



The relationships between leaf economics and hydraulic traits of woody plants depend on water availability



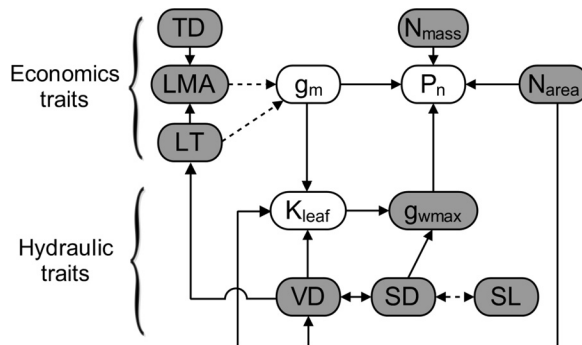
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HIGHLIGHTS

- Leaf economics and hydraulic traits were coupled on the Loess Plateau.
- The relationships between these two sets of traits depend on the changing conditions.
- Stomatal guard cell length may play a more important role than stomatal density in flexibility of plants.

GRAPHICAL ABSTRACT



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ABSTRACT

Leaf economics and hydraulic traits are simultaneously involved in the process of trading water for CO₂, but the relationships between these two suites of traits remain ambiguous. Recently, Li et al. (2015) reported that leaf economics and hydraulic traits were decoupled in five tropical-subtropical forests in China.

We tested the hypothesis that the relationships between economics and hydraulic traits may depend on water availability. We analysed five leaf economics traits, four hydraulic traits and anatomical structures of 47 woody species on the Loess Plateau with poor water availability and compared those data with Li et al. (2015) obtained in tropical-subtropical regions with adequate water.

The results showed that plants on the Loess Plateau tend to have higher leaf tissue density (TD), leaf nitrogen concentrations and venation density (VD) and lower stomatal guard cell length (SL) and maximum stomatal conductance to water vapour (g_{wmax}). VD showed positive correlations with leaf nitrogen concentrations, palisade tissue thickness (PT) and ratio of palisade tissue thickness to spongy tissue thickness (PT/ST). Principal component analysis (PCA) showed a result opposite from those of tropical-subtropical regions: leaf economics and hydraulic traits were coupled on the Loess Plateau.

A stable correlation between these two suites of traits may be more cost-effective on the Loess Plateau, where water availability is poor. The correlation of leaf economics and hydraulic traits may be a type of adaptation mechanism in arid conditions.

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1. Introduction

Leaves play an especially important role in carbon assimilation, water relations and energy balance (Ackerly et al., 2002). Studies of

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functional traits in leaves have greatly advanced our understanding of leaf function and plant performance (Sack et al., 2003; Reich, 2014; Blackman et al., 2016; Chai et al., 2015b). Among various leaf traits, those related to light capture and water and CO₂ exchange have received more attention, reflecting the crucial importance of these processes in the functioning of biosphere (Li et al., 2015). Leaf traits related to carbon economy are strongly correlated across and within biomes, such as leaf maximum photosynthetic capacity (A_{\max}), leaf dry mass per area (LMA) and leaf nitrogen concentrations, which form the leaf economics traits (Wright et al., 2004; Wright et al., 2005). Certain other groups of traits, such as venation traits and stomatal traits, are often found to be correlated across species, suggesting a balance between water demand and supply, and they form the hydraulic traits (Franks and Beerling, 2009; Zhang et al., 2012; Sack and Scoffoni, 2013; Li et al., 2015).

For land plants, the greatest biophysical barrier to carbon gain and ultimately survival is the ability of leaves to maintain high photosynthetic rate while avoiding desiccation (Simonin et al., 2012; Mitchell et al., 2013; Zwieniecki and Boyce, 2014). Water transport and CO₂ diffusion are two important processes that determine the CO₂ assimilation efficiency in leaves (Flexas et al., 2013). In fact, CO₂ uptake through stomata is inevitably coupled to water loss from photosynthetic tissue to the atmosphere (Hanson and Weltzin, 2000; Nardini and Luglio, 2014). Some studies have found coordinated relationships between leaf hydraulic and economics traits (e.g., Brodribb et al., 2005; Brodribb et al., 2007; Nardini et al., 2012; Villagra et al., 2013; Jin et al., 2016; Scoffoni et al., 2016; John et al., 2017). However, Li et al. (2015) reported that leaf economics and hydraulic traits were decoupled in five tropical-subtropical forests in China recently. To date, most of the studies about the relationships between leaf economics and hydraulic traits have been conducted in tropical and subtropical regions with adequate water. The relationship between these two sets of traits in arid regions remains unclear.

Since water is an important determinant in photosynthesis and hydraulic processes, the relationships between leaf economics and hydraulic traits might be stronger with poor water availability. We tested the hypothesis that relationships between economics and hydraulic traits depend on water availability. To test this hypothesis, we selected 47 woody angiosperms representing 38 genera and 18 families on the Loess Plateau, which is characterized by poor water availability. We then compared our results to Li et al. (2015) to detect the differences between tropical-subtropical regions and the Loess Plateau. To make a better comparison, all of the leaf economics and hydraulic traits conducted in this study were consistent with previous study in wet regions (Li et al., 2015), except for leaf stable carbon concentration. We analysed five common economics traits which suggest the carbon investments, including leaf dry mass per area (LMA), leaf thickness (LT), leaf tissue density (TD), leaf area-based N concentration (N_{area}) as well as leaf mass-based N concentration (N_{mass}). And we analysed four hydraulic traits which suggest the balance between water supply and demand, including venation density (VD), stomatal density (SD), stomatal guard cell length (SL), calculated maximum stomatal conductance to water vapour (g_{wmax}). All of the nine traits were measured according to Li et al. (2015), except that leaf stable carbon concentration was not measured in the present study. Since Li et al. (2015) guessed that the decouple of these two sets of traits may be a result of the physical separation of leaf structures but related analyses were lacking, we analysed the anatomical structures of leaves, including of palisade tissue thickness (PT), spongy tissue thickness (ST) and the ratio of PT to ST (PT/ST), through paraffin section method.

2. Materials and methods

2.1. Sites and sampling

The leaf specimens were collected from the Ziwuling Forest Region (35°09'N, 108°45'E) in the middle of the Loess Plateau, Shaanxi

Province, China. The climate is semiarid, temperate, continental monsoon, with a mean annual temperature of 9–11 °C (Chai et al., 2016a). The mean annual precipitation is approximately 560 mm (1539–2651 mm in Li et al., 2015) and mostly occurs in July, August and September. The soil type is cinnamon soil, which is rich in calcium (Liang et al., 2010). Further, the denuded lands have been abandoned to forest succession (Chai et al., 2016b). *Quercus wutaishanica* forest is the natural climax vegetation in this region (Wang et al., 2013).

Leaves were collected from 47 woody species belonging to 38 genera and 18 families. The species selected are common in the study area. For each species, at least 3–4 individuals were sampled and leaves were collected from the sun-exposed branches of each individual. After harvesting, 30–50 leaves of each species were preserved in plastic bags for analyses of economics traits and 8–10 leaves were preserved in a formalin-acetic-alcohol (FAA) solution for analyses of venation traits, stomatal traits and anatomical structures.

2.2. Economics traits

A picture of each fresh leaf surface was taken with a digital camera, and leaf surface area (LA, cm²) was measured with Motic Images Plus 2.0 (Motic China, Xiamen) software. All leaves were then placed in a drying oven for 72 h at 70 °C to determine the dry mass. Leaf dry mass per area (LMA, g m⁻²) was calculated as the ratio of dry mass to LA. Leaf thickness (LT, mm) was measured through transverse sections using Image-Pro Plus 6.0, avoiding the influence of major veins. For each section, 10–20 measurements were made. Leaf tissue density (TD, g cm⁻³) was calculated as the ratio of LMA to LT. Leaf nitrogen content were determined on a subsample of dried leaf material from each species. Leaves were ground into a fine powder, stored under desiccation, and leaf nitrogen concentrations per unit leaf mass (N_{mass} , mg g⁻¹) were determined using an elemental analyser (Euro Vector EA3000, Milan, Italy). Nitrogen per unit leaf area (N_{area} , g m⁻²) was obtained by a product of N_{mass} and LMA.

2.3. Hydraulic traits

The nail-polish imprint method was used to examine stomatal traits (Zhao et al., 2016). Clear nail polish was applied onto the middle of the abaxial leaf surface, allowed to dry, and then pulled off the leaf by using Sellotape and mounted onto a glass slide. We photographed the stomatal prints under a Classica SK200 Digital light microscope (Motic China Group Co., Ltd., China) at 200–400× magnification. SL (μm) was measured using Image-Pro Plus 6.0 (Media Cybernetics, USA) software. SD (mm⁻²) was calculated as the number of stomata per unit epidermal area by dividing leaves into grids of 100 × 100 μm. SL and SD were averaged from more than 20 randomly selected fields of view. g_{wmax} (mol m⁻² s⁻¹) was calculated according to the following equation: $g_{\text{wmax}} = d\alpha LD / (v(0.5 + 0.627\sqrt{\alpha}))$; d is the diffusivity of water in air (m² s⁻¹), L is the stomatal guard cell length (μm), D is stomata density (mm⁻²), and v is the molar volume of air (m³ mol⁻¹). A mid-range value of 0.12 for α was used for the demonstrations here (Franks et al., 2009).

After removing the nail-polish, a sample of approximately 1 cm² was excised from the leaf and then placed in 10% sodium hydroxide aqueous solution for several hours to several days, until the minor veins were exposed. Each sample was then soaked in distilled water and then stained in 1% toluidine blue for 30–60 s. The samples were then mounted onto glass slides and photographed. VD (m mm⁻²) was calculated as the total length of leaf veins per leaf area using Image-Pro Plus 6.0 by manually dividing leaves into grids of 100 × 100 μm by drawing. VD was averaged from more than 20 randomly selected fields of view.

2.4. Anatomical structures

The middle portions of leaves were excised, dehydrated in an ethanol series and then embedded in paraffin for sectioning. The transverse

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