

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/361371522>

Linking tree water use efficiency with calcium and precipitation

Article in *Tree Physiology* · June 2022

DOI: 10.1093/treephys/tpac069

CITATION

1

READS

268

7 authors, including:



Hui Li

University of Pennsylvania

605 PUBLICATIONS 9,292 CITATIONS

[SEE PROFILE](#)



Yunting Fang

Institute of Applied Ecology, Chinese Academy of Science

214 PUBLICATIONS 6,706 CITATIONS

[SEE PROFILE](#)



Yong-jiang Zhang

University of Maine

100 PUBLICATIONS 1,780 CITATIONS

[SEE PROFILE](#)



Xiaoming Zou

University of Puerto Rico at Rio Piedras

139 PUBLICATIONS 5,688 CITATIONS

[SEE PROFILE](#)

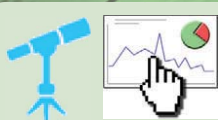
Some of the authors of this publication are also working on these related projects:



the National Research Program for Key Issues in Air Pollution Control [View project](#)



SOC Stabilization and Destabilization [View project](#)



Tree Physiology 00, 1–13
<https://doi.org/10.1093/treephys/tpac069>



Research paper

Linking tree water use efficiency with calcium and precipitation

You Yin¹, Yong-Bin Zhou², Hui Li¹, Song-Zhu Zhang¹, Yunting Fang³, Yong-Jiang Zhang^{4,6} and Xiaoming Zou^{5,6}

¹Research Station of Liaohe-River Plain Forest Ecosystem, College of Forestry, Shenyang Agricultural University, Shenyang, Liaoning 110866, China; ²Institute of Modern Agricultural Research, Dalian University, Dalian, Liaoning 116622, China; ³CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, Liaoning 110016, China; ⁴School of Biology and Ecology, the University of Maine, Orono, ME 04469, USA; ⁵Department of Environmental Sciences, University of Puerto Rico, PO Box 70377, San Juan, PR 00936-8377, USA; ⁶Corresponding authors: Y.-J.Zhang (yongjiang.zhang@maine.edu) X.Zou (xiaoming.zou@upr.edu)

Received January 19, 2022; accepted June 11, 2022; handling Editor Erich Inselsbacher

Water use efficiency (WUE) is a key physiological trait in studying plant carbon and water relations. However, the determinants of WUE across a large geographical scale are not always clear, limiting our capacity to predict WUE in response to future global climate change. We propose that tree WUE is influenced by calcium (Ca) availability and precipitation. In addition, although it is well-known that transpiration is the major driving force for passive nutrient uptake, the linkage between these two processes has not been well-established. Because Ca uptake is an apoplastic and passive process that purely relies on transpiration, and there is no translocation once assimilated, we further developed a theoretical model to quantify the relationship between tree Ca accumulation and WUE using soil-to-plant calcium ratio (S_{Ca}/B_{Ca}) and tree WUE derived from $\delta^{13}C$. We tested our theoretical model and predicted relationships using three common tree species across their native habitats in Northern China, spanning 2300 km and a controlled greenhouse experiment with soil Ca concentrations manipulated. We found that tree WUE was negatively related to precipitation of the growing season (GSP) and positively with soil Ca. A multiple regression model and a path analysis suggested a higher contribution of soil Ca to WUE than GSP. As predicted by our theoretical model, we found a positive relationship between WUE and S_{Ca}/B_{Ca} across their distribution ranges in all three tree species and in the controlled experiment for one selected species. This relationship suggests a tight coupling between water and Ca uptake and the potential use of S_{Ca}/B_{Ca} to indicate WUE. A negative relationship between S_{Ca}/B_{Ca} and GSP also suggests a possible decrease in tree Ca accumulation efficiency in a drier future in Northern China.

Keywords: leaf calcium, leaf $\delta^{13}C$, plant water use efficiency, precipitation, soil calcium, transpiration.

Introduction

Plant water use efficiency (WUE), a concept introduced about 100 years ago (Briggs and Shantz 1913), is an important functional trait that has been widely used in physiological, ecological, forestry and agricultural research (Hatfield and Dold 2019). Water use efficiency is defined as biomass production per unit of water consumption (Briggs and Shantz 1913, Stanhill 1986, Keenan et al. 2013, Limousin et al. 2015). Thus, physiologically, plant WUE is determined by both the primary productivity or photosynthetic capacity and water-use or transpiration. Water-use efficiency also changes with plant growth; larger trees with relatively higher water deficits at the top showed higher

WUE (Zhang et al. 2009). Environmentally, WUE is strongly determined by the moisture condition or precipitation of the habitat, with plants in drier habitats showing relatively higher WUE due to their more conservative water-use (Prentice et al. 2011, Zhang et al. 2021). Also, within a species, individuals or populations in drier habitats showed higher WUE (Gouveia and Freitas 2009, Li et al. 2016). Another important environmental factor determining plant WUE is the soil nutrient condition, which is poorly understood. In agricultural studies, fertilization or better nutrient management can enhance crop WUE mainly due to increased plant growth and yield (Viets 1962, Hatfield et al. 2001, Waraich et al. 2011). However, the relationship

between WUE and soil nutrient condition has rarely been tested for forest trees, with a pilot study showing a negative relationship between soil nitrogen (N) and WUE and a positive relationship between soil phosphorus (P) or calcium (Ca) and WUE within a small region across 500 km distance in northern China (Li et al. 2016). Here, we tested whether the tree WUE is determined by precipitation and by soil and plant Ca across a large geographical gradient (2300 km) in Northern China. We picked Ca because it is the only macronutrient that is apoplastically and passively taken up by vascular plants, and there is no translocation once it is incorporated into the plant structure (White and Broadley 2003). Therefore, it is tightly associated with plant biomass production and transpiration but is previously underappreciated. Calcium is required for cell wall and membrane construction, as well as being needed by some enzymes as a cofactor and as a secondary messenger in various physiological processes, including stomatal regulation and osmotic regulation (White and Broadley 2003). Additionally, Ca is a more stable nutrient and is relatively less affected by the soil moisture conditions during sampling.

Practically, plant WUE can be reflected by plant $\delta^{13}\text{C}$ value, which has been widely used to indicate intrinsic water use efficiency (iWUE) (Farquhar et al. 1982, X. Lu et al. 2018, Twohey III et al. 2019). Intrinsic WUE integrates WUE over a growing period before sampling and over a certain space where plant biomass is distributed. Plant $\delta^{13}\text{C}$ value is tightly associated with physiological processes of carboxylation efficiency and the stomatal openness that control photosynthetic gas exchange and transpiration simultaneously (Farquhar et al. 1982, Twohey III et al. 2019). Stable carbon isotope fractionation occurs dominantly during the process of CO_2 diffusion and carboxylation (Hobbie and Werner 2004) and is controlled by both the carboxylation efficiency and the openness of stomata (Farquhar et al. 1982, 1989). The higher the carboxylation efficiency, the lesser the discrimination against ^{13}C , resulting in higher $\delta^{13}\text{C}$ and iWUE values. The partial closure of stomata will also lessen discrimination against ^{13}C , resulting in relatively high $\delta^{13}\text{C}$ and iWUE values. Therefore, tissue $\delta^{13}\text{C}$ can reliably indicate plant iWUE and is used to calculate iWUE for trees (Farquhar et al. 1982, W. Lu et al. 2018). As $\delta^{13}\text{C}$ is a reliable indicator of biomass production per water consumed, it could also be used to study the linkage between WUE and passive nutrient uptake.

Although water uptake and all mineral nutrients, including Ca, are conjectured to be linked as both processes largely rely on transpiration (Barber 1962), there is a lack of solid experimental evidence. Theoretically, nutrient absorption can be promoted by transpiration-driven water flow through the rhizosphere (Barber 1962, Epstein 1972, Wright et al. 2003, Cramer et al. 2009), and high transpiration can also facilitate nutrient translocation and assimilation (Cramer et al. 2008, 2009). This relationship is supported occasionally by results that xylem sap flow rate is associated with the nutrient concentrations of the xylem sap in a tropical tree (Barker and Becker 1995), and high transpiration

is associated with high leaf nutrient concentrations in Cycads (Zhang et al. 2018). However, in most crop species, higher transpiration is not associated with higher leaf nutrient concentrations (Tanner and Beevers 1990, Tanner and Beevers 2001, Bower 2008). It is hard to detect and quantify this relationship mainly due to confounding factors of active regulation in nutrient uptake and nutrient relocation within the plant body. However, Ca uptake is an entirely passive process through transpiration-generated water flow (White 2001). In addition, Ca ions are largely transported apoplastic and immobile after incorporation into cells (White and Broadley 2003). Thus, plant tissue Ca concentration could be closely related to plant transpiration and water-use, which has not been tested. Here, we developed a conceptual model (see the Theoretical model section) to quantify the relationship between plant WUE and soil-to-plant Ca ratio. Quantifying this relationship can aid in understanding plant distribution over regional scales and the response of plant water and Ca uptake to climate change. Predicted changes in water availability and evaporative demand due to anthropogenic climate change (Dai 2013, Allen et al. 2018) will undoubtedly alter plant transpiration and water-use, consequently affecting Ca uptake, carbon assimilation, and plant distribution.

To explore the relationship between tree iWUE and precipitation, as well as plant macronutrient Ca across geographical locations, we developed a conceptual model (see the Theoretical model in Materials and Methods) and collected leaf and soil samples from 40 forest sites naturally covered by selected tree species (Figure 1; Table S1 available as Supplementary data at *Tree Physiology Online*): *Pinus tabulaeformis* Carr., *Quercus mongolica* Fisch. Ex Ledeb, and *Platycladus orientalis* (L.) Franco. These three species are widely distributed in northern China, and the sampling sites were distributed in a large graphical region acrossing 2300 km from the west to the east. To further confirm the observed relationships from the natural forests, we also conducted a greenhouse experiment to amend soil Ca concentration using *P. tabulaeformis* seedlings. Since habitat water conditions influence stomatal conductance, transpiration, WUE and calcium uptake (MacRobbie 1998, Zhang et al. 2009, 2013), we hypothesized that both iWUE and $S_{\text{Ca}}/B_{\text{Ca}}$ will be related to mean annual precipitation and the growing season precipitation. As Ca is essential for photosynthesis and plant growth, we expected a positive relationship between iWUE and both soil Ca and leaf Ca. We also hypothesized that there exists a linear relationship between iWUE calculated from leaf $\delta^{13}\text{C}$ and $S_{\text{Ca}}/B_{\text{Ca}}$ (can be defined as the reciprocal of plant Ca accumulation efficiency) based on a theoretical model we developed.

Theoretical model, materials, and methods

Theoretical model to link calcium and water

Here, we propose a conceptual model to link plant water-use with calcium accumulation. Theoretically, plant calcium content is the product of biomass production (B) and biomass calcium

concentration (B_{Ca}), and plant Ca uptake is the product of transpiration (T_r) and Ca dissolved in soil solution. Therefore, due to mass conservation and zero reuse of Ca, plant Ca content should theoretically equal to plant calcium uptake with the assumption of no organ losses (the effects of organ losses will be corrected by studying this at the leaf level) (Zhou and Zou 2017): $BB_{Ca} = T_r S_{Ca}$,

Reorganizing this, we get

$$B/T_r = S_{Ca}/B_{Ca}, \quad (1)$$

where B/T_r is WUE.

To remove the non-linear impact of saturated vapor pressure (Limousin et al. 2015), we used iWUE to reflect plant WUE and it is a linear function of $\delta^{13}C$ (Osmond et al. 1980, Farquhar et al. 1982, X. Lu et al. 2018)

$$iWUE = c * B/T_r = a_1 + b_1 * \delta^{13}C. \quad (2)$$

Combining Eqs (1) and (2) gives

$$iWUE = a + b * S_{Ca}/B_{Ca}, \quad (3)$$

where a , a_1 and b , b_1 are intercepts and slopes, respectively, and c is a constant.

In practice, representative soil solution is challenging due to limited availability and large temporal and spatial variations. We therefore replaced it with water-extractable (distilled H_2O) soil calcium. Also, it is hard to test the relationship between iWUE and S_{Ca}/B_{Ca} at the individual level for trees due to potential variation in $\delta^{13}C$ among tissues and frequent organ losses due to littering (leaf and stem shedding). Thus, it is easier to test this relationship at the leaf level. We assume that the leaf level relationship of Eq. (3) will have different a_1 and b_1 but will not alter the relationship between iWUE and S_{Ca}/B_{Ca} in Eqs (1) and (3). To test Eq. (3) at the leaf level, we collected leaf and soil samples for three widely distributed tree species from northern China (Table S1 available as Supplementary data at *Tree Physiology Online*): *P. tabuliformis* Carr., *Q. mongolica* Fisch. Ex Ledeb. and *P. orientalis* (L.) Franco. represent the area's major dominant forest trees. We also conducted a greenhouse experiment to manipulate soil Ca concentration to test this relationship for *P. tabuliformis*, which is easy to grow and highly available in nurseries as a common plantation species in the region.

Field sampling across geographical locations

Soil and tree leaf samples were collected from five provinces in northern and northeastern China across a latitude range of $35^{\circ}24' - 48^{\circ}35'N$ and a longitude range of $108^{\circ}29' - 131^{\circ}18'E$ in July and early August of 2015 (Figure 1; Table S1 available as Supplementary data at *Tree Physiology Online*). The entire region is under the strong influence of the East Asian Monsoon,

with warm and wet summers and cold and dry winters and springs. The mean annual temperature ranged from 6.2 to 9.0 °C, and the mean annual precipitation (MAP) ranged from 481 to 670 mm. Dominant soils include Inceptisols, Endisols, Aridisols and Alfisols. Three tree species, including two conifers, *P. tabuliformis* and *P. orientalis*, and one angiosperm species, *Q. mongolica*, were selected for the field study due to their commonness and wide distribution (Table S1 available as Supplementary data at *Tree Physiology Online*; Fang et al. 2011). Samples for *P. tabuliformis* were obtained from natural forests in Liaoning, Hebei, Shanxi and Shaanxi provinces (Figure 1; Table S1 available as Supplementary data at *Tree Physiology Online*), for *Q. mongolica* from Heilongjiang and Liaoning provinces, and for *P. orientalis* from Liaoning and Hebei provinces.

A total of 40 plots (20 × 20 m each) were established for these tree species in their selected natural distribution areas. Among them, 23 plots had *P. tabuliformis*, 7 plots had *P. orientalis* and 10 plots had *Q. mongolica* as dominant species, respectively. The three species differed in sampling plot numbers because their natural distribution ranges were different (Fang et al. 2011). Most forests were natural forests, about 40–80 years old (Table S1 available as Supplementary data at *Tree Physiology Online*), but some of the *P. tabuliformis* forests were possibly generated after being artificially seeded with airplanes (Wu et al. 2000). The diameter at breast height (DBH) of all tree individuals inside each plot was measured, and for each plot, two to three tree individuals that represented the average DBH were chosen for taking soil and leaf samples. A mineral soil sample was collected with a corer (42 mm in diameter) in four perpendicular directions within 2 m from each chosen tree trunk to a depth of 15 cm. The soil cores within the same plot were mixed into one composite soil sample. Meanwhile, mature leaves were also collected with the same number of current-year and fully developed leaves in four directions from the lower one-third crown for each chosen tree. Eight branchlets were randomly collected for each chosen tree by a ladder and a pole pruner (Zheng et al. 2020).

Climate data

Monthly precipitation data of all the sampling sites were acquired from the WorldClim global climate and weather database (www.worldclim.org; WorldClim 2.1) (Harris et al. 2014, Fick and Hijmans 2017). Mean annual precipitations of 6 years from 2010 to 2015 (the sampling year) were then calculated and used for the analyses. As leaf $\delta^{13}C$ is mainly related to the environmental conditions of the leaf growing season (Seibt et al. 2008), the growing season precipitation was also calculated as the total precipitation from April to June (the leaf expansion season before the sampling in 2015). Annual potential evapotranspiration (PET) and Aridity index (AI) data of all the sampling sites were extracted from the Global

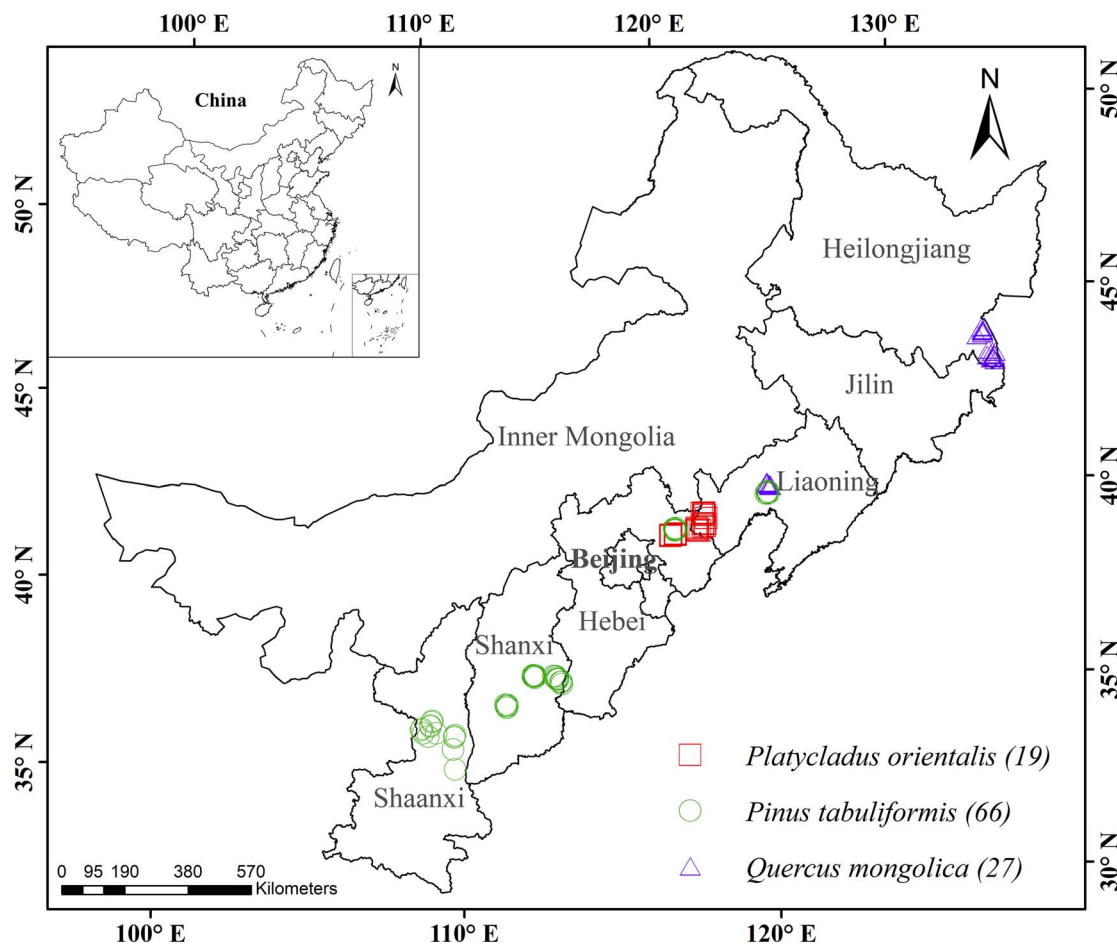


Figure 1. Sampling locations for *Platycladus orientalis* (L.) Franco, *Pinus tabuliformis* Carr. and *Quercus mongolica* Fisch. Ex Ledeb. in northern China. We obtained 2–3 soil and tree leaf samples from each of the >9 plots of 20 × 20 m from each sampling site for each tree species. Numbers in parentheses are soil and tree sample size. Symbols represent the locations of sampling plots.

Aridity Index and Potential Evapotranspiration Climate Database v2 (www.cgiar-csi.org) (Trabucco and Zomer 2019). The AI was calculated as the MAP and PET ratio.

Soil water-extractable Ca

To obtain soil water-extractable Ca (Séguin et al. 2004, Meers et al. 2006), soil samples were air-dried, ground with mortar and pestle, and sieved through 0.85 mm (20-mesh size), and then 5 g of the sieved soil was extracted with 25-ml distilled water in a rotary shaker for 30 min (Meers et al. 2006). A volume of 9.5 ml of the extractant was filtered with a filter paper to a 10 ml Eppendorf tube and spiked with 0.5 ml of 3% SrCl₂, and stored at 4 °C before analysis for Ca in a flame atomic absorption spectrometer (Z-2000, Hitachi, Tokyo, Japan) within 48 h.

Leaf Ca concentration and $\delta^{13}\text{C}$ values

Fresh mature leaves were briefly dried in an oven at 105 °C for 0.5 h and then dried to constant weight at 80 °C before leaf samples were ground with a ball mill to pass through a 100-mesh sieve. A subsample of 0.15 g of the ground leaf materials

was then digested with HNO₃-HClO₄. All digestive solution was added with 2 ml 3% SrCl₂ before diluting with deionized water to 50 ml for Ca analysis with the flame atomic absorption spectrometer (Z-2000, Hitachi). Another subsample of 7 mg of the ground leaf materials was analyzed for ¹³C in a mass spectrometer (IsoPrime 100 Isotope Ratio Mass Spectrometer, Germany). Intrinsic WUE was then calculated based on $\delta^{13}\text{C}$ (see Equation (2); W. Lu et al. 2018).

Controlled greenhouse experiment

A pot experiment with Ca amendment was conducted in a greenhouse at the Beishan Research Station of Shenyang Agricultural University (within the range of the natural distribution for *P. tabuliformis* and ~200 km away from the closest field sampling site) in 2018. Three-year-old *P. tabuliformis* saplings of similar sizes (~30 cm high, 8 mm in basal diameter) were planted in 7.5 l pots (one sapling per pot) with 6 kg sandy soils of low water-extractable Ca concentrations (<20 mg kg⁻¹) in early April. This species was selected because it is easy to grow and highly available in local nurseries. After 1 month of

establishment, 1 l of Ca-free nutrient solutions (510 mg l⁻¹ KNO₃, 240 mg l⁻¹ MgSO₄, 135 mg l⁻¹ KH₂PO₄, 850 mg l⁻¹ NaNO₃, 3 mg l⁻¹ FeSO₄, 5.7 mg l⁻¹ H₃BO₃, 1.5 mg l⁻¹ MnCl₂, 0.05 mg l⁻¹ CuSO₄, 0.12 mg l⁻¹ ZnSO₄, 0.08 mg l⁻¹ H₂MoO₄) were applied to each pot at the beginning of the experiment. The pH of the nutrient solutions varied between 5 and 6. Then the potted saplings were randomly separated into seven groups ($n = 8$ for each group), and each group was assigned randomly to one of the treatments with different concentration CaCl₂ solutions (0, 832.5, 1665, 3330, 6660, 9990 and 13,320 mg l⁻¹). All plants were watered to 70% of field water capacity by weighing every 5 days during the non-peak growing season (April to June and September to October) or every 3 days during the peak growing season (July and August). Leaf tissue sampling was carried out in July and August to test leaf Ca concentration and $\delta^{13}\text{C}$ (see methods above). Soil water-extractable Ca, leaf Ca concentration and $\delta^{13}\text{C}$ values were measured using the same methods described above.

Data analyses

A multiple linear regression model was used to test the effects of growing season precipitation (GSP), MAP, AI, PET on iWUE and $S_{\text{Ca}}/B_{\text{Ca}}$. A linear regression model of the curve estimation was also used to examine the relationship between iWUE values and $S_{\text{Ca}}/B_{\text{Ca}}$ ratios, between iWUE or $S_{\text{Ca}}/B_{\text{Ca}}$ and climate variables, and between $S_{\text{Ca}}/B_{\text{Ca}}$ and gas exchange-based WUE (A/g_s and A/T_r). A general linear model procedure was also employed to determine whether differences existed in the slope of linear regression equations, and in values of S_{Ca} , B_{Ca} , iWUE, and $S_{\text{Ca}}/B_{\text{Ca}}$ among tree species. All the above analyses were done with IBM SPSS 22 (SPSS Inc., Chicago, IL, USA).

A principal component analysis (see methods above PCA) was used to test the joint variation of the plant, soil, and climate variables including iWUE, $S_{\text{Ca}}/B_{\text{Ca}}$, S_{Ca} , B_{Ca} , MAP, GSP, and PET. The PCA was carried out using the FactoMineR package in R (Version 3.5.1) software. Furthermore, a path analysis (structural equation modeling) was used to test the potential relationships among plant, soil, and climate variables, and the contributions of soil and climate variables on iWUE. A path model was developed based on prior knowledge and bivariate relationships. Nonsignificant path relationships were removed from the model. Path analysis was conducted in AMOS 18.0 software with SPSS (SPSS Inc.).

Results

High variations in S_{Ca} , B_{Ca} , $S_{\text{Ca}}/B_{\text{Ca}}$ and iWUE were found among these three tree species (Figure 2). The concentration and variation of soil water-extractable Ca were highest for *P. tabuliformis*, which showed the widest range of natural distribution (Table S1 available as Supplementary data at *Tree Physiology*

Online), and lowest for *Q. mongolica* (Figure 2a). Leaf Ca concentration was higher for *P. tabuliformis* and *P. orientalis* than for *Q. mongolica* (Figure 2b), but differences in both concentration and variation of leaf Ca among the three tree species were much smaller than those for soil water-extractable Ca. The ratio of $S_{\text{Ca}}/B_{\text{Ca}}$ was highest for *P. tabuliformis* and lowest for *Q. mongolica* (Figure 2c). Intrinsic WUE was highest for *P. orientalis* and lowest for *Q. mongolica* (Figure 2d).

The first two axes of the PCA analysis explained 81.8% of the total variation (Figure 3). The first PCA axis (PCA1), which explained 62.0% of the total variation, was positively associated with iWUE, $S_{\text{Ca}}/B_{\text{Ca}}$, S_{Ca} , B_{Ca} and PET, and negatively associated with MAP, AI and GSP. S_{Ca} showed the most significant positive contribution to PCA1, whereas GSP showed the most significant negative contribution (Figure 3a). The PCA2, which explained 19.8% of the total variation, was positively associated with MAP, AI, $S_{\text{Ca}}/B_{\text{Ca}}$, S_{Ca} , B_{Ca} and iWUE, and negatively associated with GSP and PET. MAP showed the most significant positive contribution to PCA2, whereas PET had the largest negative contribution. The PCA1 clearly separated *P. tabuliformis* and *Q. mongolica*, with the former being in only the positive quadrants and the latter being in the negative quadrants only. In contrast, *P. orientalis* overlapped the other two species (Figure 3b).

The multiple linear regression model showed that iWUE depended on GSP and S_{Ca} significantly, while other variables included in the model (MAP, AI, PET, B_{Ca}) had no significant relationships with iWUE (Table 1). $S_{\text{Ca}}/B_{\text{Ca}}$ depended on GSP and MAP significantly but not on AI and PET (Table 1). The bivariate regression results confirmed the negative relationships between iWUE and GSP, and between $S_{\text{Ca}}/B_{\text{Ca}}$ and GSP (Figure 4a and b). Intrinsic WUE was also positively related with both S_{Ca} and B_{Ca} (Figure 4c and d). The relationships between iWUE and S_{Ca} and between iWUE and B_{Ca} were better described by a three-parameter exponential equation (Figure 4c and d). These relationships were significant in *P. tabuliformis* alone (relationships not shown), but not in the other two species if analyzed separately. These two species (*Q. mongolica*, and *P. orientalis*) are distributed in habitats with a relatively narrow range of precipitation (Figure 4).

We found positive linear relationships between iWUE (calculated from $\delta^{13}\text{C}$) and $S_{\text{Ca}}/B_{\text{Ca}}$, as expected, for all three tree species across the study forest sites (Figure 5). The slopes of iWUE against $S_{\text{Ca}}/B_{\text{Ca}}$ differed significantly among the three species (general linear model). The greatest slope was found in *Q. mongolica*, while the smallest in *P. tabuliformis*. The relationship in *P. tabuliformis* was better described by a three-parameter exponential equation (Figure 5). When all the species were combined, the relationship between iWUE and $S_{\text{Ca}}/B_{\text{Ca}}$ was well-described by a three-parameter exponential equation (Figure 5 inset). All the iWUE values of these three species were lower than 105 mg kg⁻¹ (Figures 2 and 5). Most individuals of *Q.*

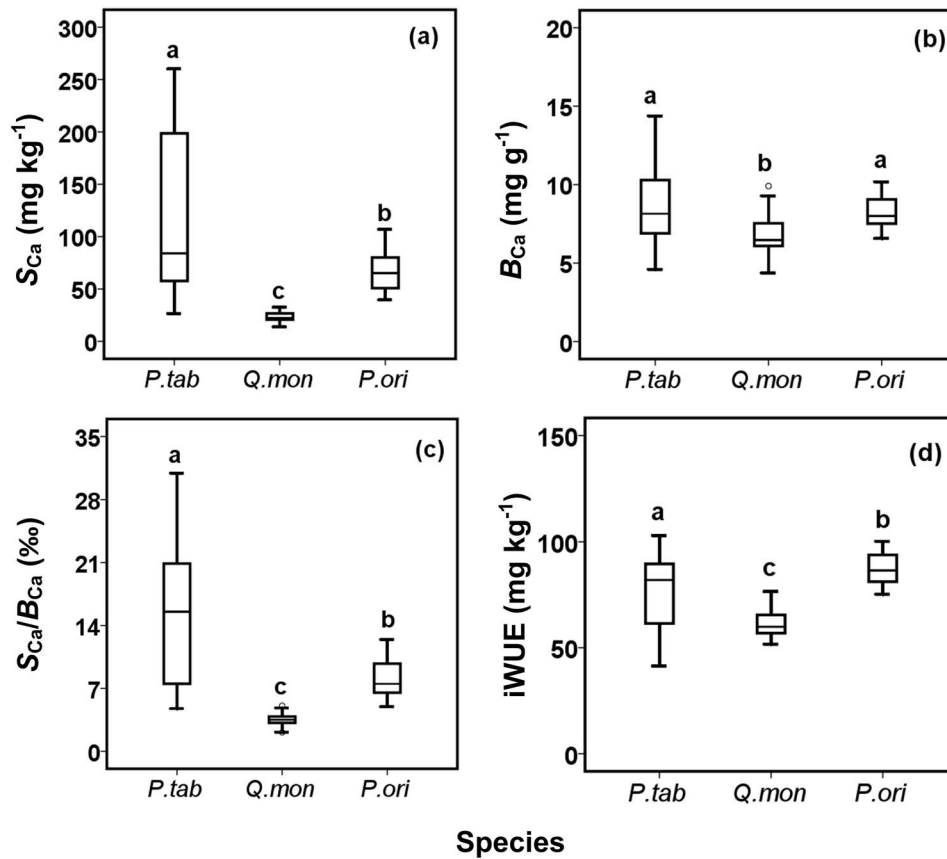


Figure 2. Boxplot of soil water-extractable calcium concentration (S_{Ca}), tree leaf calcium concentration (B_{Ca}), S_{Ca}/B_{Ca} ratio, and iWUE for three tree species from the north and northeastern China. *Pinus tabuliformis*, *Platycladus orientalis* and *Quercus mongolica*. The line inside the box is the median value, the box represents 25–75% percentile, and the vertical lines are 9–91% percentile. Different letters indicate significant differences between tree species by the linear model procedure.

Table 1. Multiple linear regression results (standardized β , t and P values) showing the dependence of iWUE derived from leaf $\delta^{13}C$ values on growing season precipitation (GSP), mean annual precipitation (MAP), Aridity index (AI), potential evapotranspiration (PET), soil calcium concentrations (S_{Ca}) and leaf calcium concentration (B_{Ca}), as well as the dependence of soil-to-plant calcium ratios (S_{Ca}/B_{Ca}) on GSP, MAP, AI and PET. For the iWUE model, $R^2 = 0.47$ and $P < 0.001$. For the S_{Ca}/B_{Ca} model, $R^2 = 0.54$ and $P < 0.001$.

	iWUE			S_{Ca}/B_{Ca}		
	β	t	P	β	t	P
GSP	-0.50	-3.03	<0.01	-0.62	-4.88	<0.001
MAP	-0.09	-0.58	0.56	0.50	4.01	<0.001
AI	0.56	0.92	0.36	-0.62	-1.13	0.26
PET	0.48	1.02	0.31	-0.24	-0.57	0.57
S_{Ca}	0.32	2.45	0.02			
B_{Ca}	-0.03	-0.30	0.76			

mongolica occurred in sites with a narrow range of S_{Ca}/B_{Ca} values between 2 and 6‰, compared with the much higher value and larger range of 6–12‰ and 6–38‰ for *P. orientalis* and *P. tabuliformis*, respectively (Figures 2 and 5).

These positive relationships between iWUE and S_{Ca} , between iWUE and B_{Ca} , and between iWUE and S_{Ca}/B_{Ca} were also found in the controlled greenhouse experiment for *P. tabuliformis* with soil Ca (S_{Ca}) manipulated (Figure 6). The relationships

were well-described by a three-parameter exponential equation (Figure 6a and c) or a linear regression (Figure 6b). The iWUE values ranged from 76 to 91 mg kg⁻¹, while S_{Ca}/B_{Ca} ranged from 1.7 to 26.0‰ across different treatments.

The path analysis model as shown in Figure 7a fitted well with the dataset (minimum fit function chi-square = 1.93, df = 2, $P = 0.452$, CFI = 1.00, AIC = 27.928, RMSEA < 0.001). The iWUE was directly influenced by both GSP and S_{Ca} , with

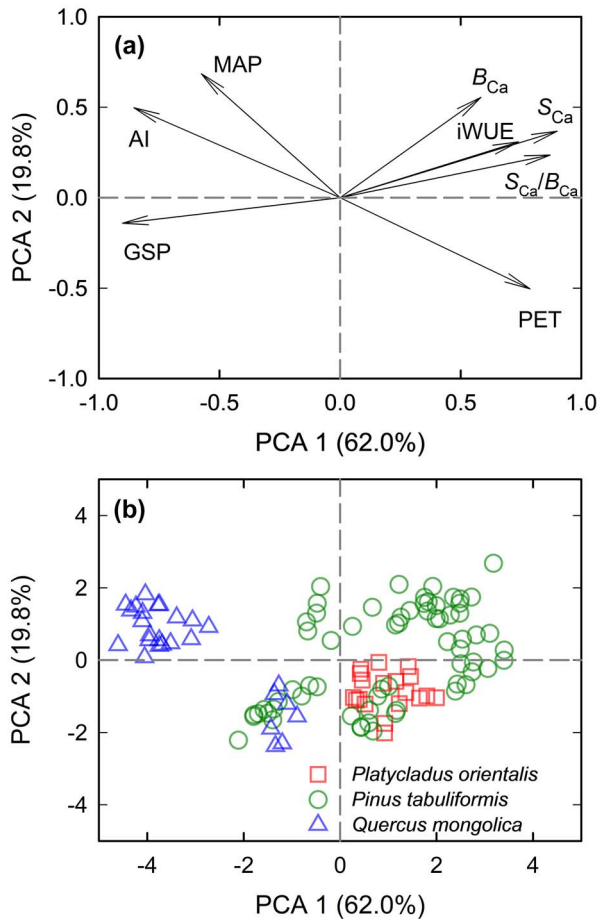


Figure 3. Principle component analysis results showing the loadings of traits (a) and three species studied (b). The traits included in the analysis were $iWUE$ derived from leaf $\delta^{13}C$ values, growing season precipitation (GSP), mean annual precipitation (MAP), Aridity index (AI), potential evapotranspiration (PET), soil calcium concentrations (S_{Ca}) and leaf calcium concentration (B_{Ca}), as well as the dependence of soil-to-plant calcium ratios (S_{Ca}/B_{Ca}). Symbols: *P. tabuliformis* (circles), *Q. mongolica* (triangles) and *P. orientalis* (rectangles).

GSP showing a significant negative effect, and S_{Ca} showing a significantly positive effect (Figure 7a). S_{Ca} showed a larger total effect on $iWUE$ compared with GSP (Figure 7b). This agrees with the multiple linear regression results. Intrinsic WUE was also significantly and positively correlated with S_{Ca}/B_{Ca} . Potential evapotranspiration showed an indirect effect on $iWUE$. Overall, S_{Ca} has the highest standardized effect on $iWUE$, followed by S_{Ca}/B_{Ca} , GSP and PET. Additionally, GSP showed a significantly positive effect on PET and a significantly negative effect on S_{Ca} . S_{Ca} also showed a significant and positive effect on PET (Figure 7a).

Discussion

Our results indicate the importance of both growing season precipitation (GSP) and soil calcium (S_{Ca}) in determining tree $iWUE$. As expected, tree $iWUE$ was related to GSP and S_{Ca} across

a large geographical gradient. Furthermore, our field sampling across native habitats of three tree species and the controlled greenhouse experiment revealed a close relationship between S_{Ca}/B_{Ca} and $iWUE$, supporting our hypothesis and conceptual model linking tree Ca accumulation and water consumption. As the reciprocal of B_{Ca} could be defined as the Ca-use efficiency (CaUE) (Vitousek 1982), the close relationship between S_{Ca}/B_{Ca} and $iWUE$ could also be described as the relationship between $S_{Ca} \cdot CaUE$ and $iWUE$. Thus, this relationship can be a reliable approach to quantifying the plant water-Ca accumulation linkage and the association between $iWUE$ and CaUE. S_{Ca}/B_{Ca} , the reciprocal of plant Ca accumulation efficiency, was sensitive to GSP. Thus, S_{Ca}/B_{Ca} can be a useful term to study the response of plant Ca accumulation efficiency to future changes in precipitation pattern and evaporative demand and provide a new perspective on understanding forest response to climate change.

Climatic and Ca effects on $iWUE$

Our results and the multivariate analyses showed strong precipitation and soil Ca contributions on $iWUE$. Here we used $\delta^{13}C$ -derived $iWUE$, a widely used index to indicate plant WUE (Farquhar et al. 1982, Guerrieri et al. 2016, Twohey et al. 2019, Tarin et al. 2020). The relationship between $iWUE$ and precipitation of the study site is confirmed in our study. As water is a relatively more limiting resource, plants in drier habitats (lower precipitation) tend to show more conservative water-use, resulting in higher WUE (Gouveia and Freitas 2009, Zhang et al. 2021). Interestingly, a negative relationship between $iWUE$ and MAP, as shown in previous studies (Gouveia and Freitas 2009, Li et al. 2016), was not found in the present study within or across three tree species studied. Instead, we found a negative relationship between $iWUE$ and GSP. A relationship between $\delta^{13}C$ and GSP was also found in other species (Leffler and Evans 2001, Van de Water et al. 2002). This could be because the leaf structural and non-structural carbon (e.g., soluble sugars) of these temperate forests are mainly produced during the active growing season, thus representing the environmental conditions of the growing season (Seibt et al. 2008). In addition, most precipitation during the non-growing season is likely lost through evaporation or groundwater in this region (Qiu et al. 2018) rather than being consumed by the trees. Meanwhile, the relationship between $iWUE$ and MAP reported in previous studies (Gouveia and Freitas 2009, Li et al. 2021) could be because of the positive relationship between MAP and GSP on a smaller geographical scale. When GSP and MAP are not closely related on a larger geographical scale, the relationship between $iWUE$ and MAP could be absent.

Besides GSP, we found that $iWUE$ of three tree species studied was also closely associated with soil Ca across a sizeable geographical gradient. Further, the path analysis model showed a larger effect of S_{Ca} on $iWUE$ than GSP, which agrees with

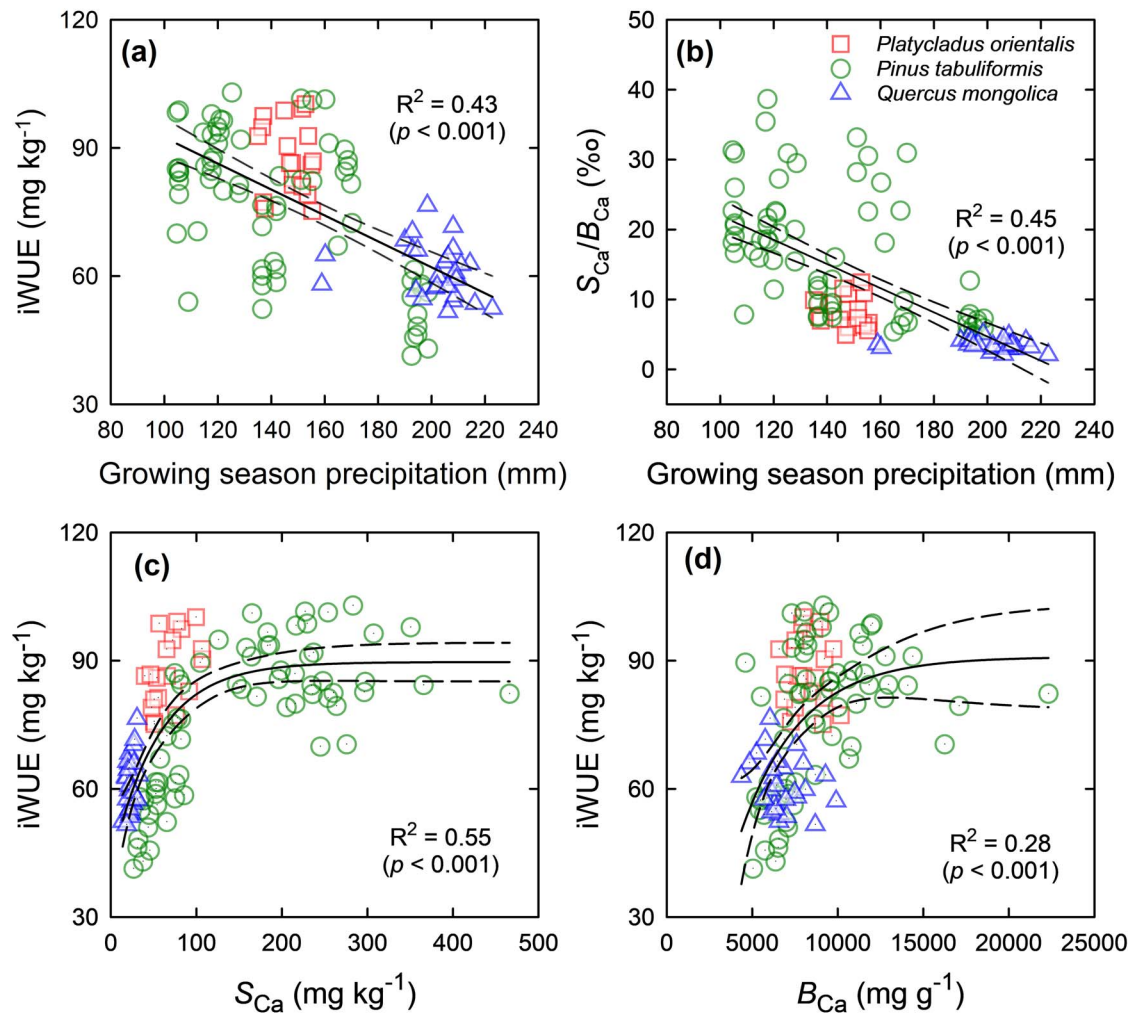


Figure 4. Intrinsic WUE derived from leaf $\delta^{13}\text{C}$ values and soil-to-plant calcium ratios ($S_{\text{Ca}}/B_{\text{Ca}}$) in relation to growing season precipitation (a, b) and iWUE in relation to S_{Ca} and B_{Ca} (c, d). Symbols: *P. tabuliformis* (circles), *Q. mongolica* (triangles) and *P. orientalis* (rectangles). Solid black lines are linear or exponential relationships fitted to values of all three species. Dashed lines indicate 95% confidence intervals (CIs).

the regression analyses showing higher explanatory power of S_{Ca} on iWUE than GSP. Thus, our results suggest that S_{Ca} could better predict iWUE than precipitation. As a macronutrient, Ca is necessary for cell wall and membrane construction (White and Broadley 2003), and Ca deficiency could result in reduced plant growth. Therefore, the positive relationship between iWUE and soil Ca, and between iWUE and leaf Ca could be because of the facilitation of increased Ca on cell development, tissue and organ growth, and ultimately primary production. In addition, once an optimum amount of Ca is achieved, a further increase in Ca will not result in a further increase in primary production and iWUE. This pattern is supported by the exponential growth to the maximum relationship between iWUE and S_{Ca} or B_{Ca} . The influence of S_{Ca} on iWUE, and no further increase in iWUE when S_{Ca} were higher than 200 mg kg^{-2} , was confirmed by our control experiment in the greenhouse with S_{Ca} manipulated. Our results also agree with a previous study showing that

enhanced soil Ca availability and Ca uptake by ectomycorrhizal symbioses increased plant WUE (Li et al. 2021). While other studies showed the influence of N, P, potassium (K) on iWUE (Cernusak et al. 2011, Matimati et al. 2014, Battie-Laclau et al. 2016), our study suggests that the effect of Ca should not be ignored.

The linkage between water-use and Ca uptake

The close association between $S_{\text{Ca}}/B_{\text{Ca}}$ and iWUE indicates the tight linkage between water and Ca uptake/transport, driven by transpiration and regulated by the stomatal aperture. The relationship between water uptake and many (likely all) other essential mineral nutrients is weakened by the active control on the Casparian strip and relocation among tissues and organs. Meanwhile, Ca uptake is a passive process (White 2001), and Ca is not translocated among plant tissues and organs after incorporation (White and Broadley 2003). Thus, Ca uptake and

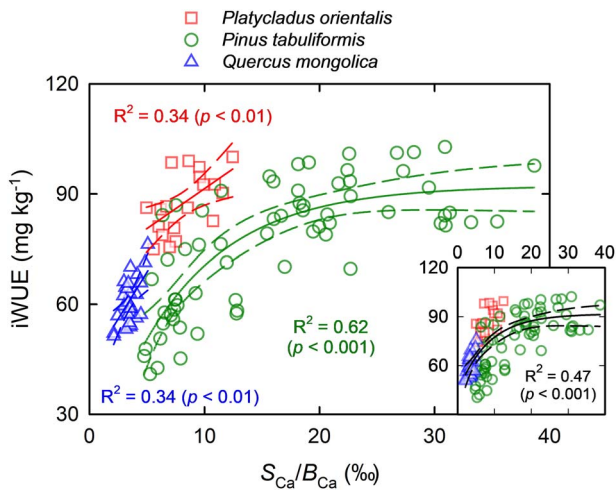


Figure 5. Linear or exponential relationships between $iWUE$ derived from leaf $\delta^{13}C$ and soil-to-plant calcium ratios (S_{Ca}/B_{Ca}) for three tree species from the north and northeastern China. Symbols: *P. tabuliformis* (circles), *Q. mongolica* (triangles) and *P. orientalis* (rectangles). Solid lines are linear or exponential relationships fitted to different species, and the break lines indicate 95% CIs.

transport could be solely determined by transpiration and Ca^{2+} in the soil solution. Although this coupling could be predicted by the Ca uptake and transportation theory, no empirical evidence has been provided to the best of our knowledge. Our results here thus provide novel empirical evidence to support the facilitation of Ca uptake and transport by transpiration (and the passive uptake of other nutrients) and suggest a tight linkage between the two (as shown in Eqs (1) and (3)).

In addition, the model indicated in Eq. (3) has advantages over conventional methods using tissue nutrient concentrations and transpiration rate to test the relationship between water and Ca uptake. Using the soil-to-plant nutrient ratio rather than tissue nutrient concentrations elucidated the soil effects and standardized tissue concentrations with soil nutrient concentrations. Furthermore, using $\delta^{13}C$ -based WUE rather than transpiration rate avoids the effects of environmental conditions on physiological measurements and standardizes the water consumption with plant biomass.

Although our theoretical model was developed for passively absorbed nutrients lacking relocation after assimilation such as Ca, testing the relationship between $iWUE$ and soil-to-plant nutrient ratio could also be applied to other mineral nutrients. Theoretically, transpiration-driven water flow drives nutrient movement from the soil to the rhizosphere as well as transport from roots to the canopy (Barber 1962, Epstein 1972, Wright et al. 2003, Cramer et al. 2008, 2009, Zhang et al. 2018). Thus, high transpiration (thus low $iWUE$) will facilitate the accumulation of other nutrients (low soil-to-leaf nutrient ratio). Indeed, $iWUE$ has been found to be related to leaf N in *Phaseolus vulgaris* (Matimati et al. 2014) and to leaf P:C ratio in tropical tree seedlings (Cernusak et al. 2011). Furthermore, an increase

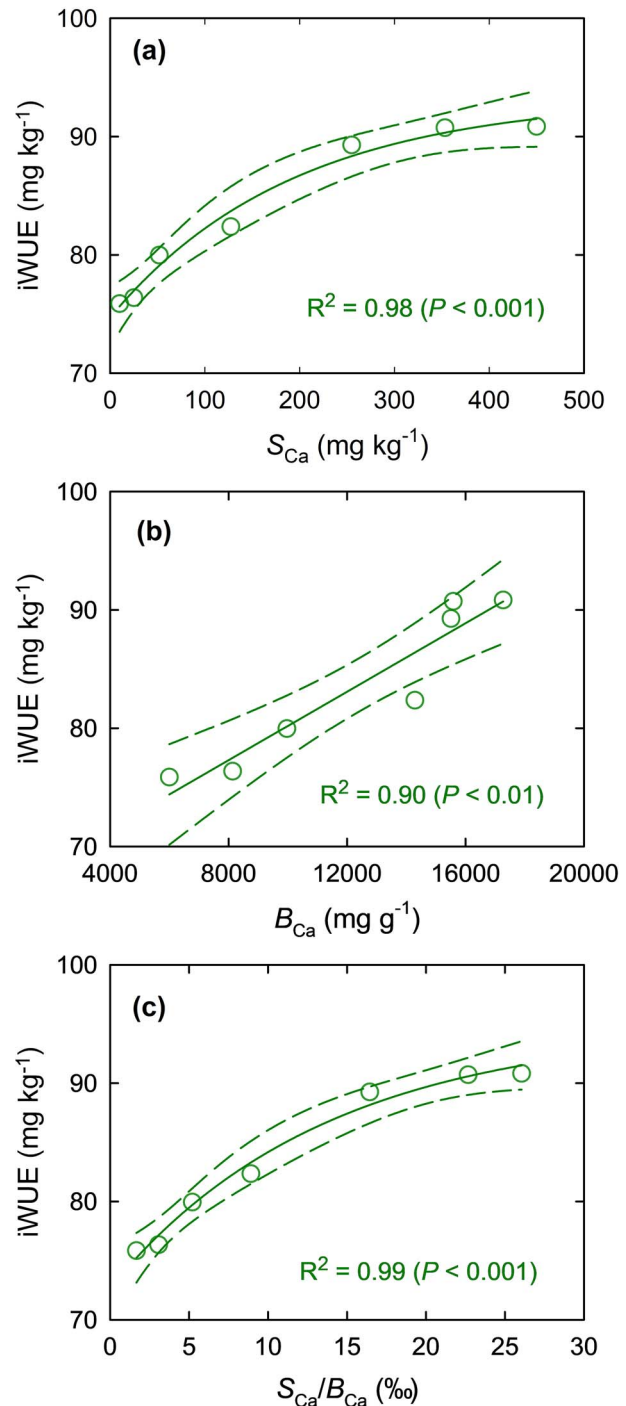


Figure 6. Leaf $iWUE$ calculated from $\delta^{13}C$ in relation to S_{Ca} , B_{Ca} and soil-to-plant calcium ratios (S_{Ca}/B_{Ca}) for *Pinus tabuliformis* in a controlled greenhouse experiment. Solid lines are linear or exponential relationships fitted to the data. Dashed lines indicate 95% CIs.

in N in rooting substrate decreases transpiration and increases $iWUE$ in maize (Wilkinson et al. 2007), and K fertilization also increases $iWUE$ in *Eucalyptus grandis* (Battie-Laclau et al. 2016). Meanwhile, an absence of a relationship between leaf transpiration rate and tissue N, P or K concentrations was reported

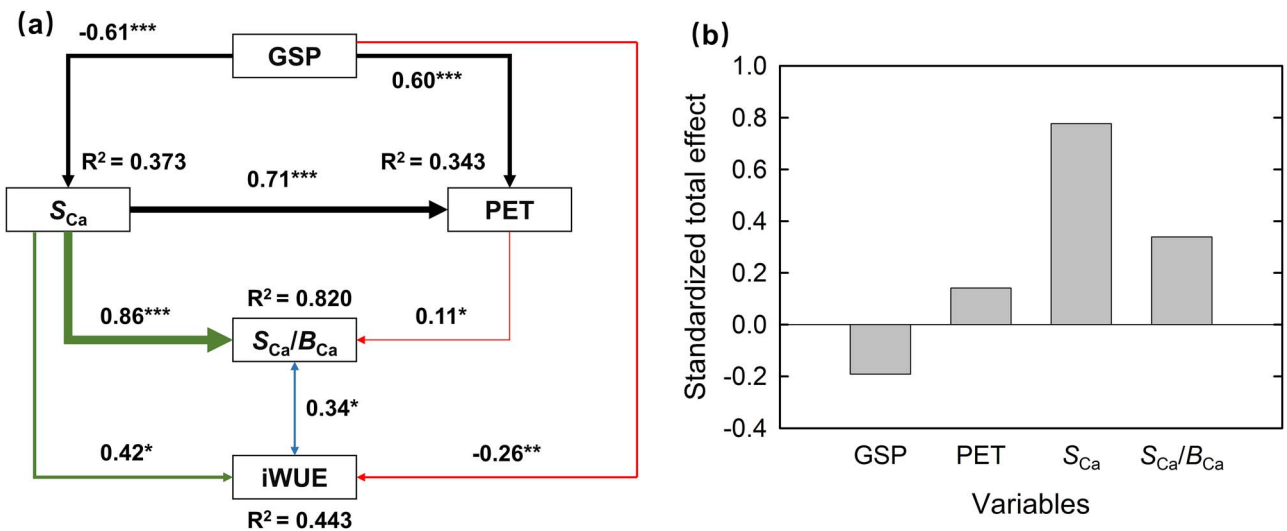


Figure 7. A path analysis model explaining the climate and calcium determinants of iWUE and soil-to-plant calcium ratio (S_{Ca}/B_{Ca}). (a) The final model. (b) The total effects of different variables on iWUE. Variables included are growing season precipitation (GSP), Aridity index (AI), potential evapotranspiration (PET), soil calcium concentrations (S_{Ca}), leaf calcium concentration (B_{Ca}) and S_{Ca}/B_{Ca} . The arrows indicate significant relationships ($P < 0.05$), and the arrow thickness denotes the strength of the relationships. Non-significant relationships were removed. Numbers on the lines indicate standardized path coefficients. Percentages close to the variables indicate the variance explained by the model (R^2). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

for multiple plant species (Tanner and Beevers 1990, Tanner and Beevers 2001, Bower 2008). The relationship between transpiration/iWUE and other nutrients could be decoupled or weaker due to active control of uptake and relocation among organs (Taiz et al. 2015), asking for further studies.

S_{Ca}/B_{Ca} in relation to environmental conditions and climate change

Our results indicate that similar to $\delta^{13}C$, S_{Ca}/B_{Ca} was also sensitive to the growing season precipitation. Under increased water deficits, WUE tends to increase (Zhang et al. 2009, Edwards et al. 2012), while transpiration and plant Ca uptake decrease concurrently, resulting in a reduced leaf Ca concentration and an increase in S_{Ca}/B_{Ca} ratio. In other words, a decrease in precipitation will decrease plant Ca uptake efficiency (the reciprocal of S_{Ca}/B_{Ca}). Further studies could be done to test whether S_{Ca}/B_{Ca} of long-lasting tissues such as stems are related to long-term water availability and whether Ca signals from tree rings indicate interannual variation in growing season precipitation. Wood $\delta^{13}C$ of tree rings has been used to study historical changes in tree WUE and related changes in water availability and atmospheric CO₂ concentrations (W. Lu et al. 2018, Ulrich et al. 2019), while our results suggest tissue Ca as a potential alternative.

The range of S_{Ca} , S_{Ca}/B_{Ca} and the iWUE– S_{Ca}/B_{Ca} relationship could also explain plant distribution range and response to changes in climate conditions. Many regions, including northern and northeastern China, are projected to be drier under global climate change in future decades (Yu et al. 2003, Shi et al.

2014). A drier environment in the future may result in a higher stomatal limitation and increased plant WUE, resulting in a decrease in plant Ca uptake and B_{Ca} value due to reduced transpiration, elevating the S_{Ca}/B_{Ca} ratio through time. Plant species may not perform well under conditions where S_{Ca} , B_{Ca} and S_{Ca}/B_{Ca} reach beyond their optimum ranges; thus, plant distribution and ecosystem composition can be expected to change. In forestry practice, this information can determine potentially suitable plantation sites for different tree species (Zhou and Zou 2017).

Acid deposition is another significant environmental change occurring globally due to the combustion of fossil fuels and the high application rates of nitrogen fertilizers (Johnson and Siccama 1983, Lindberg et al. 1986). Abundant evidence shows that acid deposition will lead to depletion of soil cations, including Ca (Watmough and Dillon 2003, Drouet et al. 2005), suggesting an increased demand on transpiration for Ca uptake and decreased plant iWUE. This is likely because depletion in soil nutrients may increase belowground carbon allocation and, consequently, water uptake and transpiration (Poorter et al. 2012). As the species showed variation in S_{Ca} and S_{Ca}/B_{Ca} range of their native habitats, change in S_{Ca} due to acidification and deviation from their native range may result in changes in water-use and nutrient economy, and consequently changes in carbon assimilation, species distribution, and ecosystem processes. We, therefore, predict that *Q. mongolica*, with a narrower range of S_{Ca} , and a steeper slope between iWUE and S_{Ca}/B_{Ca} , will probably be more sensitive to changes in S_{Ca} , due to either a change in water availability or acid deposition than

P. tabuliformis and *P. orientalis*. Finally, the non-linear relationship between *i*WUE and S_{Ca}/B_{Ca} for *P. tabuliformis* might be related to the expanded natural distribution of the species resulted from artificial seeding by airplanes when competition with other tree species was reduced or absent (Wu et al. 2000).

Conclusion

In conclusion, we revealed a significant contribution of both GSP and Ca on tree *i*WUE. We also developed a novel model to quantify the linkage between plant water consumption and calcium accumulation. The relationship established here between *i*WUE and S_{Ca}/B_{Ca} suggests the potential use of S_{Ca}/B_{Ca} (or $S_{Ca} \cdot CaUE$) to indicate WUE. We suggest that this relationship between *i*WUE and S_{Ca}/B_{Ca} can be expected to be present in other vascular plants, which can be tested in further studies. Further, understanding the relationship between *i*WUE and Ca (S_{Ca} , B_{Ca} , S_{Ca}/B_{Ca}) for different trees and crops can determine optimum soil Ca concentration for forest and crop management under a specific climate condition. In addition, the tight linkage/coupling between plant water consumption and Ca accumulation suggests new possibilities in crop water and nutrient management. Plant Ca uptake could be improved through enhancing transpiration (Yang et al. 2012), and meantime, soil Ca management could be used to improve plant WUE and drought resistance (Silva et al. 2008, Yang et al. 2012). Furthermore, S_{Ca}/B_{Ca} , which is the reciprocal of plant Ca accumulation efficiency, is also sensitive to GSP. Thus, it could be a useful term to quantify plant Ca accumulation capacity and study its response to further changes in rainfall patterns. A projected drier future in Northern China (Yu et al. 2003, Shi et al. 2014) probably will result in a decrease in tree Ca accumulation efficiency. The soil-to-plant ratio of other nutrients could also be a useful term to indicate nutrient accumulation efficiency and used to study plant response to climate change, inviting further studies. The information on S_{Ca} , S_{Ca}/B_{Ca} also highlights a reasonable evaluation and prediction of plant performance and distribution.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Acknowledgments

We thank Kallol Barai for acquiring and organizing the climate data, Keyan Zhang for help in PCA analysis and D. Binkley for his constructive comments.

Funding

This study was supported by The Special Program for Forest Scientific Research in the Public Welfare (201304216) and

the National Natural Science Foundation of China (41450007, 31700552, 31800364). Y.-J.Z. was supported by the United States Department of Agriculture, National Institute of Food and Agriculture, Hatch Project Number ME0-22021, through the Maine Agricultural and Forest Experiment Station.

Conflict of interest

The authors declare no competing interests.

Authors' contributions

X.M.Z. derived the equation for the new index. X.M.Z., Y.-J.Z., Y.-B.Z. and Y.Y. designed this study. Y.-B.Z. obtained funds and organized the research team, supervised both field and laboratory work. Y.Y., S.-Z.Z. and H.L. collected plant and soil samples in the field, performed the greenhouse experiment, and conducted chemical analyses. Y.-J.Z., H.L. and Y.T.F. analyzed the data and made figures and tables. X.M.Z., Y.-J.Z. and Y.Y. wrote the manuscript together. All authors contributed to the analyses of data and the writing of the manuscript.

Data statement

The data supporting the results are archived in Dryad: <https://doi.org/10.5061/dryad.jq2bvq87q>

References

- Allen M, Babiker M, Chen Y, Coninck HD, Connors S, Diemen RV, Zickfeld K (2018) IPCC, 2018: summary for policymakers. In: Global warming of 1.5°C an IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty, Geneva. Cambridge University Press, Cambridge, and New York.
- Barber SA (1962) A diffusion and mass-flow concept of soil nutrient availability. *Soil Sci* 93:39–49.
- Barker M, Becker P (1995) Sap flow rate and sap nutrient content of a tropical rain forest canopy species, *Dryobalanops aromatica*, in Brunei. *Selbyana* 16:201–211.
- Battie-Laclau P, Delgado-Rojas JS, Christina M, et al. (2016) Potassium fertilization increases water-use efficiency for stem biomass production without affecting intrinsic water-use efficiency in *Eucalyptus grandis* plantations. *For Ecol Manage* 364:77–89.
- Bower KE (2008) Relationship between transpiration and nitrogen uptake by pepper (*Capsicum annuum*) as mediated by vapor pressure deficit. University of Georgia, Athens, GA.
- Briggs LJ, Shantz HL (1913) The water requirement of plants. US Government Printing Office, Washington.
- Cernusak LA, Winter K, Turner BL (2011) Transpiration modulates phosphorus acquisition in tropical tree seedlings. *Tree Physiol* 31:878–885.
- Cramer MD, Hoffmann V, Verboom GA (2008) Nutrient availability moderates transpiration in *Ehrharta calycina*. *New Phytol* 179:1048–1057.
- Cramer MD, Hawkins HJ, Verboom GA (2009) The importance of nutritional regulation of plant water flux. *Oecologia* 161:15–24.

- Dai AG (2013) Increasing drought under global warming in observations and models. *Nat Clim Change* 3:52–58.
- Drouet T, Herbauts J, Demaiffe D (2005) Long-term records of strontium isotopic composition in tree rings suggest changes in forest calcium sources in the early 20th century. *Glob Chang Biol* 11:1926–1940.
- Edwards CE, Ewers BE, McClung CR, Lou P, Weinig C (2012) Quantitative variation in water-use efficiency across water regimes and its relationship with circadian, vegetative, reproductive, and leaf gas-exchange traits. *Mol Plant* 5:653–668.
- Epstein E (1972) Mineral nutrition of plants: principles and perspectives. John Wiley & Sons, New York.
- Fang J, Wang Z, Tang Z (2011) Atlas of woody plants in China: distribution and climate. Springer and High Education Press, Berlin, Heidelberg, Dordrecht, London, New York, Beijing.
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Funct Plant Biol* 9:121–137.
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Biol* 40:503–537.
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315.
- Gouveia AC, Freitas H (2009) Modulation of leaf attributes and water-use efficiency in *Quercus suber* along a rainfall gradient. *Trees* 23:267–275.
- Guerrieri R, Lepine L, Asbjornsen H, Xiao J, Ollinger SV (2016) Evapotranspiration and water-use efficiency in relation to climate and canopy nitrogen in U.S. forests. *J Geophys Res Biogeogr* 121:2610–2629.
- Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations—the CRU TS3. 10 Dataset. *Int J Climatol* 34:623–642.
- Hatfield JL, Dold C (2019) Water-use efficiency: advances and challenges in a changing climate. *Front Plant Sci* 10:103.
- Hatfield JL, Sauer TJ, Prueger JH (2001) Managing soils to achieve greater water-use efficiency: a review. *Agron J* 93:271.
- Hobbie EA, Werner RA (2004) Intramolecular, compound-specific, and bulk carbon isotope patterns in C3 and C4 plants: a review and synthesis. *New Phytol* 161:371–385.
- Johnson AH, Siccama TG (1983) Acid deposition and forest decline. *Environ Sci Technol* 17:294A–305A.
- Keenan TF, Hollinger DY, Bohrer G, Dragoni D, Munger JW, Schmid HP, Richardson AD (2013) Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499:324–327.
- Leffler AJ, Evans AS (2001) Physiological variation among *Populus fremontii* populations: short-and long-term relationships between $\delta^{13}\text{C}$ and water availability. *Tree Physiol* 21:1149–1155.
- Li J, Deng J, Zhou Y, Yin Y, Wei Y, Jing Y, Zhang R (2016) Water-use efficiency of typical afforestation tree species in Liaoning, PR China and their response to environmental factors. *Nat Environ Pollut Technol* 15:1427.
- Li Y, Zhang T, Zhou Y, Zou X, Yin Y, Li H, Liu L, Zhang S (2021) Ectomycorrhizal symbioses increase soil calcium availability and water-use efficiency of *Quercus acutissima* seedlings under drought stress. *Eur J For Res* 140:1039–1048.
- Limousin JM, Yopez EA, McDowell NG, Pockman WT (2015) Convergence in resource use efficiency across trees with differing hydraulic strategies in response to ecosystem precipitation manipulation. *Function Ecol* 29:1125–1136.
- Lindberg SE, Lovett GM, Richter D, Johnson DW (1986) Atmospheric deposition and canopy interactions of major ions in a forest. *Science* 231:141–145.
- Lu W, Yu X, Jia G, Li H, Liu Z (2018) Responses of intrinsic water-use efficiency and tree growth to climate change in semi-arid areas of North China. *Sci Rep* 8:1–10.
- Lu X, Vitousek PM, Mao Q et al. (2018) Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest. *Proc Natl Acad Sci USA* 115:5187–5192.
- MacRobbie E (1998) Signal transduction and ion channels in guard cells. *Philos Trans R Soc Lond* 353:1475–1488.
- Matimati I, Verboom GA, Cramer MD (2014) Nitrogen regulation of transpiration controls mass-flow acquisition of nutrients. *J Exp Bot* 65:159–168.
- Meers E, Laing GD, Unamuno VG, Lesage E, Tack FMG, Verloo MG (2006) Water extractability of trace metals from soils: some pitfalls. *Water Air Soil Pollut* 176:21–35.
- Osmond CB, Björkman O, Anderson DJ (1980) Physiological processes in plant ecology: toward a synthesis with Atriplex. Springer, Berlin, Heidelberg, Dordrecht, London, New York.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50.
- Prentice IC, Meng T, Wang H, Harrison SP, Ni J, Wang G (2011) Evidence of a universal scaling relationship for leaf CO₂ drawdown along an aridity gradient. *New Phytol* 190:169–180.
- Qiu GY, Zhang X, Yu X, Zou Z (2018) The increasing effects in energy and GHG emission caused by groundwater level declines in North China's main food production plain. *Agric Water Manag* 203:138–150.
- Séguin V, Gagnon C, Courchesne F (2004) Changes in water extractable metals, pH and organic carbon concentrations at the soil-root interface of forested soils. *Plant Soil* 260:1–17.
- Seibt U, Rajabi A, Griffiths H, Berry JA (2008) Carbon isotopes and water-use efficiency: sense and sensitivity. *Oecologia* 155:441–454.
- Shi P, Sun S, Wang M, Li N, Jin Y, Gu X, Yin W (2014) Climate change regionalization in China (1961–2010). *Sci China Earth Sci* 57:2676–2689.
- Silva CEMD, Gonçalves JFDC, Feldpausch TR (2008) Water-use efficiency of tree species following calcium and phosphorus application on an abandoned pasture, Central Amazonia, Brazil. *Environ Exp Bot* 64:189–195.
- Stanhill G (1986) Water use efficiency. *Advances in Agronomy* 39:53–85.
- Taiz L, Zeiger E, Møller IM, Murphy A (2015) Plant physiology and development. Sinauer Associates Incorporated, Sunderland.
- Tanner W, Beevers H (1990) Does transpiration have an essential function in long-distance ion transport in plants? *Plant Cell Environ* 13:745–750.
- Tanner W, Beevers H (2001) Transpiration, a prerequisite for long-distance transport of minerals in plants? *Proc Natl Acad Sci* 98:9443–9447.
- Tarin T, Nolan RH, Medlyn BE, Cleverly J, Eamus D (2020) Water-use efficiency in a semi-arid woodland with high rainfall variability. *Glob Chang Biol* 26:496–508.
- Trabucco A, Zomer R (2019) Global aridity index and potential evapotranspiration climate database v2. CGIAR Consortium for Spatial Information. Available at: <https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2> (30 July 2004, date last accessed).
- Twohey RJ III, Roberts LM, Studer AJ (2019) Leaf stable carbon isotope composition reflects transpiration efficiency in *Zea mays*. *Plant J* 97:475–484.
- Ulrich DE, Still C, Brooks JR, Kim Y, Meinzer FC (2019) Investigating old-growth ponderosa pine physiology using tree-rings, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and a process-based model. *Ecology* 100:e02656.

- Van de Water PK, Leavitt SW, Betancourt JL (2002) Leaf $\delta^{13}\text{C}$ variability with elevation, slope aspect, and precipitation in the Southwest United States. *Oecologia* 132:332–343.
- Viets FG (1962) Fertilizers and the efficient use of water. *Advances in Agronomy*. 14:223–264.
- Vitousek P (1982) Nutrient cycling and nutrient use efficiency. *Am Nat* 119:553–572.
- Waraich EA, Ahmad R, Ashraf MY, Ullah S, Ahmad M (2011) Improving agricultural water-use efficiency by nutrient management in crop plants. *Acta Agric Scand B Soil Plant Sci* 61:291–304.
- Watmough SA, Dillon PJ (2003) Calcium losses from a forested catchment in south-Central Ontario, Canada. *Environ Sci Technol* 37:3085–3089.
- White PJ (2001) The pathways of calcium movement to the xylem. *J Exp Bot* 52:891–899.
- White PJ, Broadley MR (2003) Calcium in plants. *Ann Bot* 92:487–511.
- Wilkinson S, Bacon MA, Davies WJ (2007) Nitrate signalling to stomata and growing leaves: interactions with soil drying, ABA, and xylem sap pH in maize. *J Exp Bot* 58:1705–1716.
- Wright IJ, Reich PB, Westoby M (2003) Least-cost input mixtures of water and nitrogen for photosynthesis. *Am Nat* 161:98–111.
- Wu Q-X, Han L-C, Wang H-S (2000) Geographical distribution and division of suitability for aerosowing Chinese pine. *J Soil Water Conserv* 14:18–23.
- Yang L, Qu H, Zhang Y, Li F (2012) Effects of partial root-zone irrigation on physiology, fruit yield and quality and water-use efficiency of tomato under different calcium levels. *Agric Water Manag* 104:89–94.
- Yu F, Price KP, Ellis J, Shi P (2003) Response of seasonal vegetation development to climatic variations in eastern Central Asia. *Remote Sens Environ* 87:42–54.
- Zhang YB, Yang D, Zhang KY, Bai XL, Wang YSD, Wu HD, Ding LZ, Zhang YJ, Zhang JL (2021) Higher water and nutrient use efficiencies in savanna than in rainforest lianas result in no difference in photosynthesis. *Tree Physiol* 42:145–159.
- Zhang YJ, Meinzer FC, Hao GY et al. (2009) Size-dependent mortality in a Neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation. *Plant Cell Environ* 32:1456–1466.
- Zhang YJ, Meinzer FC, Qi JH, Goldstein G, Cao KF (2013) Midday stomatal conductance is more related to stem rather than leaf water status in subtropical deciduous and evergreen broadleaf trees. *Plant Cell Environ* 36:149–158.
- Zhang YJ, Sack L, Goldstein G, Cao KF (2018) Hydraulic determination of leaf nutrient concentrations in cycads. *Mem NY Bot Gard* 117:179–192.
- Zheng LL, Zhao Q, Sun QY, Liu L, Zeng DH (2020) Nitrogen addition elevated autumn phosphorus retranslocation of living needles but not resorption in a nutrient-poor *Pinus sylvestris* var. *Mongolica* plantation. *For Ecol Manage* 468:118174.
- Zhou YB, Zou XM (2017) From matching site with trees towards matching calcium with trees. *J Nanjing Forestry Univ* 41:1–8.