

Research Article

Divergent leaf–root coordination between mangroves and non-mangroves

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Abstract

Interactions among roots and leaves are fundamental for plant growth and survival, yet there remains a knowledge gap in mangrove plants that experience saline stress distinct from most other vascular plants hereafter the non-mangroves. Here, we explored the coordination of above- and below-ground trait relationships among mangrove species in tropical China and compared it with those of non-mangroves. Our results show that root stele, the water-conducting tissue, was coupled with leaf water use traits and tissues outside the stele (ToS), the carbon-consuming tissues in roots, were independent of leaf economics traits in non-mangroves. However, in mangroves, root stele is independent of leaf water use traits and root ToS is coupled with leaf economics traits. The contrasting root–leaf coordination between mangroves and non-mangroves potentially arises from the existence of leaf water storage tissues in mangroves and the universal allometric relationship between root stele and ToS in both plant groups. Our findings pave a new way for understanding the ecology and vegetation dynamics of mangrove and non-mangrove plants under global environmental change.

Keywords: leaf water use traits, leaf economics traits, root traits, leaf water storage tissues, allometry, mangrove and non-mangrove plants

红树与非红树植物在根–叶关系上的趋异格局

摘要：根与叶性状之间的协调关系对植物的生长和存活至关重要，但与大多数非红树维管植物不同，盐胁迫环境下红树植物的根–叶协调机制仍不明确。本研究中，我们对比了中国热带红树植物与非红树维管植物的地上–地下性状关系。结果表明，在非红树植物中，作为根部输水组织的中柱，其大小与叶片

水分利用性状紧密耦合，而根的碳消耗组织(中柱外组织)的厚度则与叶经济学性状无显著关联。与之相反，红树植物根中柱的大小独立于叶片水分利用性状，而根中柱外组织的厚度与叶片经济学性状显著耦合。这种趋异格局可能源于红树植物普遍存在的叶片储水组织，以及两类植物根中柱与中柱外组织之间普遍存在的异速生长关系。上述研究结果为理解全球环境变化下红树和非红树植物的环境适应性策略及植被动态提供了全新视角。

关键词：水分利用性状，叶经济学性状，根性状，叶储水组织，异速生长关系，红树与非红树植物

INTRODUCTION

Coordination between roots and leaves is fundamental for plant growth and survival (Carmona *et al.* 2021; Korner 1991; Luo *et al.* 2023). From the view of material exchange, plant roots absorb water and nutrients and transport them upward to support leaf photosynthesis; meanwhile, leaf photosynthate is transported downward to meet the energy demand in root nutrient uptake. Exploration of how and why plants under contrasting habitats differ in the root–leaf coordination offers critical insights into the formation of plant strategies and responses to global change factors (Laughlin *et al.* 2010; Lu *et al.* 2022; Valverde-Barrantes *et al.* 2020; Weemstra *et al.* 2022; Zhao *et al.* 2024).

Distinct from most terrestrial plants, hereafter the non-mangrove plants, mangrove plants inhabit tropical seashores have evolved multiple strategies to tolerate high salinity-derived osmotic stress (Agduma *et al.* 2022; Huang and Huang 1989; Madhavan *et al.* 2024). For instance, many mangroves have evolved to have abundant water-storing tissues, such as hypodermis, sponge tissue and trichome layers, and phenol content in leaves (Chapman 1976; Nguyen *et al.* 2017a; Rashid *et al.* 2020; Si *et al.* 2017). These tissues can effectively store water from sources other than soil water like rainfall, fog and dew (Agduma *et al.* 2022; Lechthaler *et al.* 2016; Reef and Lovelock 2015), as such, substantially alleviating the effect of osmotic stress on leaf photosynthesis (Nguyen *et al.* 2017a, 2017b; Reef and Lovelock 2015). However, it remains unclear whether the specialized water storage tissues in mangrove leaves cause a different root–leaf relationship from that in non-mangroves that generally lack these tissues.

Global efforts over decades have identified two leading and orthogonal leaf trait spectra, i.e. leaf economics spectrum and leaf water use spectrum (Blackman 2016; Haynes 2021; Li *et al.* 2015; Mediavilla *et al.* 2020; Sack *et al.* 2013; Zhang *et al.*

2012). Leaf economics spectrum runs from quick to slow return, i.e. the production of photosynthate on investments of nutrients and dry mass in leaves (Haynes 2021; Reich 2014; Wright *et al.* 2004). The ‘fast’ species in this spectrum usually have high photosynthetic capacity, short lifespan, low leaf dry mass per area (LMA) and high leaf nitrogen concentration (N_{mass}), while the ‘slow’ species have the opposite trait syndromes, e.g. low photosynthetic capacity, long lifespan, high LMA and low N_{mass} . On the other hand, the leaf water use spectrum reflects an efficiency–safety tradeoff in water transport between the mesophyll and the vascular tissue in leaves. Species on the ‘efficiency’ end of the spectrum have leaves with wide veins and low vein density (vein length per leaf area) whereas the ‘safety’ end is characterized by thin veins (low risk of hydraulic failure) and high vein density (Baird *et al.* 2021; Feild and Brodrigg 2013; Mediavilla *et al.* 2021).

The functioning of plant roots depends on two key anatomical structures: the stele consisting mostly of vascular tissues, xylem for water-conducting and phloem for photosynthate-conducting, and the surrounding tissues outside the stele (ToS, including epidermis, exodermis and cortex), consuming photosynthetic carbon (C) from the stele (Han and Zhu 2021; Kong *et al.* 2021). Therefore, studies incorporating root anatomical structures are critical for our understanding of the functional coordination between roots and leaves. For example, for non-mangrove trees, there is a correlation between root and leaf water use traits, e.g. thicker root stele are associated with wider leaf veins (Feild and Brodrigg 2013; Kong *et al.* 2019; Valverde-Barrantes *et al.* 2020). Likewise, we can expect independence of root ToS (C-consuming tissue) and leaf economics traits (indicating carbon production (Wright *et al.* 2004)) (Hypothesis 1) given the common independence of leaf economics and water use traits in non-mangroves (Li *et al.* 2015; Sack *et al.* 2013). If so, it is intriguing to explore why roots and leaves are

decoupled in terms of C consumption (roots) and C production (leaves) since both organs lie separately in the ends of the continuous photosynthate-conducting vascular system in plants.

In contrast to non-mangrove plants, we expect different root–leaf relationships in mangrove plants. Specifically, we predict a decoupling of root stele (water-conducting tissue) from leaf water use traits in mangroves (Hypothesis 2) because water storage tissues in mangrove leaves with prominent external water sources can relieve the selection pressure to drive leaf vein variation by the water-conducting tissue in roots, i.e. the stele (Agduma *et al.* 2022). If Hypothesis 2 is validated, we also predict a coupling of root ToS (C-consuming tissue) with leaf economics traits (Hypothesis 3) given the observed decoupling of leaf economics and water use traits in mangroves (Agduma *et al.* 2022).

Here, by considering root anatomical structures and dual functions of roots in water (and nutrients) transport and C consumption, we aim to test the above three hypotheses regarding the root–leaf relationships between non-mangroves and mangroves. To fulfill this purpose, we construct two plant trait datasets: one is on non-mangrove plants including absorptive root anatomical structures, leaf economics traits and leaf water use traits, aiming to test Hypothesis 1; the other is on mangrove plants with the above traits as well as the size of leaf water storage tissues, aiming to test Hypothesis 2 and Hypothesis 3.

MATERIALS AND METHODS

Non-mangrove plants: data collection

We collected studies on non-mangrove plants with all the trait data accessible for the leaf economics, leaf water use and root anatomical traits including root diameter, stele radius, ToS thickness and the stele to root diameter ratio. Leaf economics traits were selected following a classical paper by Li *et al.* (2015) including LMA, specific leaf area (SLA, leaf area per leaf dry mass), N_{mass} , leaf thickness (LTh), leaf tissue density (LTD), and leaf carbon isotope composition ($\delta^{13}\text{C}$) that indicates the long-term water use efficiency (Li *et al.* 2015). Leaf water use traits refer to the minor vein diameter and density that are closely related to the efficiency and safety of water transport, respectively, in leaves (Cao *et al.* 2022; Feild and Brodribb 2013). While vein diameter was seldom measured in previous studies compared with the widely used vein density. To compensate for

the paucity of data on vein diameter, we considered adding literature with measured vein density and stomatal traits (size and density). This is because of an evolutionary balance between leaf water demand (represented by stomata traits) and leaf water supply (represented by vein traits) in non-mangrove plants including mangroves (Brodribb and Jordan 2011; Brodribb *et al.* 2013; Carins Murphy *et al.* 2014; Pan *et al.* 2022; Tian *et al.* 2016; Wen *et al.* 2020). As for roots, we concentrated only on the first-order roots, the main root segment of a root branch responsible for resource absorption (water and nutrients) and compared it to the resource absorption (CO_2) organ aboveground, the leaves (Guo *et al.* 2008). In total, 78 non-mangrove species were collected and used for later analyses (Supplementary Table S1).

Mangrove plants: sampling

There are few studies on mangrove plants with all the above leaf and root traits available. Here, we collected leaves and roots of 17 typical mangrove species (see Supplementary Table S2 for details) growing in the intertidal zones of the seashore of the Dongzhai Harbor National Natural Reserve (19°51′–20°01′ N, 110°30′–110°37′ E), Hainan Island, China in May 2015. This reserve harbors the most representative and pristine natural mangroves in China (Xiong *et al.* 2016). The area has a tropical monsoon climate. The mean annual temperature is 23.5 °C, with the highest mean monthly temperature, 28.4 °C, in July and the lowest, 17.1 °C, in January. The annual precipitation is 1676 mm, and more than 80% is concentrated between May and October.

Five mature individuals were selected for each species. We selected 15–20 mature and intact canopy leaves for each species, and three to five intact root branches including three most terminal root branch orders responsible for water and nutrient absorption were also collected for this species (Guo *et al.* 2008; Pregitzer *et al.* 2002). All the root branches and three to five leaves were immediately placed in FAA fixation solution (90 mL 70% alcohol, 5 mL 100% acetic acid, and 5 mL 37% methanol) for root and leaf anatomy measurements. For each species, five to six leaves were placed in NaOH solution to determine the leaf's minor vein diameter and density. The remaining leaf samples were used to examine and measure leaf morphological and chemical traits. All the leaf samples except those in the FAA solution were sealed in a plastic bag before putting them into an ice-containing incubator, and then immediately taken into the lab for leaf trait measurements.

Mangrove plants: trait measurements

We first determined *leaf thickness* for each species using fresh leaves by a digital caliper (Masterproof, E.H.G Lucas GmbH, Germany). The leaves were then scanned before the individual leaf area was calculated using IMAGE J software (NIH Image, Bethesda, MD, USA). The leaves were oven-dried at 60 °C for 48 h and then weighed to determine *specific leaf area* (leaf area per unit leaf dry mass, SLA), *leaf dry mass per area* (LMA), and *leaf tissue density* (LTD). *Leaf mass-based nitrogen concentration* (N_{mass}) and *leaf C isotope composition* ($\delta^{13}\text{C}$) were measured using an elemental analyzer interfaced with isotope ratio mass spectrometry (EA1112 coupled with Delta-XP, Thermo Fisher Scientific, Bremen, Germany). The above leaf morphological and chemical traits are usually considered leaf economics traits (closely related to leaf photosynthesis). Leaf *total phenol content*, an indicator of leaf defense function, usually shows a trade-off with leaf photosynthesis (Eallonardo Jr *et al.* 2013). Therefore, we considered *total phenol content* (Tphol) as a leaf economics trait, which was measured by referring to the method in a classical study (Hättenschwiler and Jørgensen 2010).

Because mangrove leaves are usually thick and cuticle-rich for resistance to alkali decay, we first removed the epidermis and upper layers of the mesophyll to expose the leaf minor veins using a sharp knife or needle. The leaves were then dipped into a 5%–7% NaOH solution for hours to expose the leaf minor veins. The leaf veins were stained red and photographed using a camera (Eclipse Ni-U; Nikon). For each species, 5–6 leaves and at least six fields of view per leaf were selected between the midrib and the margin to calculate *leaf minor vein diameter* (LV_{dia} , μm) and *density* (LV_{den} , mm mm^{-2}) using IMAGE J (NIH Image, Bethesda, MD, USA) (Li *et al.* 2015). The LV_{dia} was calculated by dividing LV_{den} by vein surface area per leaf area (SA_v) (Feild and Brodribb 2013). SA_v is calculated according to the area for a field of view and the length of the minor veins in the field of view.

Leaf and root anatomical structures were determined using a common method for paraffin sectioning. Briefly, for each species, three to five leaves and 15–20 first-order roots, were taken from the FAA solutions and were then processed in a suite of procedures, including dehydration, embedding in paraffin, cutting into sections (8 μm thickness), staining and then photographing using a compound microscope (Leica DM2700 M, Germany) (Cao *et al.* 2022; Kong *et al.* 2014). For leaves, only

the cross-sectional area between the midrib and the margin was photographed. First-order root and leaf anatomical structures were determined using IMAGE J software (NIH Image, Bethesda, MD, USA). Specifically, we measured *root diameter* (Diam), *root stele diameter* (Stele), and *thickness of root tissues outside the stele* (ToS, including epidermis, exodermis, and cortex), as these traits are closely related to water and nutrient absorption and transportation (Freschet *et al.* 2021; Valverde-Barrantes *et al.* 2020). The *stete to root diameter ratio* (Stele: Diam), a key trait for root traits, was also calculated (Kong *et al.* 2014).

Leaf water storage tissues have been widely observed in mangrove leaves including the hypodermis, sponge tissue and trichome layer (Chapman 1976; Huang and Huang 1989). The palisade tissue in mangrove leaves was not considered as water storage tissues (Nguyen *et al.* 2017a; Rashid *et al.* 2020) because cells in this tissue are densely compacted without swelling for water storage. The size of *leaf water storage tissues* of a species was calculated based on leaf anatomy photos of at least three leaves from different individuals. Specifically, we defined the *relative size of leaf water storage tissues* ($LWST_{\text{rs}}$) as the proportion of leaf cross-sectional area accounted by the sum of the cross-sectional areas of the hypodermis, sponge tissue and trichome layer (Nguyen *et al.* 2017a, 2017b). As the *water storage tissues* distribute evenly along the leaf lamina, $LWST_{\text{rs}}$ can be regarded as the proportion of *leaf thickness* (LTh) accounted by the *leaf water storage tissues*. Then, we calculated the absolute value of the *leaf thickness* accounted by the *leaf water storage tissues* ($LWST_{\text{as}}$) as follows: $LWST_{\text{as}} = LWST_{\text{rs}} \times LTh$. In this study, the size of *leaf water storage tissues* was an important trait, seemingly linked with both leaf economic traits and leaf water use traits. To determine which trait spectra *leaf water storage tissues* belongs to, we first separately examined the correlations of *leaf water storage tissues* ($LWST_{\text{as}}$ and $LWST_{\text{rs}}$) with leaf economics and leaf water use traits. Then, the results of *leaf water storage tissues*-based pairwise correlations were further validated using a trait permutation analysis developed in a previous study (Li *et al.* 2015) (see Data analyses section for details). All the traits and abbreviations are listed in Table 1 and Supplementary Tables S3 and S4.

Phylogenetic tree construction

For the non-mangrove plants with a large species pool (Supplementary Table S1), the phylogenetic tree was constructed based on the DNA sequences of the Rubisco large subunit (*rbcL*) and the maturase K

Table 1: Leaf and root traits used in this study

Plant traits	Abbreviations
Leaf thickness	LTh
Leaf dry mass per area	LMA
Leaf mass-based nitrogen concentration	N _{mass}
Leaf carbon isotope composition	δ ¹³ C
Specific leaf area	SLA
Leaf minor vein density	LV _{den}
Leaf minor vein diameter	LV _{dia}
Stomatal guard cell length	SL
Stomatal density	SD
Maximum stomatal conductance to water vapor	g _{wmax}
total phenol content	Tphol
Proportion of leaf cross-sectional area accounted by leaf water storage tissues	LWST _{rs}
Absolute value of the leaf thickness accounted by the leaf water storage tissues	LWST _{as}
Root diameter	Diam
Thickness of root tissues outside the stele	ToS
Root stele diameter	Stele
Stele to root diameter ratio	Stele:Diam

(*matK*) which were available from previous studies (Kong *et al.* 2014; Li *et al.* 2015). Both the phylogenetic trees for the non-mangrove (Supplementary Fig. S1) and mangrove plants (Supplementary Fig. S2) were separately constructed using the R package “V. PhyloMaker” (Jin and Qian 2019; 2022) with the backbone topology of the phylogenetic tree derived from (Zanne *et al.* 2014). Plant names in the phylogenetic tree were referenced against The Plant List (<http://www.theplantlist.org/tpl/search>).

Data analyses.

We calculated the mean, minimum, maximum, standard error and coefficient of variation (CV) of each root and leaf trait. We calculated the

phylogenetic signal by employing Blomberg’s *K* test, assuming a Brownian evolution model (Li *et al.* 2015). A larger *K* value for a trait indicates more phylogenetic conservatism (i.e. more influence of the trait by a common ancestor than by environments) (Blomberg *et al.* 2003). All the original data of non-mangrove plants and partial data of mangrove plants that did not confirm to a normal distribution, were log-transformed, such as *root diameter*, *root stele diameter*, *thickness of root tissues outside the stele*, *leaf minor vein diameter and density*, *specific leaf area*, and *leaf mass-based nitrogen concentration*. Pairwise trait relationships were assessed using Pearson’s correlation. We also explored trait relationships using phylogenetic generalized least square (PGLS), which exclude the influence of a common ancestor on trait relationships. This analysis is performed using the “*pgls*” function in the “*caper*” package.

To explore the relationships between leaf water use and economics in leaves, and the relationships between root anatomical traits and leaf water use and economics, we used a multivariate ordination method developed in a previous study (Li *et al.* 2015). All the data were standardized, and three separate PCAs were conducted using three different trait groups (i.e. leaf economics, leaf water use, and root traits) (Fig. 2a, b). Subsequently, we created a sampling distribution using the scores of 10 000 permutations of the first principal component axis (PC1) of each PCA. Each PC1 accounted for over 50% of the total trait variation in each of the above PCA (data unshown). Finally, the relationships among leaf economics, leaf water use and root traits were assessed based on the permutation results.

We also explored the relationship between root anatomical structures given its instructiveness for our understanding of the coordination between roots and leaves. Specifically, we first determined whether there were linear relationships of the stele radius and the thickness of the *tissues outside the stele* (ToS) with root diameter. If the linear relationships are confirmed, the difference between the two slopes of the above two linear relationships will be tested using standardized major axis (SMA) (Kong *et al.* 2019) in R package ‘*smatr*’. All the analyses were performed using R software (v.4.3.2) (Revell 2024).

Compared with non-mangrove plants, only three additional leaf economics traits were included in the mangrove plants: the size of *leaf water storage tissues* (LWST_{as} and LWST_{rs}), and *total phenol content* (Tphol). The trait relationships within leaves and between leaves and roots were almost the same even after

removing the above three additional leaf economics traits in mangroves (Supplementary Figs S10 and S11). This suggests that it is feasible to compare mangrove and non-mangrove plants. Further, the relationship between root diameter and leaf economics traits for the non-mangrove plants of our study (see the Result section) was similar to those using over 1000 species (Vleminckx *et al.* 2021) even on a global scale (Weigelt *et al.* 2021).

RESULTS

Leaf traits variation

For non-mangrove leaves, the first two principal components (PC) of the principal component analysis (PCA) accounted for 63.68% of the total leaf trait variation. PC1, accounting for 38.40% of the variance, was mainly represented by leaf economics traits; PC2, accounting for 25.28% of the variance, was mainly represented by leaf water use traits (Fig 1a; Supplementary Table S5). Of the leaf economics traits, *leaf dry mass per area* was negatively correlated with *leaf mass-based nitrogen concentration* ($P < 0.001$) and positively correlated with *leaf thickness* ($P < 0.001$); of the leaf water use traits, *leaf minor vein density* was negatively correlated with *stomatal guard cell length* ($P < 0.001$) (Supplementary Table S6; Fig 1a). The permutation analysis showed independence of leaf economics and leaf water use traits in the non-mangroves ($P = 0.073$, Supplementary Figs S5a and S6).

For the mangrove leaves, the first two PC of the PCA accounted for 77.11% of the total leaf trait variation. Permutation analysis showed a strong coupling of the size of the *leaf water storage tissues* (LWST_{as} and LWST_{rs}) only with the leaf economics (both P values < 0.001 , Supplementary Fig. S7a, c) as well as a decoupling between leaf economics and leaf water use (Supplementary Figs S8a and S9). PC1 accounted for 59.18% of the variance and was mainly represented by leaf economics traits; PC2 accounted for 17.94% of the variance and was mainly represented by leaf water use traits (Fig 1b; Supplementary Table S7). Of the leaf economics traits, both LWST_{as} and LWST_{rs} were positively correlated with *leaf thickness* and *leaf dry mass per area*, and negatively correlated with *leaf mass-based nitrogen concentration* (P values < 0.001 , Supplementary Table S8 and Fig. S5b). For leaf water use traits, *leaf minor vein density* was negatively correlated with *leaf minor vein diameter* ($P < 0.001$, Supplementary Table S8; Fig 1b).

Leaf-root traits coordination

When the leaf and root traits were pooled in non-mangrove plants, the first two PC of the PCA accounted for 54.58% of the total trait variation. PC1 accounted for 35.03% of the variance and was mainly represented by leaf water use and root traits; PC2 accounted for 19.56% of the variance and was mainly represented by leaf economics traits (Fig. 2a; Supplementary Table S9). Permutation analyses showed that root traits were decoupled from leaf economics ($P = 0.088$, Supplementary Fig. S5b) but coupled with leaf water use traits ($P = 0.012$, Supplementary Fig. S5c) in the non-mangroves.

For mangrove leaf and root traits pooled together, the first two PC of the PCA accounted for 69.52% of the total trait variation. PC1, accounting for 55.19% of the variance, was mainly represented by leaf economics and root anatomical traits; PC2, accounting for 14.32% of the variance, was mainly represented by leaf water use traits (Fig 2b; Supplementary Table S10). Permutation analyses showed that root traits were coupled with leaf economics ($P = 0.001$, Supplementary Fig. S8b) and the size of *leaf water storage tissue* (LWST_{as} and LWST_{rs}) ($P = 0.005$, Supplementary Fig. S10a; $P = 0.003$, Supplementary Fig. S10b) and were decoupled from leaf water use ($P = 0.085$, Supplementary Fig. S8c) in mangroves.

In non-mangrove plants, the phylogeny had significant effects on root traits (Supplementary Table S3), and there were significant relationships of root traits with leaf economics traits using phylogenetic generalized least square (PGLS) ((Supplementary Table S6 and Fig. S11a). Overall, mangroves traits showed little phylogenetic conservatism (Supplementary Table S4), and the root-leaf trait relationships using PGLS were similar to those using the original trait data (Supplementary Table S8 and Fig. S5b).

Allometry in root structures

Both the non-mangrove and mangrove species (Fig. 3) followed an allometric relationship between root structures: the slope for the regression of the thickness of *root tissues outside the stele* with root diameter was larger than the slope for the regression of the stele radius with root diameter (0.43 vs. 0.076, $P < 0.001$ for non-mangroves; 0.40 vs. 0.097, $P < 0.001$ for mangroves).

DISCUSSION

Although studies have frequently reported coordination of root diameter with leaf economics and hydraulics traits (Carmona *et al.* 2021; Ding *et*

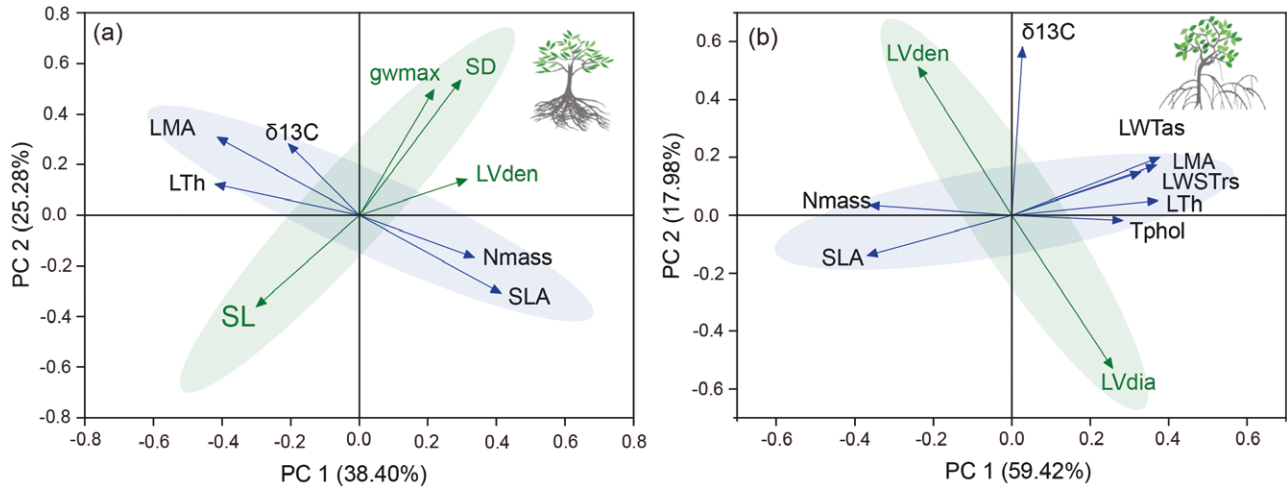


Figure 1: Decoupling of leaf economics and hydraulics traits for non-mangrove and mangrove species. (a) In 78 non-mangrove species, leaf economics traits (e.g. LMA, Nmass) do not align with leaf water use traits (e.g. SD, SL), suggested by the largely orthogonal alignment between the two groups of traits. (b) In 17 mangrove species, leaf economics traits are also decoupled from leaf water use traits. Trait abbreviations: LTh, leaf thickness; LMA, leaf dry mass per area; Nmass, leaf mass-based nitrogen concentration; $\delta^{13}\text{C}$, leaf carbon isotope composition; SLA, specific leaf area; Tphol, total phenol content; LWSTrs, the proportion of leaf cross-sectional area accounted by leaf water storage tissues; LWSTas, the absolute value of the leaf thickness accounted by the leaf water storage tissues, measured by LWSTrs \times LTh; LVdia, leaf minor vein diameter; LVden, leaf minor vein density; SL, stomatal guard cell length; SD, stomatal density; gwmax, maximum stomatal conductance to water vapor.

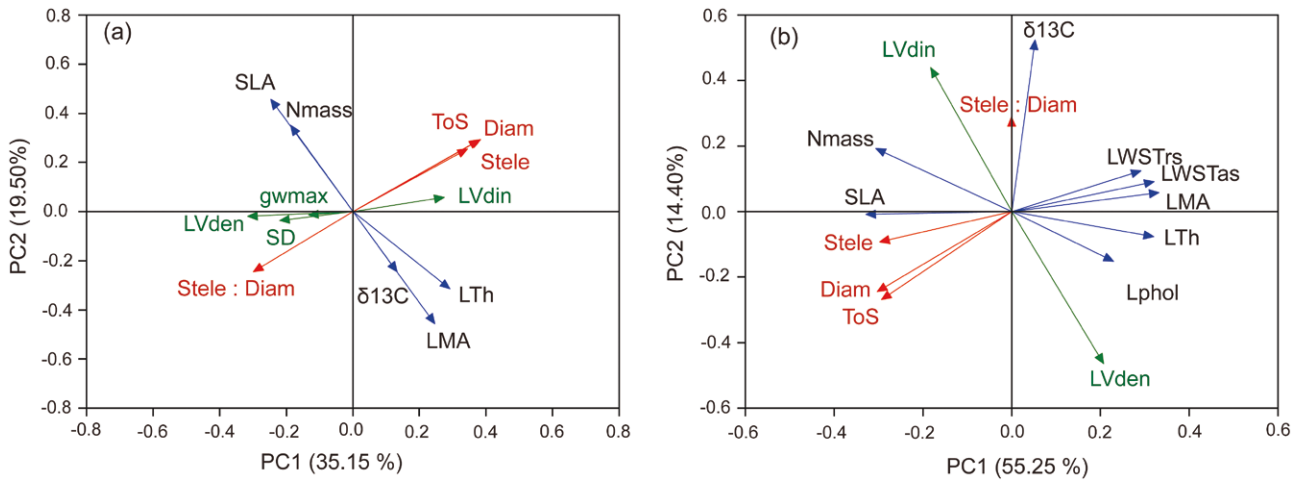


Figure 2: Coordination of leaf and root traits for non-mangrove and mangrove species. (a) In non-mangrove species, root traits (e.g. ToS, Stele:Diam) appear orthogonal to leaf economics traits (in blue) and coupled with leaf water use traits (e.g. SLA, LTh). (b) In contrast with non-mangrove plants, root traits of mangrove species align with majority of leaf economics traits and largely orthogonal to leaf water use traits. Abbreviations for leaf traits are the same as Figure 1. Abbreviations for root traits: Diam, root diameter; ToS, thickness of root tissues outside the stele; Stele, root stele diameter; Stele: Diam, stele to root diameter ratio.

al. 2023; Wang and Huang 2024; Weigelt et al. 2021, 2023), few have explored how and why the root-leaf relationships in non-mangrove plants differ from that in mangrove plants. By introducing the dual functions of roots in water-conducting (via stele) and carbon-consuming (via tissues outside the stele, i.e. ToS), we demonstrate contrasting root-leaf relationships between non-mangroves

and mangroves. For non-mangrove plants, the stele radius is coupled with leaf water use traits and ToS thickness is independent of leaf economics traits that indicate leaf carbon (C) production (supporting Hypothesis 1), whereas in mangroves root stele radius is independent of leaf water use traits (supporting Hypothesis 2) and ToS thickness is coupled with leaf economics traits (supporting Hypothesis 3). Here,

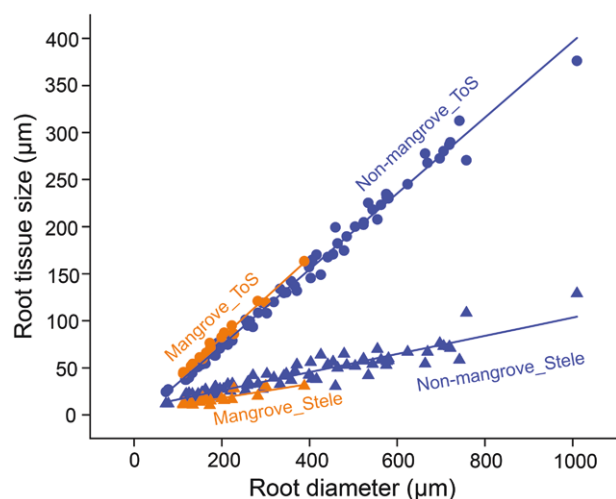


Figure 3: Allometric relationships between root stele radius (triangles) and the thickness of root tissues outside the stele (circles) with increasing root diameter in non-mangrove and mangrove species. Abbreviations: ToS, thickness of root tissues outside the stele; Diam, root diameter.

we aim to uncover how the contrasting root–leaf relationships emerge with the example of plants growing in wet environment.

Decoupled root–leaf relationship in non-mangroves regarding root water use

Compared with plants in dry environments, plants in wet conditions are generally taller by producing thicker absorptive roots with thicker steles for more efficient transport of water and nutrients to leaves, which can result in a better competition for light harvest in the canopy (Chen *et al.* 2013; Fan *et al.* 2012; Joswig *et al.* 2022; Preston *et al.* 2006; Wahl and Ryser 2000). Producing *fast* leaves (i.e. low LMA, high N_{mass}) in wet conditions can confer the plants with *fast* growth by the high photosynthetic capacity of these leaves. However, what is often ignored is that the *fast* leaves are susceptible to damage from high wind, pests and diseases in the canopy (Grime 1974; Reich 2014), which precludes the monopolization of the canopy by the *fast*-leafed species. While, the *slow*-leaf species (i.e. high LMA and low N_{mass}) survive better under these environmental stresses in the canopy. Therefore, the *fast*- and the *slow*-leafed species can both coexist in the canopy with a similar water transport system in adaptation to diverse selective pressures of the wet environment (water *vs.* wind, pests or diseases); this could eventually lead to the independence of the leaf water use traits from the leaf economic traits.

Decoupled root–leaf relationship in non-mangroves regarding root carbon consumption

As mentioned above, *fast*-leafed non-mangrove plants in wet environments could provide more photosynthate and hence afford the high C demand for building a thicker root ToS with more metabolically active cells (Kong *et al.* 2021; Lu *et al.* 2022) whereas *slow*-leafed plants with less photosynthate production might produce thin root ToS with low C cost. If so, root ToS thickness is expected to be coupled with the leaf economic traits like LMA and N_{mass} that indicates C production. However, our results show decoupling rather than coupling of such root–leaf relationship in non-mangroves. Notably, we find an allometric relationship in absorptive roots here as well as in many other studies (Kong *et al.* 2019; Zhang *et al.* 2023), i.e. the ToS thickness increased much faster than the stele radius with increasing root diameter (Fig. 3a). Importantly, such root anatomical allometry persists irrespective of species in the *fast* or *slow* end of the leaf economics spectrum (Fig. 2). That is to say, in wet environment, whether plant species are *fast*-leafed or *slow*-leafed, they tend to produce thick absorptive roots with thick ToS in this environment. Therefore, contradictory to our above expectation, C supply from non-mangrove leaves could not be the driving force to shape thick root ToS in wet conditions.

Compared with *fast*-leafed species that could provide roots more C to form thick ToS, it is puzzling to see that *slow*-leafed species also tend to have thick root ToS. One possible reason is that thick ToS of the *slow*-leafed species in wet environment is formed to be associated with high mycorrhizal colonization and hence high nutrient absorption via mycotrophy. Such mycotrophy through thick ToS has been regarded to match with the high nutrient transport capacity as conferred by thick root stele in wet environment (Kong *et al.* 2021, 2017). It is well-known that such nutrient-related functional balance (i.e. nutrient absorption *vs.* transportation) underlies the formation of root anatomical allometry in both the *fast*-leafed or *slow*-leafed species (Kong *et al.* 2017). Therefore, the independence of root ToS thickness from leaf economic traits could be used for the aforementioned nutrient balance rather than the balance between C supply (via leaf photosynthesis) and C consumption (via root construction and maintenance). In other words, this root and leaf independence could be dominated by nutrient—rather than C-related process.

Furthermore, after removing the influence of plant phylogeny, the above root–leaf relationship also holds. From an evolutionary perspective, the mesophyll (corresponding to the leaf economics traits) appeared a long time after the landing of early plants over 400 million years ago (Beerling 2005; Beerling *et al.* 2001); this suggests a coupling of the roots with the aboveground non-mesophyll shoot branches (similar to the leaf veins) at that time. Therefore, the independence of root ToS thickness and leaf economics traits could also be an evolutionary imprint of the independent appearance of leaf veins and mesophyll (Li *et al.* 2015).

Decoupled roots from leaf water use traits in mangroves

Our results revealed for the first time the independence of root stele radius and leaves in water use traits in mangrove plants. This independence could be related to *leaf water storage tissues* in mangroves. Generally, mangrove plants have thick leaves with high LMA in sites with high soil salinity (John *et al.* 2017; Poorter *et al.* 2009). Our results showed that *leaf water storage tissues* (LWST_{as} and LWST_{ts}) were larger in mangroves bearing thicker leaves with higher LMA (Fig. 1b); this is why the size of *leaf water storage tissues*, although storing water, is coupled with the leaf economic traits (Fig. 4). Such coupling could increase the adaptation of the mangroves to the high salinity conditions. Moreover, *leaf water storage tissues* in mangroves could also contribute to the independence of leaf veins from root stele, the water-conducting tissue. This is because the larger selection pressure on leaf vein traits by less root water supply under higher soil salinity, the larger extent of the selection could be counteracted by the construction of leaves with larger water storage tissues in this condition (Fig. 2b).

Coupled roots with leaf economics traits in mangroves

Different from non-mangrove plants, mangrove plants with thicker absorptive roots in conditions sufficient water availability (i.e. low salinity) tend to form *fast* leaves (thin LTh, low LMA) (Fig. 2b), rather than forming both *fast* and *slow* leaves as aforementioned for non-mangroves in wet environment (Fig. 2a). The paucity of *slow*-leafed mangroves (thick LTh, high LMA) in low salinity with sufficient water availability could be due to the fact that mangroves do not need to build thick leaves to store water in this condition (Fig. 1b). Furthermore, mangrove plants, even the *fast*-leafed mangroves in habitats

with low salinity, usually have thicker leaves with higher LMA than non-mangrove plants (Aritsara *et al.* 2022; Poorter *et al.* 2009). This could contribute to the dominance of *fast*-leafed mangroves facing frequent environmental disturbances (e.g. wind, pests or diseases) in conditions with sufficient water (low salinity). Consequently, we could speculate that the dominant *fast*-leafed mangroves in low salinity could afford the high C cost of producing thick root ToS, and hence leading to the coupling of root ToS thickness with leaf economics traits.

Nevertheless, we also note that leaf water use traits are decoupled from both leaf economics and root traits (Fig. 2). Besides being as the water conducting agent, leaf veins also function as transporting photosynthate belowground to roots. This suggests that *fast*-leafed mangroves in low salinity could be accompanied with leaf veins either with high or low C transport capacity (Fig. 2b). Under the limitation of low C transport capacity via leaf veins, the *fast*-leafed mangroves even with high C production in low salinity might not build thick root ToS with high C cost. Notably, root anatomical allometry is also observed in the mangroves (Fig. 3b); and this suggests that thick root ToS must be produced in the low salinity condition. As we argued previously, building thicker ToS in non-mangrove roots is used to reach a functional balance between nutrient absorption and transportation in thicker absorptive roots. Therefore, the coupling of root ToS thickness with leaf economic traits in mangroves (e.g. *fast*-leafed mangroves are accompanied with thick root ToS) could also be due to the existence of root anatomical allometry, which, as aforementioned, is dominated by nutrient- rather than C-driven process.

CONCLUSIONS

Here, we systematically reveal the contrasting patterns and mechanisms of the root–leaf coordination between non-mangrove and mangrove plants. Briefly, root anatomical structures, stele radius and ToS thickness, are coupled with leaf water use traits and decoupled from leaf economics in non-mangroves, whereas the root structures are decoupled from leaf water use traits and coupled with leaf economics in mangroves.

When plants are regarded as a continuum for water supply (roots) and demanding (leaves), the contrasting root–leaf relationships between mangroves and non-mangroves could lie in the

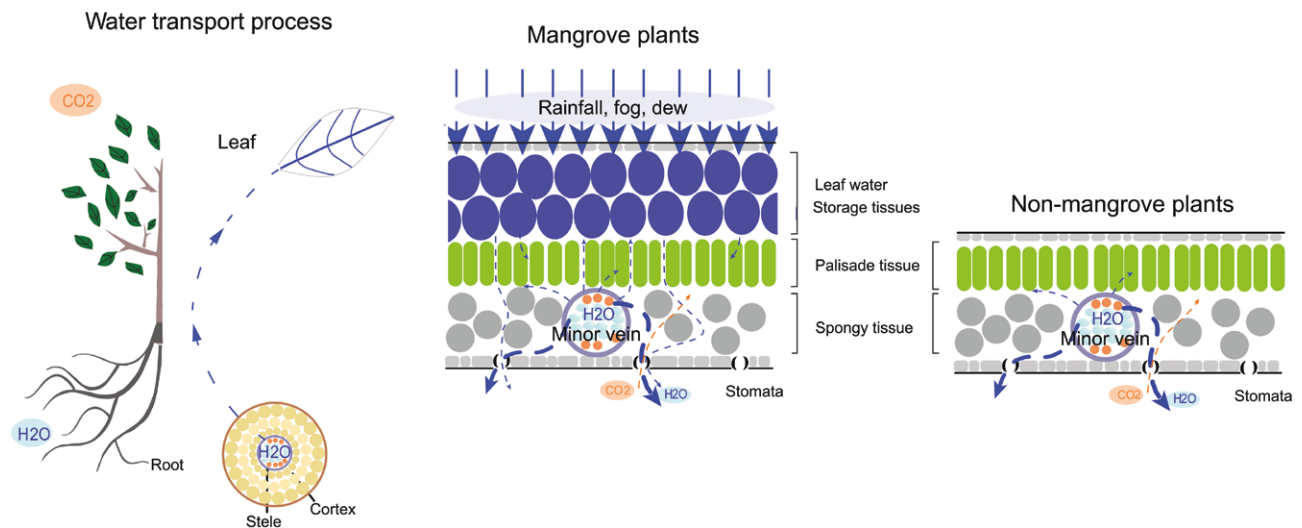


Figure 4: A conceptual framework for the comparison of water transport and partition from roots to leaves between mangrove and non-mangrove plants. The blue dashed lines in leaves represent water sources at leaf end: (1) water supply from roots both mangrove and non-mangrove plants: transported from roots to leaf minor veins, mainly supplied to stomatal transpiration, and a small amount used for photosynthesis in palisades (and water storage in mangrove *leaf water storage tissues*; for simplicity, only the hypodermis is shown as the mangrove leaf water storage tissue); (2) water supply outside the root of mangrove plants, such as rainfall, fog and dew, which are mainly used to refill the *leaf water storage tissues* in mangrove plants. The CO_2 fixation and hence the photosynthate are indicated with solid circles and dashed lines in orange. The relative amount of water used in the above partition ways, by referring to studies on mangrove plants (Nguyen *et al.* 2017a, 2017b; Pan *et al.* 2022; Reef and Lovelock 2015), was roughly represented by different-sized dashed lines in blue.

existence of *leaf water storage tissues* in the former and absence in the latter. Alternatively, when plants are considered as a continuum for C consumption (roots) and production (leaves), the distinct root–leaf relationships between mangroves and non-mangroves could be due to the universal allometric relationship between root stele and ToS. Uncovering the distinct root–leaf relationships and the underlying mechanisms are important for our understanding of and predicting the changes of vegetation composition and functions of mangrove and non-mangrove ecosystems under future environmental changes such as global warming and sea-level rising. Future studies could test the generality of the findings in mangroves in many other mangrove forests around the world. Last but not the least, leaf water storage tissues have been widely observed in many desert plants. It is interesting to learn about how the roots and leaves are coordinated in these desert plants, and whether this coordination is similar to the mangrove plants.

Supplementary Material

Table S1: Summary information for the 78 non-mangrove plant species in study.

Table S2: Summary information for the 17 mangrove plant species in study.

Table S3: Variation in 13 root and leaf functional traits measured from 78 non-mangrove plant species.

Table S4: Variation in 14 root and leaf functional traits measured from 17 mangrove species.

Table S5: Reports from principal components analysis on the 9 leaf traits of 78 non-mangrove species, including the proportion of variation explained (top table) and loading scores of traits on each component (bottom table).

Table S6: Pearson correlation coefficients (lower diagonal) and Phylogenetic Generalized Least Square models (upper diagonal) among 13 root and leaf functional traits for 78 non-mangrove species.

Table S7: Reports from principal components analysis on the 10 leaf traits of 17 mangrove species, including the proportion of variation explained (top table) and loading scores of traits on each component (bottom table).

Table S8: Pearson correlation coefficients (lower diagonal) and Phylogenetic Generalized Least Square models (upper diagonal) among 14 root and leaf functional traits for 17 mangrove species.

Table S9: Reports from principal components analysis on the 13 root and leaf traits of 78 non-mangrove species, including the proportion of variation explained (top table) and loading scores of traits on each component (bottom table).

Table S10: Reports from principal components analysis on the 4 root traits and 10 leaf traits of 17 mangrove species, including the proportion of variation explained (top table) and loading scores of traits on each component (bottom table).

Figure S1: Phylogenetic tree of 78 non-mangrove species.

Figure S2: Phylogenetic tree of 17 mangrove species.

Figure S3: Principal component analysis of mangrove leaves and roots.

Figure S4: Correlation of leaf traits distribution in 17 mangrove species.

Figure S5: Correlation between PC1 scores of leaf water use traits and root anatomical traits and distribution of 17 mangrove species.

Figure S6: Correlation and distribution of leaf water use traits and root anatomic traits in 78 non-mangrove species after phylogenetic removal.

Figure S7: Correlation between PC1 scores of leaf traits and distribution of 17 mangrove species.

Figure S8: Correlation between PC1 scores of leaf water use traits and root anatomical traits and distribution of 17 mangrove species.

Figure S9: Correlation and distribution of leaf water use traits and root anatomic traits in 17 mangrove species after phylogenetic removal.

Figure S10: Correlation and distribution of PC1 scores of leaf and root anatomic traits in 178 mangrove species.

Figure S11: The principal components of leaves and roots of mangrove and non-mangrove plants were analyzed using phylogenetic generalized least squares model.

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Authors' Contributions

Huifang Wu (Data curation, Writing—original draft), Qingpei Yang (Data curation, Formal analysis, Visualization), Jing Chen (Conceptualization), Mingzhen Lu (Conceptualization, Writing—review & editing), Weizheng Ren (Formal analysis), Yanmei Xiong (Formal analysis), Yuxin Pei (Investigation), Preetika Chand

(Writing—review & editing), Oscar Valverde-Barrantes (Writing—review & editing), Jingjing Cao (Conceptualization, Writing—original draft), and Deliang Kong (Conceptualization, Writing—original draft, Writing—review & editing)

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Conflict of interest statement. The authors declare that they have no conflict of interest.

Data Availability

Data of mangrove species are available in Dryad Digital Repository, a publicly available database, or acquirable on request of the corresponding author. Data of root and leaf traits for non-mangrove species can be assessed in the supporting information of two previous studies (Kong *et al.* 2014; Li *et al.* 2015).

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