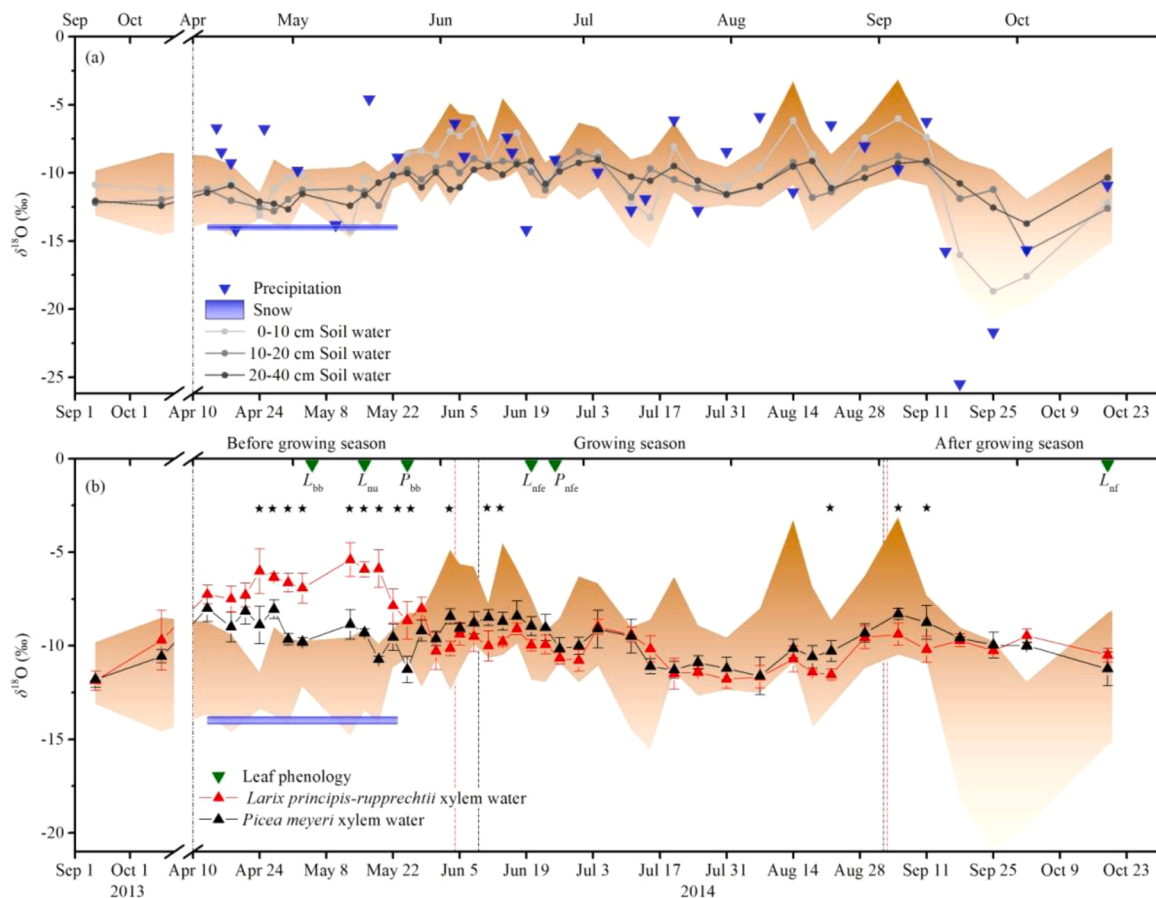
### 3.4. Seasonal variation of trees water sources

#### 3.4.1. Water utilization before growing season

During the period of snow cover (before May 5), xylem  $\delta^{18}\text{O}$  of larch showed a strong positive correlation to daily mean soil temperature ( $r = 0.818$ ,  $p < 0.05$ ,  $N = 6$ ), whereas a positive correlation was observed between spruce and daily minimum air temperature with a time lag of approximately 3–7 days ( $r = 0.885$ ,  $p < 0.05$ ,  $N = 6$ ). These findings support the interpretation that the initial trend of high xylem  $\delta^{18}\text{O}$  values is a result of winter evaporative enrichment in twigs (Fig. S2, larch:  $\delta D = 3.04 \delta^{18}\text{O} - 37.71$ ,  $R^2 = 0.664$ ,  $N = 205$ ,  $p < 0.001$ ; spruce:  $\delta D = 4.12 \delta^{18}\text{O} - 27.99$ ,  $R^2 = 0.702$ ,  $N = 240$ ,  $p < 0.001$ ). Such an enrichment could occur for both evergreen and deciduous species. Considering that

soil water is likely frozen during the winter (Fig. S3), evaporative water demand would be unable to be filled through root uptake, but was more likely to have been derived from other sources of water, i.e. stem water storage in trunk. After twig evaporation, water stored in trees may mix with enriched xylem water, which likely leads to a gradual decline of xylem  $\delta^{18}\text{O}$  under snow cover period (Fig. 6).

During the period of snowmelt (May 5 to May 23), xylem  $\delta^{18}\text{O}$  of larch had a strong relationship with daily maximum soil temperature ( $r = -0.844$ ,  $p < 0.05$ ,  $N = 5$ ). No such relationship, however, was observed for spruce. As the snow melts, it appears the trees began to use the isotopic depleted snowmelt water (-14‰). Our data indicates that larch depended on this more than spruce.



**Fig. 6.** Seasonal variation in  $\delta^{18}\text{O}$  of (a) precipitation, snow water, soil water, and (b) tree xylem water (*Larix principis-rupprechtii* and *Picea meyeri*) during the growing and non-growing seasons. Standard error bars for snow water ( $N = 5$ ) and xylem water ( $N = 5$ ) are also shown. For a clear display, standard error bars for soil water in three vertical depths are not shown. Instead, horizontal bands (brown) depict the standard error ranges for soil water  $\delta^{18}\text{O}$  values ( $N = 16$ ) of three depths during sampling period. Dashed red and black vertical lines represent the transition between the growing and non-growing seasons of *Larix principis-rupprechtii* and *Picea meyeri*, respectively. Black five-pointed star indicate significant differences between two species in  $\delta^{18}\text{O}$  xylem on each sampling date. Green triangles represent the dates of leaf phenology. bb, bud burst; nu, needle unfolding; nfe, needle full elongation; nf, needle fall.

### 3.4.2. Contribution of winter precipitation for tree growth

Before the growing season, but after late April, trees mainly use the winter-sourced water (negative seasonal origin index values). During growth initiation (around late May/early June), the seasonal origin index values were lower in larch than in spruce (Fig. 7,  $-0.24 \pm 0.23$  versus  $0.02 \pm 0.16$ , respectively), indicating larch used more winter precipitation than spruce for growth initiation. From June to August, the seasonal origin index was  $>0$  for 95% larch and 67% spruce, implying trees increased summer precipitation utilization during the growing season.

### 3.4.3. Estimation of tree water sources in growing season

Because the isotopic values in xylem water were affected by evaporation before the growing season (Fig. 6), isotopes in the xylem water do not likely represent the water sources from soil. Therefore, we calculated trees' water uptake at different soil layers from June to August because plant uptake was generally not strongly fractionating during growing season (Fig. S4, Fig. S5).

Based on the Bayesian mixing model, the main water-absorbing layer of larch and spruce were both found in the deeper soil layer, below 10 cm. On average, 76.8% of the water in larch and 73.8% of the water in spruce was from this layer (Fig. 8).

In June, larch relied much more on the water from the 10 to 20 cm and 20–40 cm soil layers (38.0% and 40.5%, respectively) and much less water from 0 to 10 cm soil layer (13.9%). Unlike larch, spruce used water almost equally from each soil layer, with mode values of 30.2%,

36.5%, and 34.5% for the 0–10 cm, 10–20 cm and 20–40 cm layers, respectively. Although both species increased water-absorption from the 0 to 10 cm top layer (30.2% and 35.0% for larch and spruce, respectively) during the rainy July of 2014, they still maintained absorbing a large proportion of water from deeper soil layers. Similarly, during the August drought, larch continued to absorb water relatively evenly from each soil layer. In contrast, spruce reduced its absorption of water from the 0 to 10 cm of soil in half during the August drought (31.9% vs. 14.3% for larch and spruce in August, respectively).

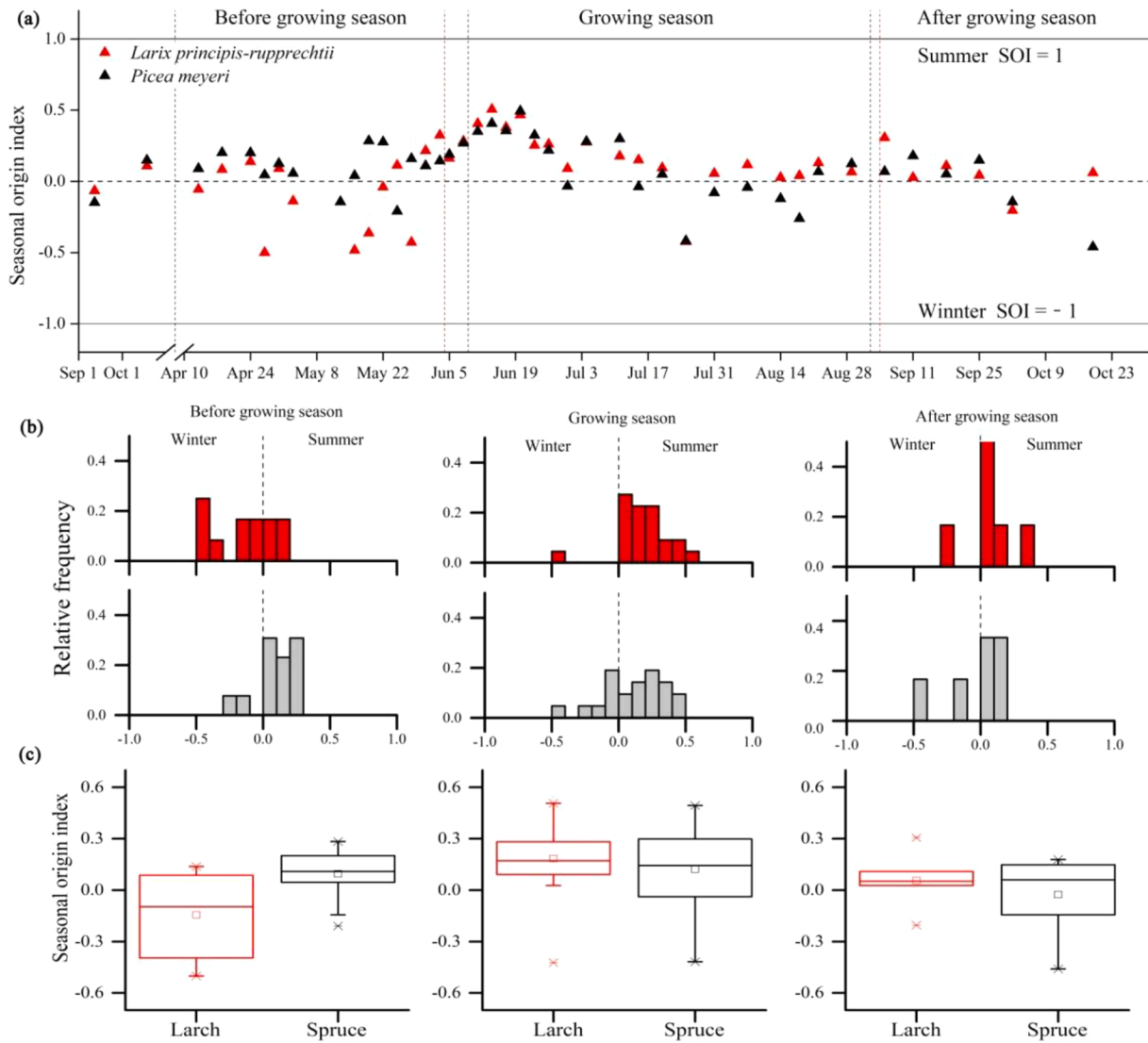
During both the accelerating and decelerating growth stages, the behavior of source water between larch and spruce followed the patterns observed in June (Fig. 9). During the accelerating stage, larch used more water from deeper soil layers (below 10 cm 82.5%) while spruce used water generally equally from each soil layer. During the decelerating stage, both extracted water from the below 10 cm soil layers (77.2% and 75.1%, respectively).

Species differed in their water sources, as reflected by differences in their root distribution (Fig. 10). Larch is considered to be deeper-rooted, with its roots concentrated mainly in the 10–30 cm soil layer (58.5%), compared to spruce, whose fine roots mostly occur in the 0–10 cm top soil layer (50.8%).

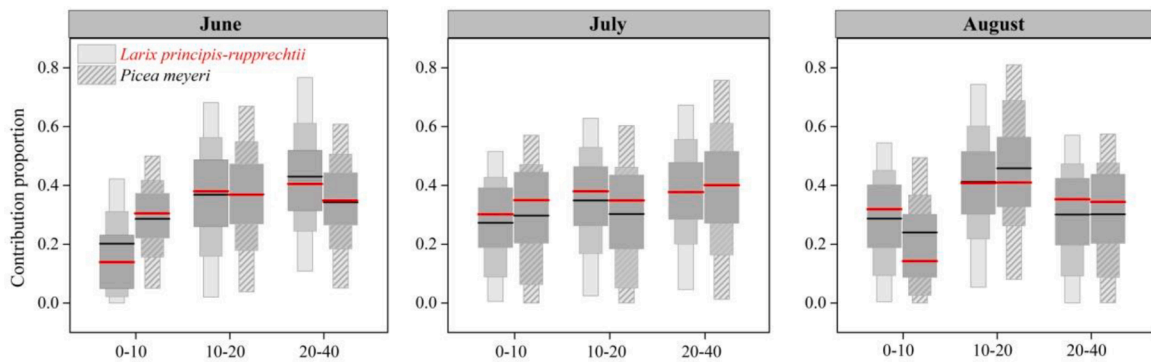
## 4. Discussion

Before our study, the simultaneous monitoring of tree wood growth and water use strategies had rarely been conducted (Sánchez-Costa





**Fig. 7.** (a) Temporal variations of seasonal origin index (SOI) values in xylem water, (b) distributions and (c) boxplots of SOI values for xylem water in different phases. Boxplots show the maximum, 75th percentile, average (square), median (horizontal line), 25th percentile, and minimum. Larch: *Larix principis-rupprechtii*, Spruce: *Picea meyeri*.



**Fig. 8.** Proportional source contributions of different soil depths to xylem water of *Larix principis-rupprechtii* and *Picea meyeri* from June to August. Results were derived by SIAR (Stable Isotope Analysis in R, version 4.2) based on the Bayesian model. Boxplots illustrate the 50th, 75th, and 95th percentile confidence intervals from dark to light. Under the 95th percentile confidence interval, the mean and median values are indicated by black and red lines, respectively. Number of replicates in June, July and August are  $N = 10$ ,  $N = 6$ , and  $N = 5$ , respectively.

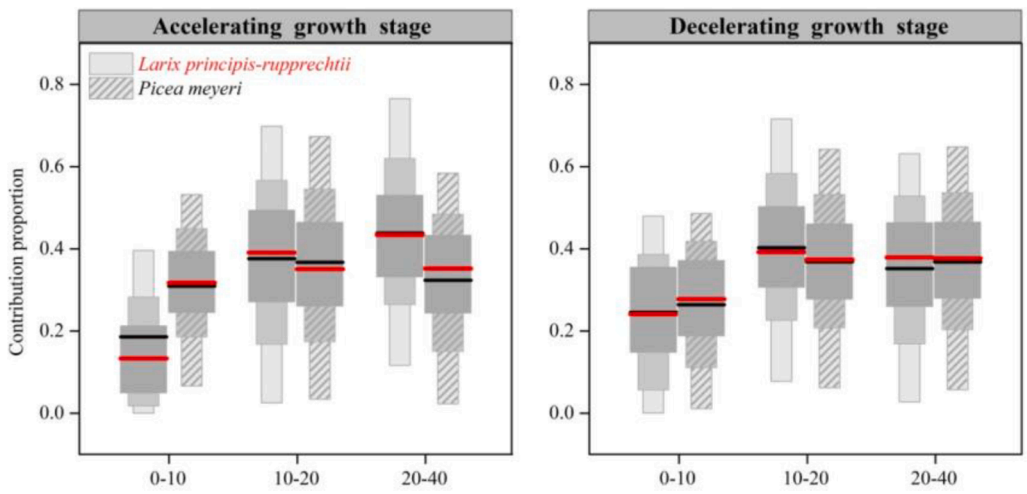


Fig. 9. Proportional source contributions of different soil depths to xylem water of *Larix principis-rupprechtii* and *Picea meyeri* at the accelerating and decelerating growth stages. These two growth stages were defined from weekly to biweekly microcoring and our analyses of these cores where we fed observations and measurements of cell development into the Gompertz model of intra-annual dynamics of wood formation. Model output helps us determine trees growth rates at high temporal resolution.

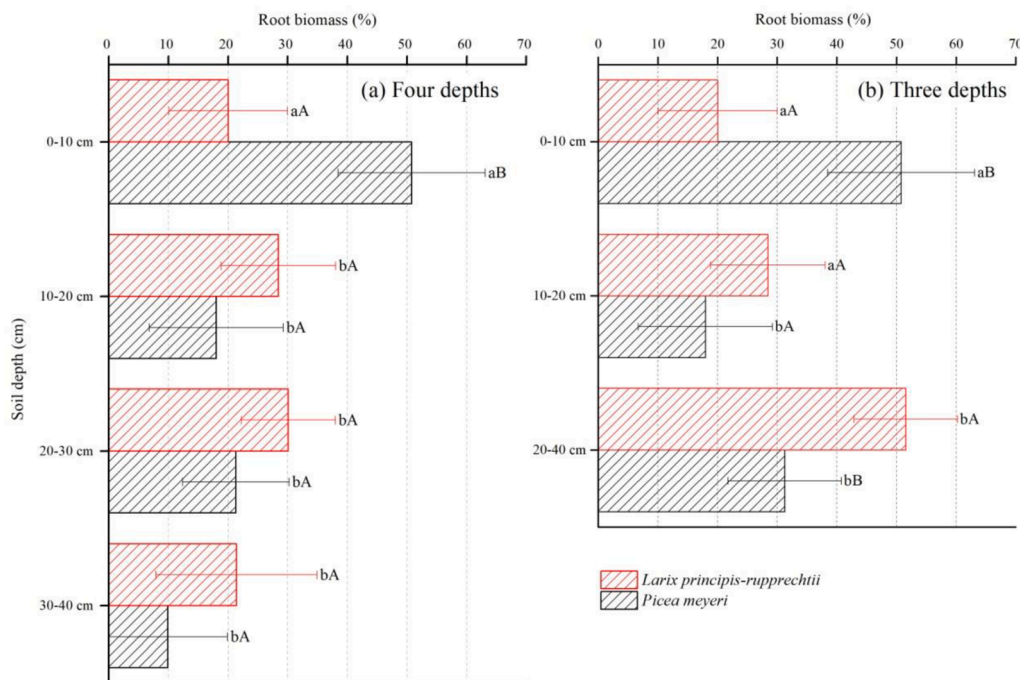


Fig. 10. Vertical distributions of fine root biomass (< 2 mm) of *Larix principis-rupprechtii* and *Picea meyeri* under the alpine habitat (Luya Mountains, China) in September 2014. The lowercase (a, b) and the uppercase (A, B) represent significant differences among soil depths or species, respectively ( $p < 0.05$ ). Standard error bars for each soil layer ( $N = 60$ ) are shown.

et al., 2015). We found that *Larix principis-rupprechtii* appears to use a larger proportion of winter snowmelt water for growth initiation than *Picea meyeri*, partially supporting our first hypothesis, because utilization of water stored in stems can be observed within time periods of snow cover. We also found that both larch and spruce mainly absorbed water from 10 to 20 cm soil depths. However, as evidenced during the August drought, spruce appears to have a greater plasticity in soil water uptake than larch. This flexibility suggests that spruce is more sensitive and responds more quickly to decreased water availability than larch. Opportunistic water source flexibility might be important for spruce as it adapts to increased water stress (Obojes et al., 2018). Likewise, the fact that larch did not substantially shift its water source during the August drought at our site indicates that less flexibility could make larch more vulnerable to transient, late-season droughts. Counter to this apparently level of reduced flexibility, however, access to deeper water that is less variable over time (Chitra-Tarak et al., 2018), might help larch persist in

prolonged and severe droughts.

From late-May to early June, winter snowfall seems to play an important role for the onset of tree growth. Low seasonal origin index (i. e., winter) values in xylem water suggested trees broadly rely on winter precipitation (Fig. 7); larch used more winter precipitation than spruce for growth initiation. Consistent with the expected trend deriving from the influence of isotopic depleted snowmelt water (-14‰), xylem  $\delta^{18}\text{O}$  displayed a marked decreasing trend after larch needle unfolding (Fig. 8). The influence of soil water, especially thawed topsoil water (0–10 cm), can be excluded, since  $\delta^{18}\text{O}$  soil values appeared with an opposite and increasing trend. Our findings combined with previous findings indicate that winter snow is an important driver for subsequent growing-season tree growth across temperate forests in China (Zhang et al., 2019b). Both the amount and rate of winter snowmelt strongly affected pre- and early growing-season soil water availability (Yu et al., 2013). Such infiltration dynamics may shape the ecological hysteresis of

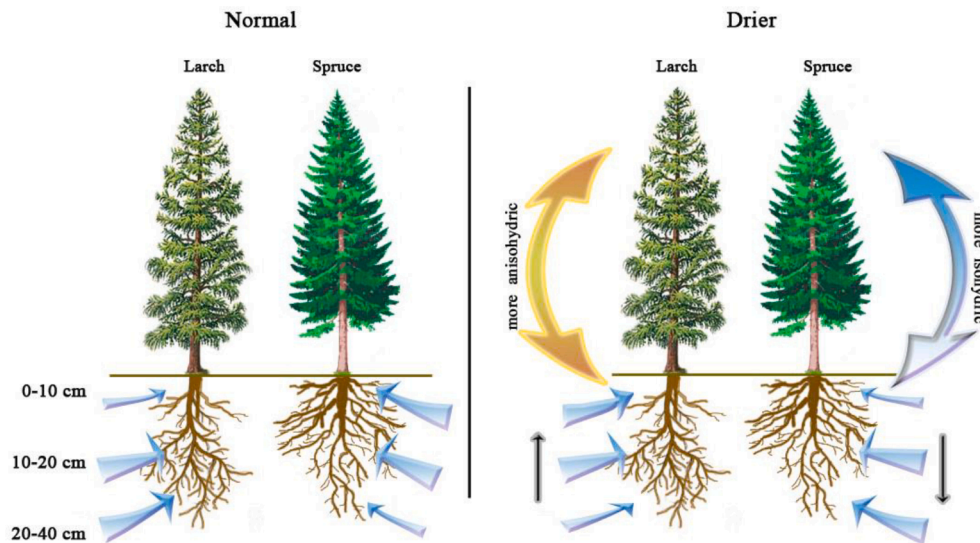


Fig. 11. Conceptual diagram of divergent water-use strategies in *Larix principis-rupprechtii* and *Picea meyeri*. Black arrows represent the water source movement between upper soil layer and deeper soil layer for larch and spruce under drier condition. The thickness of blue one-way arrows represents the proportional water source contributions of different soil depths to trees.

trees, thus controlling their response to climate (Da Silveira Lobo Sternberg, 2001; Staal et al., 2020), which plant-tissue isotope proxies may capture winter climate signals (Shamir et al., 2020). On the other hand, having more flexibility in water sourcing may result in greater tree growth stability and resilience to adverse transient meteorological events (Mazza et al., 2018).

#### 4.1. Role of tree-stored water before snow melting

Previous studies reported that instead of taking water from the soil, trees could rely on water stored in the stem or extract snowmelt water in wintertime for short periods (Boyce and Lucero, 1999). In boreal forest, Scots pine was prone to use more stem water storage if low soil temperature made accessibility to soil water difficult (Sevanto et al., 2006). In our study, isotopic enrichment in xylem (high values) occurred under snow cover period and intensified when temperature increased, suggesting that trees may have used stored water or mixed water for evaporative water loss when soil water was frozen. However, this utilization of stored water seemed to become weakened or masked after snowmelt because the snowmelt water was isotopically depleted.

Stronger xylem evaporation occurred in larch than in spruce, which led to more isotopically enriched water of approximately +2‰ (in  $\delta^{18}\text{O}$ ) for larch. Nevertheless, it is hard to distinguish whether larch used more stored water than spruce without other additional data (stem diameter variation, sap flow and stem water potential, etc.) (Čermák et al., 2007; Nehemy et al., 2021). Because we know little about the degree of within-tree mixing between stored water and xylem water, the isotopic characteristics of stored waters, and trees evaporation dynamics and how these uncertainty influences our interpretation of isotopic xylem water are still relatively unknown (Hu et al., 2018; Knighton et al., 2020; McDonnell, 2014). It was reported that the contribution of tree-stored water to total daily transpiration may range from 10 to 50% (Steppe and Lemeur, 2004). Carrasco et al. (2015) observed the contribution was greater for deciduous species than evergreen species, which may provide a clue to improve understanding of stored water dynamics differing in species.

#### 4.2. Larch relies more on winter snowmelt than spruce for growth initiation

Larch appeared to use a larger proportion of winter snowmelt water

than spruce. The lower seasonal origin index values and the two-fold reduction of  $\delta^{18}\text{O}$  in larch than that in spruce (Fig. 6, 7), suggests larch used more winter precipitation than spruce for growth initiation. This finding falls in line with evidence for a significant correlation between tree-ring width in our study region and previous-year autumn/winter precipitation for larch, but not spruce (Jiang et al., 2014). Unlike evergreen spruce, deciduous larch has a stronger resource demand for canopy reconstruction, which likely creates more dependence on snowmelt water for growth initiation, especially before the soil thaws (Antonova and Stasova, 1997). Warmer winter ground temperature appears to trigger rapid growth of *Larix* sp. at high altitudes and latitudes (Zhang et al., 2019a), further suggesting snowmelt is an important early-season source of water.

Considering xylem stem water evaporation was much greater in larch than in spruce (Sugimoto et al., 2002; Zhang et al., 2018a), larch may be subjected to higher water stress by the reduced snowpack under warmer spring conditions (Kharuk et al., 2015; Schuur et al., 2015). Based on our findings that larch depends on snowmelt water to rebuild its canopy, we hypothesize that a shorter season of frozen soil, greater soil moisture from thawing soil, and increased snowmelt might aid more rapid construction of the larch canopy. In the absence of severe drought during the growing season, a larger canopy could lead to a greater competitive advantage in growth for larch, matched by more dominant in water and nutrients acquisition for belowground investment (Jiang et al., 2020).

#### 4.3. Higher plasticity of water resource acquisition in spruce than in larch

Isotopic evidence showed that both larch and spruce mainly absorbed water from 10 to 20 cm soil depths, which are coupled with the maximum soil water (Fig. 4) and maximum soil organic carbon storage at 10–20 cm (Wu et al., 2014). Previous studies showed there was a soil texture transition in this layer (10–20 cm) (Wu et al., 2011), which allows for a longer mean residence time and an efficient mixing of new and old water. This observation is further supported by our evidence that soil  $\delta^{18}\text{O}$  at 10–20 cm did not differ significantly with either the 0–10 cm or 20–40 cm layers. Based on the soil texture, the water in the 10–20 cm layer is probably a mixture of summer precipitation and previous-year autumn and winter precipitation (Zhang et al., 2018b).

Although both larch and spruce mainly used water from the same soil layer (10–20 cm), their abilities to absorb current year precipitation

from the 0 to 10 cm layer of soil differed. The higher xylem  $\delta^{18}\text{O}$  and lower lc-excess (line-conditioned excess, Fig. S5) of spruce relative to larch indicated spruce extract more upper soil water that is typically enriched in  $\delta^{18}\text{O}$  (Lévesque et al., 2013). Equally, the significant correlation between xylem  $\delta^{18}\text{O}$  and soil  $\delta^{18}\text{O}$  at 0–10 cm was detected only in spruce ( $r = 0.446$ ,  $p < 0.05$ ), not larch ( $r = 0.296$ ,  $p = 0.205$ ), suggesting spruce absorb more water from the 0 to 10 cm layer of soil. Moreover, the Bayesian stable isotope mixing model results showed that the contribution from the top soil layer water during the rainy and then dry months of July and August of 2014 were coupled in spruce (35.0% and 14.3%, respectively), but uncoupled in larch (30.2% and 31.9%, respectively) (Fig. 8). This means that spruce could shift to uptake water from the top layer of soil during wet periods. Root biomass data support this finding, which shows spruce has more shallow roots.

Our findings indicate that larch absorbs water primarily from deeper soil layers while spruce had greater plasticity in shifting water resources between layers. These different water uptake abilities may be partly explained by their different vertical root distribution (Ehleringer et al., 1991). Larch distributed more fine roots ( $< 2$  mm) at depths below 10 cm (approximately 80.0%, Fig. 10), whereas spruce distributed almost half of its fine roots above 10 cm. In line with our results, Bischetti et al. (2009) pointed out that the average rooting depth of *Larix decidua* was much deeper than that of *Picea abies* in mixed stands of the Italian Alps. Research in the Swiss Alps found European larch used deep and stable soil water resources and had the most negative response to soil–water limitations (Eilmann and Rigling, 2012). Therefore, beside preferentially acquiring water from soil layers with the highest water content, shallower-rooting spruce appear to be more responsive to more recent rainfall conditions than deeper-rooting larch (Schmid and Kazda, 2002). To compete with fast-growing species, shallower roots allow spruce to acquire more nutrients from top soil layer (Ugawa et al., 2010), because nutrient availability often declines (Wu et al., 2014), whereas bulk density tends to increase with soil depth.

#### 4.4. Divergent water-use strategies

The physiological traits of trees likely help to account for species difference in patterns of water source usage. According to our short-term (one-day) leaf gas exchange measurements on three trees per species, the daily average transpiration rate of larch and spruce were 2.86 and 2.67  $\text{mmol m}^{-2} \text{s}^{-1}$ , and stomatal conductance 0.13 and 0.11  $\text{mol m}^{-2} \text{s}^{-1}$ , respectively. Net photosynthesis rates were 7.27 and 10.67  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and water use efficiency 2.64 and 4.19  $\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}^{-1}$  for larch and spruce, respectively (Dong, 2011). Compared with larch, spruce is considered to have a more conservative water consumption strategy and more sensitive stomatal regulation (Oberhuber et al., 2015).

As a pioneer species, deciduous larch tends to increase resource accumulation early in the growing season via high transpiration and, simultaneously, high photosynthesis. Sustaining these fluxes requires more water from a stable source in the deeper soil layer (Treydte et al., 2014). Our results reveal that the xylem  $\delta^{18}\text{O}$  of larch was lower ( $-10.37\%$ ) than those of spruce ( $-9.80\%$ ), supporting higher stomatal conductance of larch in correspondence with access to deeper soil water pools (Hartl-Meier et al., 2015). Nevertheless, larch in other settings seems to be capable of increasing assimilation rates irrespective of soil water stress in summer (Lévesque et al., 2014). Supporting evidence of this ability was reported by Anfodillo et al. (1998) in the northeastern Italian Alps, where the mean daily maximum sap flux density of *Larix decidua* stayed relatively high under moderate water deficits, was nearly three times of that of *Picea abies*. Considering water-use strategy and physiological traits, this seems logical. *Picea abies* is more shade tolerant and can reduce sap flow density up to 47% under drought conditions (Leo et al., 2014). Such abilities may partially contribute to its plasticity in water-use source between shallow and deep soil layers. On the other hand, *Picea abies* can decrease sap flow, and sufficiently and quickly

access internal stem water to deal with soil drought (King et al., 2013). Growth analysis on stem radial variations at our site, based on six-year point dendrometer monitoring, also shows greater daily stem water movement in spruce (unpublished data). This implies that spruce utilize internal stem water reserves more quickly than larch at a diurnal period, thus leads to greater daily amplitudes (Oberhuber et al., 2015).

Although the leaf gas exchange parameters were not measured either at the same time or over a long-term period, analysis of xylem water isotopes and leaf photosynthetic traits still provide some insight into the water-use strategies of larch and spruce. Our work and the work of others indicate that spruce has more conservative water-use strategy. Shallower roots and tighter stomatal control reflect greater sensitivity to soil water availability in spruce, suggesting it has a stronger water-saving strategy than larch. Compared to spruce, larch is found to have larger tracheid sizes, especially in the lumen of earlywood cells (Fonti and Babushkina, 2016). Larger lumen can enable higher water transport capacity (Valentini et al., 1994), but it also constitutes a trade-off due to reduced transport safety (e.g., increased risk of cavitation in tracheids with larger lumen area). However, larch maintains a relatively high transpiration even during moderate water deficit periods due to its less conservative stomatal control (Anfodillo et al., 1998). Consequently, when soil water availability is insufficient to meet the higher water demand, this anisohydric strategy can make larch prone to cavitation and increases the risk of hydraulic failure (King et al., 2013). In contrast, by closing their stomata relatively early under conditions of low plant water availability and reducing sap flux, spruce behaves isohydrically (Wieser et al., 2016). The decreased transpiration caused by reducing stomatal conductance during water deficits may be an adaptive behavior to protect the conducting system against hydraulic failure while restricting the entry of  $\text{CO}_2$  (Chen et al., 2015; McDowell et al., 2008).

#### 4.5. Implications for alpine trees' future growth

Vegetation modeling forecasts from the IPCC suggest that global temperature changes are relatively uneven and are occurring more quickly in the northern high latitudes and altitudes than in the tropics (IPCC, 2013). As such, northern high latitudes and altitudes can be thought of as an "indicator area" for climate change (Mankin et al., 2019). Trees here have likely been adapted to moist conditions or, at least, conditions with less evaporative demand than in the recent decades. Even a moderate water deficit may lead to a strong reduction in transpiration. Differences in water-use strategies between co-existing species could alter population-level competition in the future (Gros-siord et al., 2019), although it might also allow for greater coexistence if different sources of water can be utilized at the stand scale.

If short-term water stress occurs more frequently under projected future warming, we may infer that spruce will have a greater competitive advantage over larch due to spruce's high plasticity in the acquisition and allocation of water and carbon resources (Zhang et al., 2019c, Figure 11). Pollen data indicates that *Picea meyeri*, which used to have a limited distribution in high mountains because of its higher humidity requirement, has moved up in elevation to meet the *Larix* timberline in recent centuries at Qingling Mountains in Northern China (Liu et al., 2002). Consistent with this finding, more spruce than larch seedlings were naturally regenerating within our study site. However, these data were only collected for one year and it is almost certain that under different conditions these responses might change substantially. The differences between species plasticity in water use patterns might emerge, shift or even disappear under inconsistent environmental stressors (Goldsmith et al., 2019; Jiao et al., 2019b). Therefore, integrating investigation of the complex interactions between species and water source and biomass accumulation with long time series of dataset (i.e. tree-ring, FLUXNET, and remote sensing data) will be critical to accurately understand species dynamics and to estimate alpine forest resilience to environmental stress (Soh et al., 2019).

## 5. Conclusions

Our findings reveal that co-occurring larch and spruce show different water use strategies in a monsoonal climate. In this region, it appears that spruce has a greater ability to cope with short-term variations in water availability than larch. Trees may rely on stored water for evaporative water loss when soil water was frozen in wintertime. During growth initiation, winter snowmelt appeared to be the source water for growth initiation for larch more than spruce. Considering that xylem water evaporation was much stronger in larch than spruce, larch may be subjected to higher water stress due to the reduced snowpack under warmer conditions. During the growing season, however, both species exhibited similar stem growth dynamics and weak water source partitioning, with most water taken up from the same soil layer (10–20 cm). These dynamics may amplify inter-specific competition for water. Later during the growing season and during a drought, spruce showed a greater plasticity in water acquisition among multiple soil layers, a shift we did not observe in larch. Shallower roots and tighter stomatal control reflect greater sensitivity to soil water availability in spruce, suggesting it has a stronger water-saving strategy than larch. We find that combined analyses of tree growth and isotopic tracing of water sources reveals not only the seasonal variation in the response of trees to water availability, but also enables identification of inter-specific differences in water-use strategies. Such analyses will help in understanding the future growth responses that determine the resistance and resilience of these two species to the anticipated decrease in water availability.

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## CRedit authorship contribution statement

**Yiping Zhang:** Investigation, Writing – original draft, Writing – review & editing. **Junliang Xu:** Writing – original draft. **Yuan Jiang:** Investigation. **Tessa Mandra:** Writing – review & editing. **Tim T. Rademacher:** Writing – review & editing. **Feng Xue:** Writing – review & editing. **Manyu Dong:** Writing – review & editing. **Neil Pederson:** Writing – review & editing.

## Declaration of Competing Interest

None declared.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108696.

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