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# The role of heartwood water storage for sem-arid trees under drought

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ABSTRACT

Stem water storage is an important water pool in forests. However, we know little about the heartwood water use processes and the water use strategies of trees in semi-arid temperate forests. We investigated Simon poplar (*Populus simonii*), a heartwood water storage tree species. A combination of methods (sap flow, the dendrometer and the soil–plant–atmosphere canopy model were used to trace the water use dynamics of Simon poplar trees. The aim was to understand how this heartwood water storage tree species survives under drought stress.

Our field data showed that *P. simonii* had significantly higher heartwood water content (60%) than other tree species (30%) in the same region. The enhanced tree water deficit (TWD) and continuous stem shrinkage showed that the heartwood water supply was able to maintain sap flow (1.5–4.6 mm/d) during early growing season droughts. The strong water absorption ability of the roots resulted in the quick recovery of TWD, which caused the rain water could hardly reach 50 cm depth in the soil. The weakened link between transpiration and root water assimilation of heartwood water storage trees meant that sap flow was more sensitive to drivers such as air temperature ($R = -0.71$, $p < 0.01$) and vapor pressure deficit ($R = 0.69$, $p < 0.01$).

These results suggest that heartwood water storage may buffer drought events during the growing season and reduce the wide fluctuation in interannual precipitation. Therefore, heartwood water storage needs to be taken into account when calculating the soil–plant–atmosphere continuum and creating tree survival models.

## 1. Introduction

Recent global tree mortality and forest die off has been attributed to climate change; increases in the frequency, duration, and/or severity of drought; and heat stress (Barber et al., 2000, Klos et al., 2009, Allen et al., 2010, Dulamsuren et al., 2010, Choat et al., 2012, McDowell et al., 2016). Water stress during the growing season, caused by warming-induced increases in atmospheric moisture demand, has induced tree growth declines in the semi-arid forests of Inner Asia (Liu et al., 2013). Recent tree mortality has been observed in low-elevational temperate and southern boreal forest regions distributed close to the xeric tree line in Asia (Kharuk et al., 2013; Liu et al., 2013). Trees are a very important part of the soil–plant–atmosphere continuum (SPAC) in forest ecosystems because 60%–80% of terrestrial evapotranspirational water loss is directly controlled by plants (Schlesinger and Jasechko 2014). Therefore, the forest mortality risk can affect water cycling besides reduce the carbon sink process.

*Populus* species are widely distributed across the world and are known to be water-consuming species (Manzanera and Martínez-Chacón 2007, Beniwal et al., 2010). Simon poplar (*Populus simonii*) is one of the main species in the “Three-North Shelter Forest Program” (Zhang et al., 2016), which has been instigated in a semi-arid area close to the xeric tree line in China. Previous studies have shown that Simon poplar could maintain sap flow during the leaf-flushing period before useable precipitation had occurred (soil moisture < 8% above 1 m) (Hu et al., 2010) and during the dry growing season (soil moisture < 7% above 2 m) (Zhang et al., 2013).

Tree water use strategies focused on the response of stoma conduction (leaf transpiration, or leaf water potential) to soil drought (decrease of soil water content or potential) (McDowell et al., 2008, Parolari et al., 2014). Isohydric trees reduce stoma conduction as soil water potential decreases, while anisohydric species allow leaf transpiration as soil water potential declines with drought (McDowell et al., 2008). However, this hypothesis gives no explanation on the effect of

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tree water storage. Succulent trees, which store withdrawable water in living cells (Griffiths and Males, 2017), also have sensitive response of leaf to soil drought (De Smedt et al., 2012). However, rare studies focused on the effects of heartwood water storage in non-succulent trees on water use strategies, which may improve the isohydric hypothesis and provide widely adaptable implications for modelling research.

This study compared the water use dynamics of Simon poplars during growing season by taking field measurements and by using the soil–plant–atmosphere canopy model (SPA) where the water inputs were soil water from rainfall rather than stem water storage, because soil water is the main water source used in most stand-level models (Williams et al., 1996, Hanson et al., 2004). The water use process and soil dynamics of Simon poplars was also compared to two afforested coniferous species, larch (*Larix principis-rupprechtii*) and pine (*Pinus sylvestris* var. *mongolica*). We hypothesized that stem water storage may weaken the sensitivity of leaf transpiration to soil drought. The aims were to investigate (1) how stem water storage affects the transpiration process in the soil-plant-atmosphere continuum containing Simon poplar trees during drought, and (2) how Simon poplar trees use soil water. The results from this study could provide new information about forest responses to climate change, and improve our understanding of the water cycle process in the SPAC.

## 2. Materials and methods

### 2.1. Experimental site

Our experiment was located in the forest-steppe ecotone on the edge of the Otindag sandy land in southeastern Inner Mongolia, China (42°09′N; 116°17′E; 1350 m a.s.l. Fig. 1). Mean annual temperature (MAT) is 2.28 °C (1953–2013), which has significantly increased by 0.39 °C/10a ($R^2 = 0.49$, $p < 0.05$) during this period (Fig. S1). Mean annual precipitation is 364 mm (1953–2013), but annual precipitation (AP) widely fluctuates and has not shown any significant trends between 1953 and 2013 (Fig. S2). Our experiment was carried out in afforested *Populus simonii*, *Larix principis-rupprechtii*, and *Pinus sylvestris* var. *mongolica* forests (Fig. S3). All the three investigated tree species were planted on similar stands with entisols, in which sand (grain size 0.063–2 mm) takes over 40% of the soil materials and roots were mostly distributed within the top 30 cm of the soil (Fig. S4). These afforested forests are parts of the "Three-North Shelter Forest Program", which is a series of human-planted wind-shelter forest strips (shelterbelts) in North, Northeast, and Northwest China. A 20 m × 20 m plot was planted with Simon poplar, whereas 10 m × 10 m plots were used for the two needle leaf species as these two species were planted at a greater density than the Simon poplar (Table S1).

### 2.2. Meteorology

Air temperature (Ta) and relative humidity (RHa) were measured and recorded with HOBO U23 pro v2 sensors (Onset Computer, Inc., Bourne, MA, USA). The device was placed at the bottom of the canopy on the north side of the stem to avoid direct sunlight. Precipitation data was recorded by a nearby weather station (Fig. 1). Shortwave radiation data was measured at Peking University Saihanbai Ecological Station (PKU station, Fig. 1), which was located at a similar altitude to our experimental site. Soil temperature and moisture were measured and recorded by an EM50 with TDR-type 5 TM sensors (Decagon Devices, Inc. Pullman, WA, USA). The sensors were placed at soil depths of 10, 30, 50, 100, and 150 cm. The temperature and moisture were interpolated each 10 cm soil layer down to 150 cm.

### 2.3. Sap flow measurement

Sap flow (SF, L/h) was measured in six trees per plot with SF-L (Ecomatik, Inc, Munich, Germany) Granier type thermal dissipation

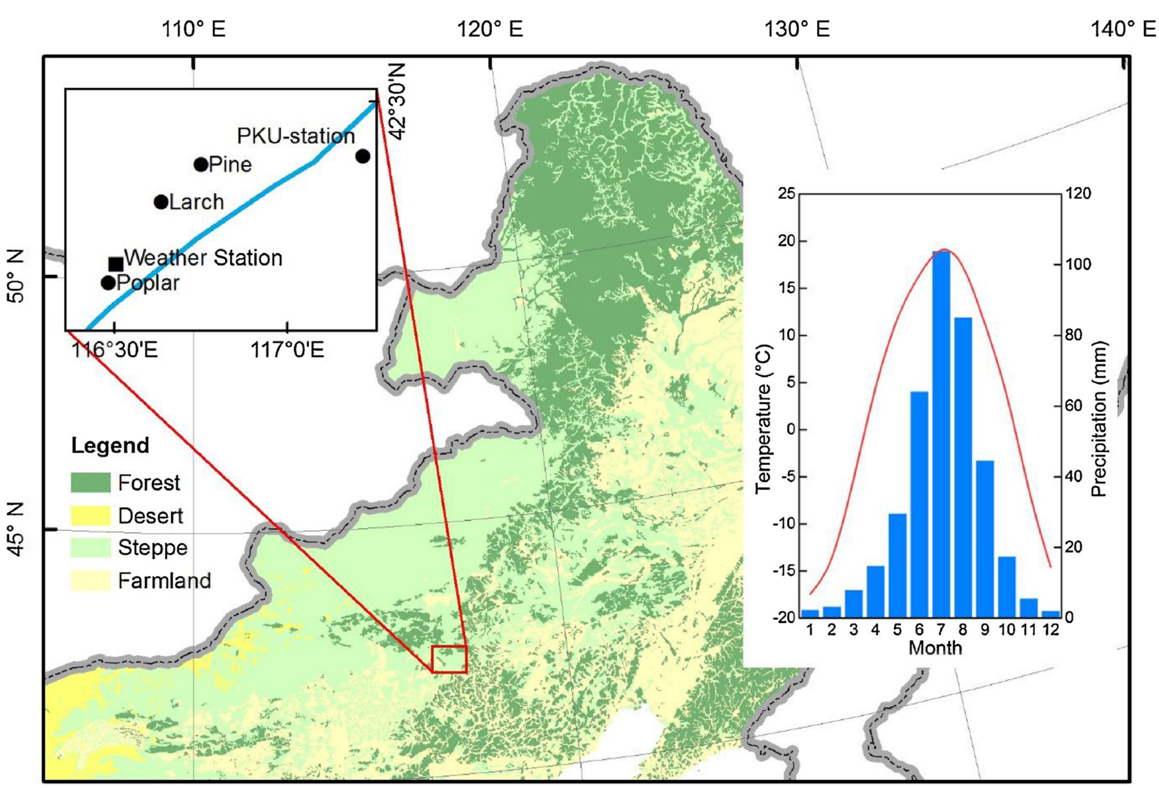


**Fig. 1.** The study area was located in the forest-steppe ecotone where there was a 400 mm precipitation isoline (blue line on the sites map) across the area. The study area had a typical continental climate and most precipitation occurred in summer (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).