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Not all sweetness and light: Non-structural carbohydrate storage capacity in tree stems is decoupled from leaf but not from root economics

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ABSTRACT

1. Non-structural carbohydrates (NSC) are considered as indicators of the balance between tree carbon sources and sinks and reflect functional strategies throughout different biomes. However, little is known about the contribution of NSC to tree economics, and in particular, whether leaf, stem and coarse root traits coordinate together into a whole-tree economics spectrum.

2. Twenty-four functional traits (including NSC content) were measured in leaves, stem and coarse root xylem of up to 90 angiosperm tree species in temperate, Mediterranean and tropical climates. By performing principal component analysis and standardized major axis regression, we explored the relationships between NSC and other functional traits, as well as the effects of climate and phylogeny on these relationships.

3. Our results revealed a covariation between leaf and coarse root NSC content and leaf economic traits, whereas stem NSC content was largely decoupled from the leaf economics spectrum that was mostly driven by leaf nitrogen content and leaf mass per area. Coarse root xylem traits were closely correlated with leaf traits, while most stem xylem traits were independent from the leaf economics spectrum but covaried with coarse root traits. Trade-offs among traits in tropical species opposed those from other climates. Evolutionary history affected relationships among certain traits but did not change overall patterns.

4. We conclude that due to leaf habit, an extended growing season and heightened defences, tropical species form distinct conservative resource acquisition strategies. Across all climates, as the stem must provide an efficient transport route between roots and leaves, while maintaining the display of branch and leaf organs,

stem xylem design and NSC storage capacity lead to a stem economics spectrum that is largely independent from the leaf spectrum, but is coupled with that of coarse roots due to anatomical continuity.

1 | INTRODUCTION

Functional traits that impact tree fitness indirectly via their effects on growth, reproduction and survival are widely studied to understand plant ecological strategies (Díaz et al., 2016; Violle et al., 2007). Trait patterns have been described using various concepts, with the 'economics spectrum' currently being one of the most popular models to describe how traits related to resource economics (Chave et al., 2009; Reich, 2014; Wright et al., 2004). For example, the leaf economics spectrum describes leaf-level resource use trade-offs, opposing species with acquisitive or conservative leaf traits based on leaf nutrient concentrations, leaf mass per area (LMA) and leaf life span (Onoda et al., 2017; Osnas et al., 2013; Wright et al., 2004).

In analogy with the leaf economics spectrum, several studies have reported resource economics trade-offs in different tissues, e.g. wood (Chave et al., 2009; Fortunel et al., 2012) and root (Carmona et al., 2021; Prieto et al., 2015; Roumet et al., 2016) tissues, as well as at the whole-tree level (de la Riva et al., 2016; Díaz et al., 2016; Freschet et al., 2010). Some studies have suggested that the traits of leaves, stems and roots are co-ordinated and thus provide a useful framework for exploring the trade-off between acquisition and conservation of resources at the whole-tree level (Reich, 2014). However, other studies on tropical species have shown that trait variation may be decoupled among different organs, suggesting that a consistent, whole-tree economics spectrum is difficult to identify or would at least involve several functional axes (Baraloto et al., 2010; Fortunel et al., 2012). These studies indicate that the economics spectrum model is not ubiquitous at a whole-tree level and across climates. However, differences in the spatial scales considered may contribute to discrepancies among studies on the topic of trait relationships (Escudero & Valladares, 2016). Therefore, further understanding as to whether an economics spectrum exists at the whole-tree level is necessary, especially across a broad range of species and climates and by embracing broader functions related to nutrient and water use.

Non-structural carbohydrates (NSC) are the primary substrates and key energy sources for tree metabolic processes, and play a vital role in multiple functions such as growth, osmoregulation, defence and survival (Hartmann & Trumbore, 2016; Kozlowski, 1992; Sala et al., 2012). NSC produced by photosynthesis can be quickly used for immediate functions or stored for reserves and defence (Klein & Hoch, 2015; Weber et al., 2019), which suggests an allocation-based trade-off between carbon demand and supply. Thus, the content of NSC and allocation patterns in leaves, stems and roots are considered as indicators of balance between carbon sources and sinks (Martínez-Vilalta et al., 2016). For example, species with a lower LMA tend to have greater light capture potential and net photosynthetic rate, which may result in an increase in photosynthates that are then transported as soluble sugars (SS) for rapid plant growth (Li et al., 2016; Wright et al., 2002). Additionally, tree species with tough leaves and high LMA usually have more carbon investment in reserves and defence, allowing individuals to persist when carbon demand is greater than supply (e.g. under severe drought stress) (Anderegg & Anderegg, 2013; Poorter & Kitajima, 2007). However, few studies have directly examined the relationship between NSC and the economics spectrum in trees, and whether NSC in different organs co-ordinates with economic traits (e.g. LMA, nitrogen content and wood density) that define ecological strategies, is still poorly understood. Due to the diverse roles played by NSC in different tree organs (Hartmann & Trumbore, 2016), NSC in leaf and woody organs are likely to exhibit different dimensional characteristics in resource allocation strategies.

We explored the coordination of functional traits by measuring suites of traits characterizing leaves, stems and coarse roots across 60–90 angiosperm tree species from temperate, Mediterranean and tropical forests. Specifically, we sought to test the following hypotheses: (H1) As a product of photosynthesis, NSC may be co-ordinated with economics strategies, but due to the role played by NSC in different organs, we hypothesize that leaf NSC content would co-ordinate with leaf economic traits, while stem and root NSC content would be independent of acquisitive and conservative resource strategies in these organs. (H2) Functional differences between leaves and wood may lead to independent functional trade-offs at the leaf versus stem and coarse root levels. However, given the anatomical continuity of xylem tissues between stem and root systems in woody plants, we hypothesize that leaf, stem and coarse root traits would not be integrated along a whole-tree economics spectrum, but coarse root structural traits such as wood density and anatomical traits would be co-ordinated with stem structural traits.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

This study was conducted in a temperate forest (Luz-Saint-Sauveur, France; 43°08′N, 0°03′E), a Mediterranean forest (Montpellier, France; 43°42′N, 4°00′E) and a tropical forest (Paracou, French

Guiana; 5°15′ N, 52°55′ W). The Luz-Saint-Sauveur site has a temperate climate, with the heaviest rainfall in the first half of the year; the Montpellier site has a typical Mediterranean climate with hot dry summers and cool wet winters; and the Paracou site has a tropical climate with a distinct dry season from mid-August to mid-November and a long rainy season. The mean annual precipitation (MAP) is 1217, 588 and 3035 mm and the mean annual temperature (MAT) is 11.8, 15.4 and 26.9°C for temperate, Mediterranean and tropical sites, respectively. The temperature and precipitation data were calculated using mean monthly data from the past 31 years (see Zhang et al., 2023).

A total of 90 species of angiosperm trees was selected, with 20 species each in temperate and Mediterranean climates and 50 species in the tropical climate, spanning 33 deciduous species and 57 evergreen species (Table S1). For each species, three healthy, adult, single-stemmed trees were identified, with a distance of at least 20 m between them. We collected leaf and stem samples for each tree, and coarse root samples for 60 tree species (20 species in each climate). Samples were collected at the end of the growing season in 2019 and 2020. We sampled all trees between 7 AM and midday, to reduce variability in NSC content linked to photosynthate production. Leaves were chosen from the same side of the tree where stem and root samples were collected and divided into two groups. At a height of 1.3 m, three 0.05 m long cores were extracted from tree stems with a 4.3-mm diameter increment borer. To collect samples of coarse roots, we excavated a single lateral root (0.02–0.05 m in diameter) and at a distance of 0.3–0.5 m from the base of the tree, we extracted three increment cores or removed three 0.02-m-long segments of root, depending on accessibility. We also collected one stem core for temperate and Mediterranean trees in March 2021 (before bud burst) to capture variability in seasonal dynamics of NSC. However, we found that stem NSC content did not show any significant differences between the two sampling times, except for the stem SS of Mediterranean trees (Figure S1). Therefore, the following analyses were based on the autumnal NSC data, since they may be a better indicator of the current year's carbon balance (Martínez-Vilalta et al., 2016). In total, 540 leaf samples, 930 stem cores and 540 coarse root segments were collected, and 24 functional traits were measured for each individual tree (Table 1). Samples collected from temperate and Mediterranean forests did not require permissions other than the landowner's consent, while the collection of samples from tropical forests in French Guyana was authorized by the French government (APA No. 1371201).

2.2 | Trait measurements

2.2.1 | NSC, carbon and nitrogen content

Immediately on returning to the laboratory, increment cores/root sections were trimmed and a 0.02-m-long section was taken from the outer sapwood. Then, these sections and one of two groups of leaf samples were heated in a microwave oven (90 s at 700 W) to stop enzymatic activity (Quentin et al., 2015) and oven-dried at 60°C for at least 72 h. Dried samples were ground into powder using a ball mill (Retsch MM400, Germany), and the ground samples were stored in sealed plastic tubes until chemical analyses were performed.

We collected a total of 270 leaf samples, 390 stem samples and 180 coarse root samples, but could not perform time-consuming analytical methods on all samples. Therefore, we used the near-infrared spectroscopy (NIRS) method to predict NSC, carbon (C) and nitrogen (N) content (Ramirez et al., 2015). Near-infrared spectra were first obtained for all samples on powders previously stabilized in a conditioning room at a temperature of $20 \pm 2°C$ and air humidity of $65 \pm 5\%$ (methods described by Zhang et al., 2022).

SS and starch content were determined on all leaf samples ($n = 270$) and a sub-sample of stems ($n = 113$) and coarse roots ($n = 140$) using a colorimetric method (Zhang et al., 2022) and were used to calibrate the NIRS method. The selected sub-sample comprised most species and represented a broad range of data. We used the NIRS calibrations to predict SS and starch content for all the leaf, stem and coarse root samples. SS and starch content were expressed as a dry weight ($mg\,g^{-1}$) and their sum is referred to as the total NSC content.

Similarly, C and N contents per unit mass (%) were determined in a sub-sample of leaves ($n = 110$), stems ($n = 113$) and in all coarse root samples ($n = 180$) using an elemental analyser (CHN model EA 1108, Carlo Erba Instruments, Italy) and were used to calibrate NIRS readings.

Partial least squares regression (PLSR) was used to develop calibrations for the prediction of SS and starch contents (Table S2), and C and N contents (Table S3), in leaves, stems and coarse roots separately. The R^2 values of calibration ranged between 0.75 and 0.95 for SS and starch, and between 0.87 and 0.92 for C and N, respectively.

2.2.2 | LMA and wood density

Another group of fresh leaf samples ($n = 270$) were scanned using a scanner (Epson V39, Epson Inc., Japan) and the leaf area was determined using ImageJ 1.52 software (https://imagej.nih.gov/ij/). The leaves were then dried at 60°C for at least 72 h and the weight used to determine LMA (leaf dry mass divided by leaf area, $g\,m^{-2}$) was calculated. We used the mean LMA value obtained from five leaves of the same tree as the mean value for each tree. The LMA and N content per unit mass in leaves are hereafter called 'leaf economic traits', being the two major traits among the six considered by Wright et al. (2004), that structure the leaf economics spectrum.

Stem ($n = 270$) and coarse root ($n = 180$) samples (with outer bark removed) were used for stem wood density (SWD) and root wood density (RWD) measurements. Stem and coarse root samples were soaked in water for 24 h and the saturated volume was determined using the water displacement method. After determining the saturated volume, samples were dried in a well-ventilated oven at 105°C for more than 72 h and then the dry mass was determined. Wood

TABLE 1 Summary and functional role of the 24 measured traits across 90 tree species for leaf and stem (coarse roots were measured in 60 tree species).

Organ	Trait	Abbreviation	Unit	Functional role
Leaf	Leaf carbon content	Leaf C	%	Resource capture
	Leaf nitrogen content	Leaf N	%	Resource capture
	Leaf mass per area	LMA	$g\,m^{-2}$	Resource capture and defence
	Leaf soluble sugars	Leaf SS	$mg\,g^{-1}$	Resource capture and defence
	Leaf starch	Leaf ST	$mg\,g^{-1}$	Resource capture and defence
	Leaf non-structural carbohydrates	Leaf NSC	$mg\,g^{-1}$	Resource capture and defence
Stem	Stem carbon content	Stem C	%	Storage, Structure and defence
	Stem nitrogen content	Stem N	%	Storage, Structure and defence
	Stem wood density	SWD	$g\,cm^{-3}$	Transport, structure and defence
	Stem soluble sugars	Stem SS	$mg\,g^{-1}$	Storage, structure and defence
	Stem starch	Stem ST	$mg\,g^{-1}$	Storage, structure and defence
	Stem non-structural carbohydrates	Stem NSC	$mg\,g^{-1}$	Storage, structure and defence
	Stem total parenchyma fractions	Stem RAP	—	Storage, structure and defence
	Stem vessel fractions	Stem VF	—	Transport, structure and defence
	Stem fibre (including tracheid) fractions	Stem FFT	—	Transport, structure and defence
Coarse root	Root carbon content	Root C	%	Storage, Structure and defence
	Root nitrogen content	Root N	%	Storage, Structure and defence
	Root wood density	RWD	$g\,cm^{-3}$	Transport, structure and defence
	Root soluble sugars	Root SS	$mg\,g^{-1}$	Storage, structure and defence
	Root starch	Root ST	$mg\,g^{-1}$	Storage, structure and defence
	Root non-structural carbohydrates	Root NSC	$mg\,g^{-1}$	Storage, structure and defence
	Root total parenchyma fractions	Root RAP	—	Storage, structure and defence
	Root vessel fractions	Root VF	—	Transport, structure and defence
	Root fibre (including tracheid) fractions	Root FFT	—	Transport, structure and defence

density was calculated as dry mass divided by saturated volume ($g\,cm^{-3}$; Williamson & Wiemann, 2010).

2.2.3 | Wood anatomy

Stem ($n=270$) and coarse root ($n=180$) sections were placed in a 50% solution of alcohol and water. We used a sliding microtome to cut 15–20 μm thick cross sections. Cross-sections were stained with a mixture of safranin and alcian blue (0.35 g safranin in 35 mL 50% alcohol with 0.65 g alcian blue in 65 mL deionized water) and dehydrated using ethanol series (50%, 75%, 95% and 100%). Finally, sections were mounted on glass slides and observed under a light microscope (Olympus BX 60F; Olympus Co. Ltd, Japan). Three microphotographs of transversal sections for each stem and coarse root sample were taken (one or two microphotographs were taken for very few sections) with an APO x5 lens using a digital camera

(Canon EOS 500D; Canon Inc., Tokyo, Japan). The proportion of total radial and axial parenchyma (RAP, i.e. the sum of radial parenchyma and axial parenchyma, %) and vessel fraction (VF, i.e. the total vessel area divided by xylem cross-section area) was then estimated using ImageJ software. The remaining tissues fraction including fibres, fibre-tracheids and tracheids (FFT) was calculated as: 1-RAP-VF.

2.3 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individuals	Species	3 individuals per species
Climates	Climates	3 climates

2.4 | Statistical analyses

Data were transformed using natural logarithms to correct for deviations from normality except for SWD and RWD that were normally distributed. We performed a principal component analysis (PCA) on leaf traits using LMA and leaf N content that relate to the leaf economics spectrum and leaf C content to examine differences between species from different climates. To examine the degree of associations between leaf, stem and coarse root traits, we used the standardized major axis (SMA) regression method (Warton et al., 2006) to determine the relationships among leaf economics spectrum proxied by the principal component of the first axis (LESPC1) and other traits (e.g. NSC, SS, starch, wood density, chemical and anatomical traits). We also performed SMA regression analysis directly on leaf N content and LMA to determine their relationships with other traits. We performed PCA on each organ and at the whole-tree level to examine overall trait co-ordination. PCA analysis with phylogenetically independent contrasts (PICs, Felsenstein, 1985) included was also conducted to account for the influence of species evolutionary histories. We constructed a phylogenetic tree (Figure S2) including all 90 species using the R package V.PhyloMaker (Jin & Qian, 2019), with the GBOTB phylogeny as the backbone (Smith & Brown, 2018). In addition, a mixed effects linear model was performed to examine the effect of climates (temperate, Mediterranean and tropical) on first axis (PC1) scores of leaf, stem, coarse root and whole-tree PCAs. We included climates as fixed factor and species as random factor. Tukey's honestly significant difference (HSD) post hoc tests were then performed to identify variation among these groups when significant differences were found. All statistical analyses were performed in R version 4.0.2 (R Core Team, 2022).

3 | RESULTS

3.1 | Relationships between leaf economic traits, NSC content and xylem traits

For the PCA on leaf traits for 90 tree species (Figure S3), the first axis accounted for 56.3% of variation, running from species with acquisitive leaf traits (high leaf N and low LMA) to species with conservative leaves (low leaf N and high LMA). The SMA regressions showed that there was a significant and negative relationship between LESPC1 and leaf NSC (as well as SS and starch content) when all species were grouped. There was also a significant and negative relationship between LESPC1 and coarse root NSC, but not with stem NSC (Figure 1a–i). When focusing on climates, LESPC1 was significantly associated with leaf NSC in tropical species and with root NSC in Mediterranean species.

With all species pooled together, LESPC1 was not associated with stem C, N or SWD (Figure 2a–c) but was positively related to coarse root C and RWD and negatively with coarse root N (Figure 2d–f). When focusing on climates, significant and positive relationships were found between LESPC1 and SWD and RWD in

Mediterranean species, but negative relationships between LESPC1 and RWD in tropical species (Figure 2c,f). There were significant and positive relationships between LESPC1 and stem and coarse root RAP but negative relationships between LESPC1 and stem and coarse root VF with all species pooled (Figure S4). Negative relationships between LESPC1 and coarse root VF were also found in temperate and Mediterranean species, while the opposite trend was found in tropical species (Figure S4).

When using SMA regressions to directly test the relationships between leaf N content and LMA with other traits, the patterns between traits (especially for LMA) were similar to those using LESPC1 as a proxy (Figures S5–S7).

We also found that leaf NSC was not associated with either stem or coarse root NSC, but stem NSC was significantly related to coarse root NSC (Figure S8). Additionally, SWD was positively associated with RWD, and positive relationships were also observed between corresponding stem and coarse root xylem cell fractions (Figure S8).

3.2 | Trait correlation among leaves, stems, coarse roots and at the whole-tree level

When we performed PCAs for leaf, stem, coarse root and at the whole-tree level, we found that relationships between NSC and functional traits differed in each organ (Figure 3a–d). At the whole-tree level, PC1 and PC2 explained 20.0% and 15.9% of the trait variation, respectively (Figure 3d). The first PCA axis was defined by leaf and root N, VF, leaf NSC, C, LMA, SWD and RWD, while the second PCA axis was defined by stem and root NSC, RAP, FFT, stem N and root C. Stem C was not strongly associated with either axis (Figure 3d). When including PICs in the PCA, although the percentage of explained variation and the relationships between certain traits changed, the overall pattern of co-ordination among leaf, stem and coarse root traits remained largely consistent. For example, leaf traits covaried with coarse root traits, while stem traits were independent from leaf spectrum (Figure S9).

Tree species in the three climates showed different resource allocation strategies (Figure 3). The score on the first PCA axis of temperate and Mediterranean species was significantly lower than that of tropical species at the leaf, coarse root and whole-tree level, while no significant difference in the first PCA axis score was found at the stem level (Figure S10).

4 | DISCUSSION

4.1 | Links between NSC and leaf economics spectrum

Partially in agreement with our first hypothesis, we found that leaf economic traits covaried with leaf and coarse root NSC, but not with stem NSC. This finding is partly consistent with those found by Ramirez et al. (2021), who showed that the position of
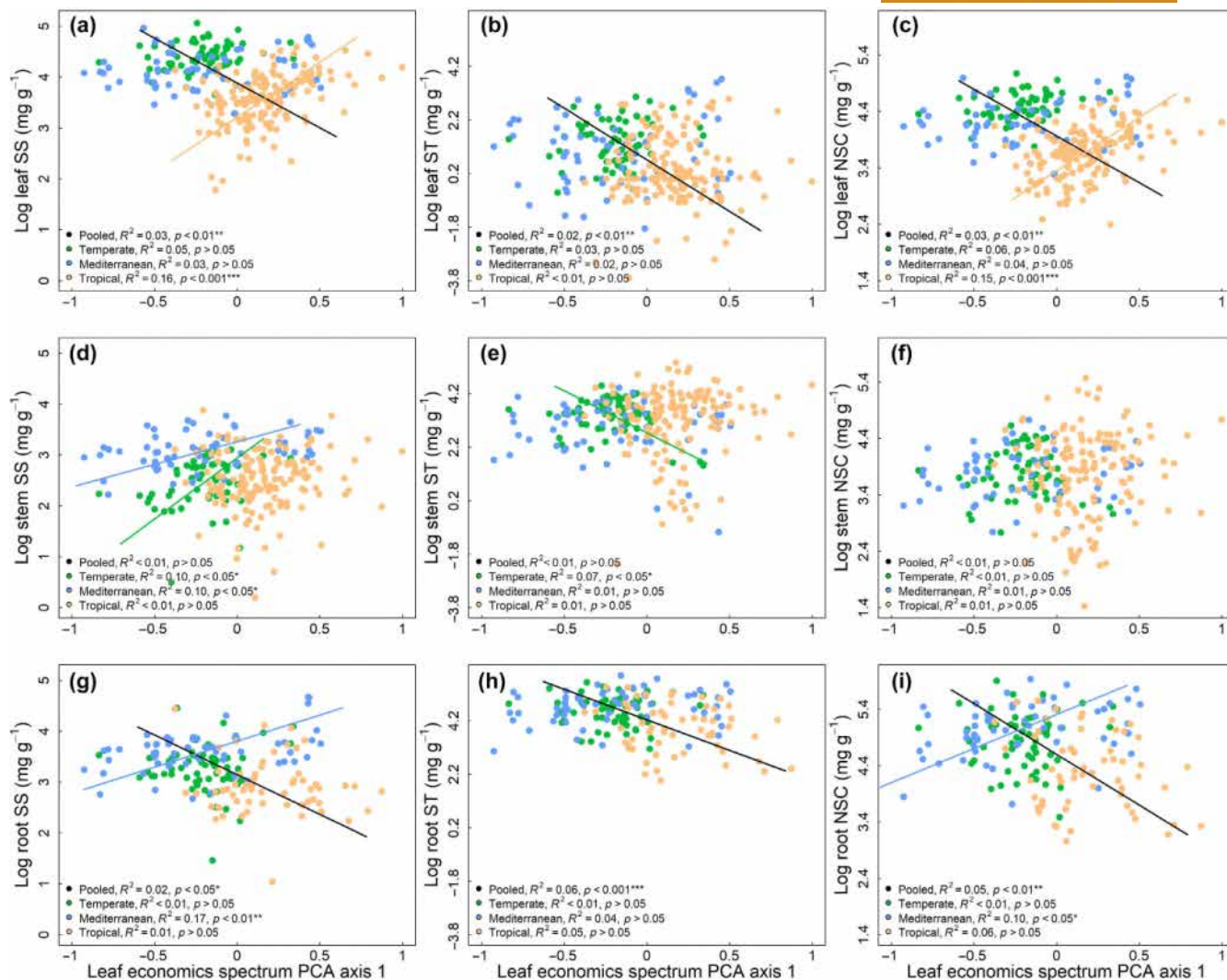
FIGURE 1 Standardized major axis (SMA) regressions (a–c) between LESPC1 and leaf NSC, (d–f) stem NSC for 90 species and (g–i) between LESPC1 and root NSC for 60 tree species across climates. Green points represent temperate species; blue points represent Mediterranean species; and orange point represents tropical species. Regression lines are shown when the correlation is significant. The black lines represent the relationships across all species; the green lines represent the relationships within temperate species; the blue lines represent the relationships within Mediterranean species and the orange lines represent the relationships within tropical species. LESPC1, leaf economics spectrum PCA axis 1; NSC, non-structural carbohydrates; SS, soluble sugars; ST, starch.

tree species along the plant acquisition and conservative strategy spectrum was a predictor of NSC in leaves, but not in stems and coarse roots. Additionally, we also showed that leaf NSC augmented with increasing leaf N and decreasing LMA, suggesting that species with an acquisitive resource strategy could accumulate more NSC in their leaves than those with a conservative resource strategy. Lower LMA and higher leaf N is usually associated with higher net photosynthetic rate (Onoda et al., 2017; Wright et al., 2004), and thus the increase in leaf NSC with increasing N possibly resulted from increased carbon uptake (Li et al., 2016; Wright et al., 2002).

We found that stem NSC displayed an orthogonal trend with leaf economics spectrum (along the first PCA axis), which may be due to the stem's distinct functional roles compared to leaves or roots. Leaves and fine roots acquire resources that need to be transported

to organs located at the opposing extremities of the tree. The stem must provide a transport route that is efficient, while maintaining the display of branch and leaf organs. Therefore, the design of the xylem space must reflect an optimized route for water and nutrient transport that takes into account seasonal demands for NSC, as well as climatic constraints, such as prolonged dry and cold periods (Kawai et al., 2022).

The dynamics of NSC in stem xylem are relatively slow and NSC can accumulate over periods of many years (Hartmann & Trumbore, 2016). This 'older' NSC could contribute to annual growth, especially in temperate deciduous species (such as *Fagus* and *Quercus* species), where storage of NSC occurs before the winter months and can be remobilised the following spring (Barbaroux & Bréda, 2002; El Zein et al., 2011). Therefore, stem NSC remains relatively immobile and varies little unless a disturbance occurs, and
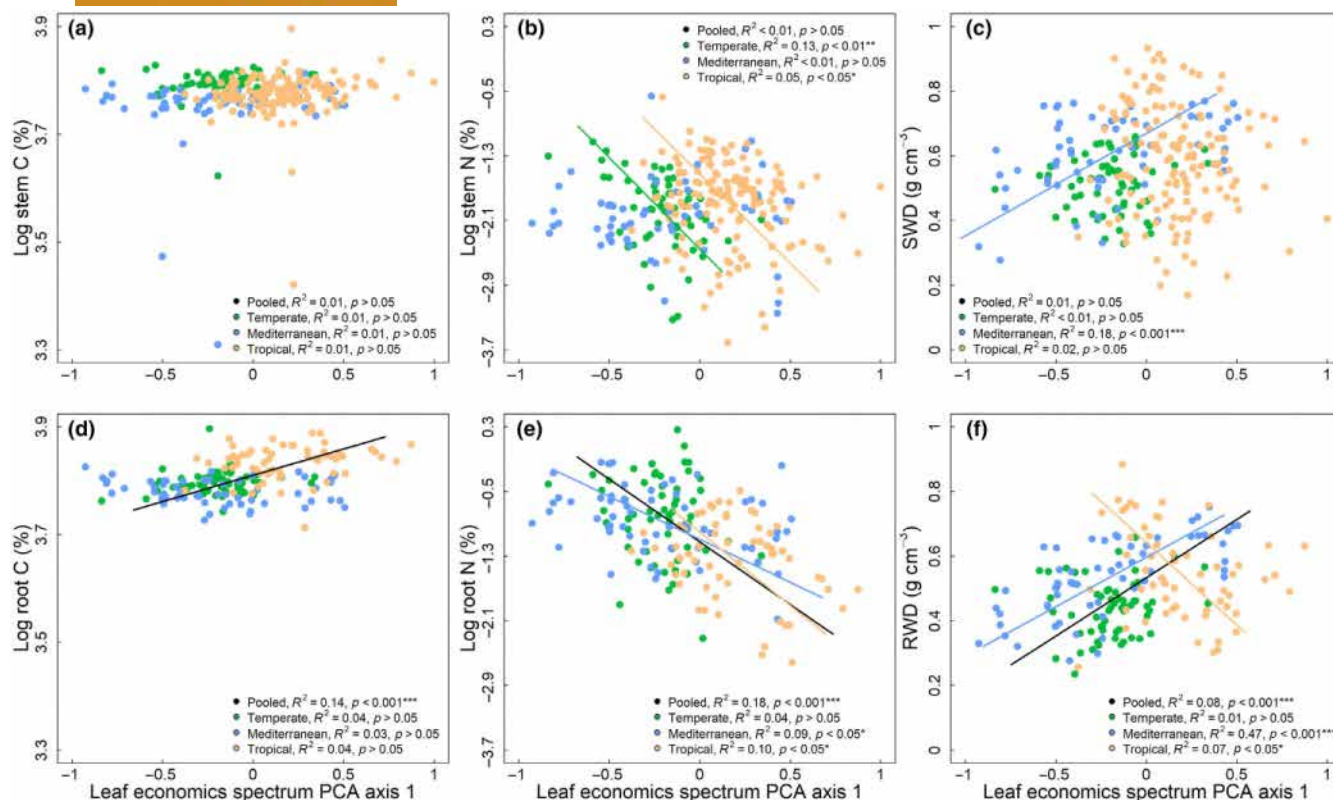
FIGURE 2 Standardized major axis (SMA) regressions (a–c) between LESPC1 and stem C, N and wood density for 90 species and (d–f) between LESPC1 and root C, N and wood density for 60 tree species across climates. Green points represent temperate species; blue points represent Mediterranean species; and orange points represent tropical species. Regression lines are shown when the correlation is significant. The black lines represent the relationships across all species; the green lines represent the relationships within temperate species; the blue lines represent the relationships within Mediterranean species and the orange lines represent the relationships within tropical species. C, carbon; LESPC1, leaf economics spectrum PCA axis 1; N, nitrogen; SWD, stem wood density; RWD, root wood density.

so contributes to the lack of co-ordination with functional traits associated with the leaf economics spectrum.

Compared to the stem, the NSC in coarse roots is usually much greater and similar to that of fine roots (Wang et al., 2018), whose growth partially depends on the carbohydrates produced by the leaves (Liu & Wang, 2021). This may explain why a negative relationship between coarse root NSC and leaf economics spectrum was found (i.e. greater root NSC with increased leaf N content but lower LMA).

4.2 | Partial correlation of leaf, stem and root traits not associated with whole-tree economics spectrum

Consistent with our second hypothesis, we found that leaf traits and certain coarse root traits (chemical traits and wood density) were associated with each other to a certain extent, whereas most stem traits were independent of leaf economic traits, revealing an absence of a consistent whole-tree economics spectrum in the species we studied. Our PCA results with and without PICs confirmed this point, especially at the whole-tree level, with leaf and several coarse root traits loading on the first axis, while stem

traits primarily loaded on the second axis. A possible reason for the coupling of leaf and coarse root traits is that nutrient storage is an important function of roots (Drew, 1987) and tree species with high storage function would have lower leaf lifespan. However, although coarse root NSC was closely associated with leaf economic traits, we did not find a significant relationship between coarse root NSC and leaf NSC, but between coarse root NSC and stem NSC. NSC stored in woody organs (stems and coarse roots) may only be mobilized to a small extent during normal functioning and are not used for immediate metabolism to the extent that they are in leaves (Hartmann & Trumbore, 2016). Our results are also in agreement with previous studies that reported a decoupled relationship between leaf and stem economics in tropical woody species (Baraloto et al., 2010), even when phylogenetic contrasts were considered with species-level data, demonstrating that the different investment in leaf and wood tissues optimized tree growth and survival. As shown by multiple dimensions of traits' trade-offs, a study of plant strategies must integrate certain combinations of leaf and wood economic traits (Baraloto et al., 2010). Although stem traits are orthogonal to leaf economic traits, we found close associations between stem and coarse root structural traits, which are also in agreement with previous studies (Fortunel et al., 2012). There are several functional analogies between stems
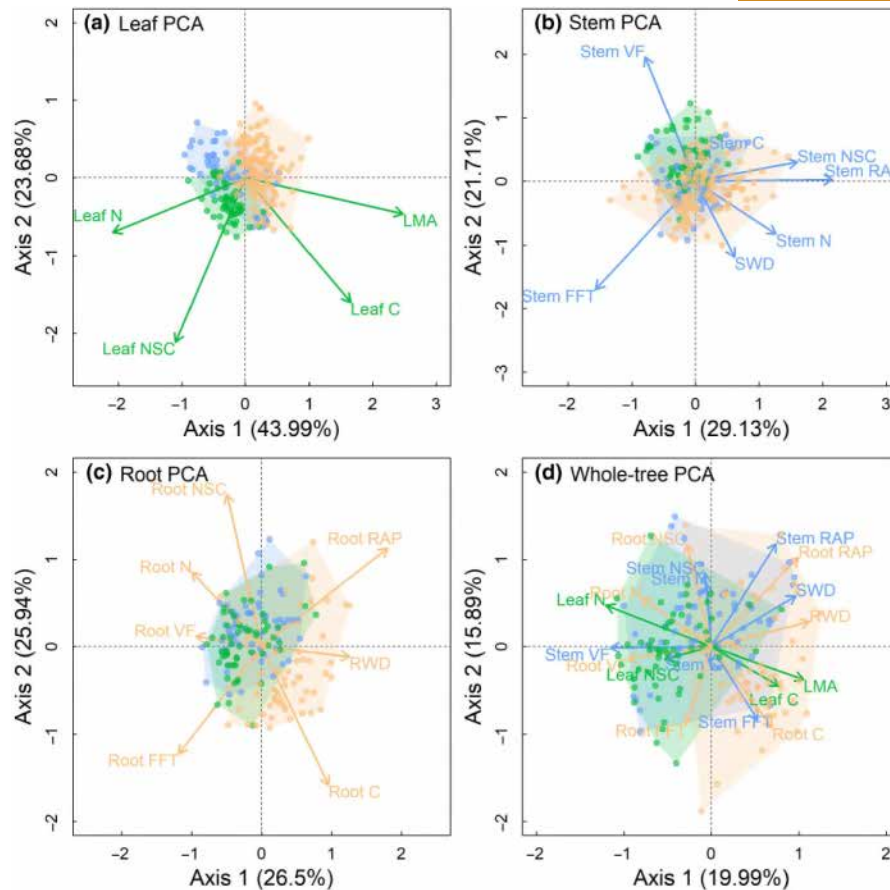
FIGURE 3 Principal component analysis (PCA) of functional traits among 90 species for (a) leaves and (b) stems, and among 60 species for (c) coarse roots and (d) the whole-tree. Green points represent temperate species; blue points represent Mediterranean species; orange points represent tropical species. Green, blue and orange arrows represent leaf, stem and root traits, respectively. See Table 1 for trait abbreviation.

and coarse roots, such as transport and storage. The anatomical and hydraulic continuity of xylem between stem and root systems (Fortunel et al., 2014; Tyree & Ewers, 1991) likely explains the co-variation of stem and root structural traits, which indicates a similar investment strategy in wood tissues.

Although recent studies have also shown that there are conspicuous patterns of integration for leaf and wood traits toward a whole-tree economics spectrum (de la Riva et al., 2016; Freschet et al., 2010; Zhao et al., 2017), the inconsistent results regarding resource economics suggest that trait co-ordination may be contingent on the traits examined and the environmental conditions (Méndez-Alonzo et al., 2012; Reich, 2014). For example, biotic factors, such as the impact of herbivores and pathogens, may contribute to the lack of a consistent, whole-tree economics spectrum, as the physiological response of different organs to natural enemies may differ, leading to different patterns of growth, photosynthesis and primary metabolism (Johnson et al., 2016). Further studies including empirical data and meta-analyses, taking into account biotic and abiotic factors, are still needed to disentangle plant ecological strategies across multiple scales (Freschet et al., 2010).

Another important caveat is that we only considered coarse roots as a below-ground organ. A complete understanding of plant

responses to global environmental change requires an integrated definition of the whole-tree economics spectrum covering all relevant organs (Fortunel et al., 2012; Vleminckx et al., 2021), and the lack of measurements on fine roots is a limitation of our study. Further work should address the relationships between leaf economic traits, NSC and tissue fractions in a more complete set of organs including fine roots, which in many regards are the below-ground analogues to leaves.

4.3 | Effects of climate zones on plant strategies

We found substantial variation in tree resource strategy across climates, which is likely structured by leaf habits (Zhao et al., 2017). As many of the deciduous species we studied are found in the Mediterranean, but are equally common in temperate biomes with low LMA, it is not surprising that temperate and Mediterranean tree species are inclined to the resource strategy of rapid acquisition. Deciduous species with thinner lamina and greater stomatal conductance should have higher rates of photosynthesis per unit leaf mass, associated with high N content, compared to evergreen species (Givnish, 2002). Most of the tropical tree species

we studied were (semi)-evergreen species (42 out of 50) and had high LMA and are more likely to exhibit relatively conservative resource acquisition strategies because photosynthesis and growth can be maintained throughout the year and thus resources are relatively abundant. Furthermore, we also demonstrated that in tropical species, the relationships between leaf economic traits and leaf NSC, root wood density and root VF opposed those species from other climates or when species from all climates were pooled together, which indicates strong regional effects on trait patterns. In general, temperate acquisitive species should have more sugars but low wood density for a faster metabolism. However, in tropical forests there is considerably greater taxonomic diversity (Cunningham & Read, 2002), with large variation in the light requirements across species (e.g. shade-tolerant vs. light-demanding species), which mediates a trade-off between growth and survival.

In addition, natural enemies such as herbivores and pathogens may also influence trait associations with changing herbivory rates across latitudinal gradients, particularly for evergreen species with long leaf lifetimes. For example, trees experience little or no winter attack from invertebrates in the temperate zone, but in the tropics they can be damaged by herbivores for several months throughout the year (Lim et al., 2015) resulting in decreased water and nutrient uptake. Thus, the associations among functional traits and economics strategy could change across latitudinal sites, which means that the study of economics strategies should not be limited to a single climate but should be performed across different climatic regions. Future studies that avoid the concentration of tree species with similar ecological strategies in one climatic zone and the uniform distribution of tree species with different leaf habits across climatic zones will be important towards reaching this goal.

5 | CONCLUSIONS

We investigated the co-ordination of functional traits including NSC content that are associated with tree economic traits, across 90 deciduous and evergreen angiosperm species growing in three contrasting climates. We found that leaf and coarse root NSC were co-ordinated with leaf economic traits, while stem NSC was independent from the leaf economic traits. In addition, we found there was a decoupled relationship between leaf and stem economic traits, and a coupled relationship between stem and several coarse root traits. We conclude that stem xylem design and NSC storage capacity lead to a stem economics spectrum that is largely independent from leaf but not from the coarse root spectrum. We highlight that species from different climates had distinct resource allocation strategies at both the organ and whole-tree levels, suggesting a strong effect of region on trait trade-offs. Further studies including empirical data and meta-analyses, and accounting for the effects of biotic factors, are still needed to understand tree strategies across scales.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

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REFERENCES
Anderegg, W. R. L., & Anderegg, L. D. L. (2013). Hydraulic and carbohydrate changes in experimental drought-induced mortality of

saplings in two conifer species. *Tree Physiology*, 33, 252–260. https://doi.org/10.1093/treephys/tpt016

Baraloto, C., Timothy Paine, C. E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A. M., Hérault, B., Patiño, S., Roggy, J. C., & Chave, J. (2010). Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, 13, 1338–1347. https://doi.org/10.1111/j.1461-0248.2010.01517.x

Barbaroux, C., & Bréda, N. (2002). Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology*, 22, 1201–1210. https://doi.org/10.1093/treephys/22.17.1201

Carmona, C. P., Bueno, C. G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A. D., Pärtel, M., Zobel, M., & Tamme, R. (2021). Fine-root traits in the global spectrum of plant form and function. *Nature*, 597, 683–687. https://doi.org/10.1038/s41586-021-03871-y

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Cunningham, S., & Read, J. (2002). Comparison of temperate and tropical rainforest tree species: Photosynthetic responses to growth temperature. *Oecologia*, 133, 112–119. https://doi.org/10.1007/s00442-002-1034-1

de la Riva, E. G., Tosto, A., Pérez-Ramos, I. M., Navarro-Fernández, C. M., Olmo, M., Anten, N. P. R., Marañón, T., & Villar, R. (2016). A plant economics spectrum in Mediterranean forests along environmental gradients: Is there coordination among leaf, stem and root traits? *Journal of Vegetation Science*, 27, 187–199. https://doi.org/10.1111/jvs.12341

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. https://doi.org/10.1038/nature16489

Drew, M. C. (1987). *Function of root tissues in nutrient and water transport. Root development and function* (pp. 71–101). Cambridge University Press.

El Zein, R., Maillard, P., Bréda, N., Marchand, J., Montpied, P., & Gérant, D. (2011). Seasonal changes of C and N non-structural compounds in the stem sapwood of adult sessile oak and beech trees. *Tree Physiology*, 31, 843–854. https://doi.org/10.1093/treephys/tpr074

Escudero, A., & Valladares, F. (2016). Trait-based plant ecology: Moving towards a unifying species coexistence theory. *Oecologia*, 180, 919–922. https://doi.org/10.1007/s00442-016-3578-5

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125, 1–15. https://doi.org/10.1086/284325

Fortunel, C., Fine, P. V. A., & Baraloto, C. (2012). Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology*, 26, 1153–1161. https://doi.org/10.1111/j.1365-2435.2012.02020.x

Fortunel, C., Ruelle, J., Beauchêne, J., Fine, P. V. A., & Baraloto, C. (2014). Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients. *New Phytologist*, 202, 79–94. https://doi.org/10.1111/nph.12632

Freschet, G. T., Cornelissen, J. H. C., Logtestijn, R. S. P. V., & Aerts, R. (2010). Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, 98, 362–373. https://doi.org/10.1111/j.1365-2745.2009.01615.x

Givnish, T. (2002). Adaptive significance of evergreen vs. deciduous leaves: Solving the triple paradox. *Silva Fennica*, 36, 703–743. https://doi.org/10.14214/sf.535

Hartmann, H., & Trumbore, S. (2016). Understanding the roles of non-structural carbohydrates in forest trees – From what we can measure to what we want to know. *New Phytologist*, 211, 386–403. https://doi.org/10.1111/nph.13955

Jin, Y., & Qian, H. (2019). V. PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, 42, 1353–1359. https://doi.org/10.1111/ecog.04434

Johnson, S. N., Erb, M., & Hartley, S. E. (2016). Roots under attack: Contrasting plant responses to below-and aboveground insect herbivory. *New Phytologist*, 210, 413–418. https://doi.org/10.1111/nph.13807

Kawai, K., Waengsothorn, S., & Ishida, A. (2022). Sapwood density underlies xylem hydraulics and stored carbohydrates across 13 deciduous tree species in a seasonally dry tropical forest in Thailand. *Trees*, 1, 1–11. https://doi.org/10.1007/s00468-022-02364-3

Klein, T., & Hoch, G. (2015). Tree carbon allocation dynamics determined using a carbon mass balance approach. *New Phytologist*, 205, 147–159. https://doi.org/10.1111/nph.12993

Kozlowski, T. (1992). Carbohydrate sources and sinks in woody plants. *The Botanical Review*, 58, 107–222. https://doi.org/10.1007/BF02858600

Li, N., He, N., Yu, G., Wang, Q., & Sun, J. (2016). Leaf non-structural carbohydrates regulated by plant functional groups and climate: Evidences from a tropical to cold-temperate forest transect. *Ecological Indicators*, 62, 22–31. https://doi.org/10.1016/j.ecolind.2015.11.017

Lim, J. Y., Fine, P. V., & Mittelbach, G. G. (2015). Assessing the latitudinal gradient in herbivory. *Global Ecology and Biogeography*, 24, 1106–1112. https://doi.org/10.1111/geb.12336

Liu, R., & Wang, D. (2021). C: N: P stoichiometric characteristics and seasonal dynamics of leaf-root-litter-soil in plantations on the loess plateau. *Ecological Indicators*, 127, 107772. https://doi.org/10.1016/j.ecolind.2021.107772

Martínez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S., Piper, F. I., & Lloret, F. (2016). Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. *Ecological Monographs*, 86, 495–516. https://doi.org/10.1002/ecm.1231

Méndez-Alonzo, R., Paz, H., Zuluaga, R. C., Rosell, J. A., & Olson, M. E. (2012). Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology*, 93, 2397–2406. https://doi.org/10.1890/11-1213.1

Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tosens, T., & Westoby, M. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist*, 214, 1447–1463. https://doi.org/10.1111/nph.14496

Osnas, J. L. D., Lichstein, J. W., Reich, P. B., & Pacala, S. W. (2013). Global leaf trait relationships: Mass, area, and the leaf economics spectrum. *Science*, 340, 741–744. https://doi.org/10.1126/science.1231574

Poorter, L., & Kitajima, K. (2007). Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology*, 88, 1000–1011. https://doi.org/10.1890/06-0984

Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Roupsard, O., Thammahacksa, C., & Stokes, A. (2015). Root functional parameters along a land-use gradient: Evidence of a community-level economics spectrum. *Journal of Ecology*, 103, 361–373. https://doi.org/10.1111/1365-2745.12351

Quentin, A. G., Pinkard, E. A., Ryan, M. G., Tissue, D. T., Baggett, L. S., Adams, H. D., Maillard, P., Marchand, J., Landhäusser, S. M., Lacointe, A., Gibon, Y., Anderegg, W. R. L., Asao, S., Atkin, O. K., Bonhomme, M., Claye, C., Chow, P. S., Clément-Vidal, A., Davies, N. W., ... Woodruff, D. R. (2015). Non-structural carbohydrates in woody plants compared among laboratories. *Tree Physiology*, 35, 1146–1165. https://doi.org/10.1093/treephys/tpv073

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ramirez, J. A., Craven, D., Posada, J. M., Reu, B., Sierra, C. A., Hoch, G., Handa, I. T., & Messier, C. (2021). Non-structural carbohydrate concentrations in woody organs, but not leaves, of temperate and tropical tree angiosperms are independent of the 'fast-slow' plant economic spectrum. *BioRxiv* https://doi.org/10.1101/2021.04.20.440698

Ramirez, J. A., Posada, J. M., Handa, I. T., Hoch, G., Vohland, M., Messier, C., & Reu, B. (2015). Near-infrared spectroscopy (NIRS) predicts

non-structural carbohydrate concentrations in different tissue types of a broad range of tree species. *Methods in Ecology and Evolution*, 6, 1018–1025. https://doi.org/10.1111/2041-210X.12391

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K., & Stokes, A. (2016). Root structure-function relationships in 74 species: Evidence of a root economics spectrum related to carbon economy. *New Phytologist*, 210, 815–826. https://doi.org/10.1111/nph.13828

Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: Feast or famine? *Tree Physiology*, 32, 764–775. https://doi.org/10.1093/treephys/tpr143

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105, 302–314. https://doi.org/10.1002/ajb2.1019

Tyree, M. T., & Ewers, F. W. (1991). The hydraulic architecture of trees and other woody plants. *New Phytologist*, 119, 345–360. https://doi.org/10.1111/j.1469-8137.1991.tb00035.x

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vleminckx, J., Fortunel, C., Valverde-Barrantes, O., Timothy Paine, C. E., Engel, J., Petronelli, P., Dourdain, A. K., Guevara, J., Béroujon, S., & Baraloto, C. (2021). Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species. *Oikos*, 130, 1193–1208. https://doi.org/10.1111/oik.08284

Wang, Y., Mao, Z., Bakker, M. R., Kim, J. H., Brancheriau, L., Buatois, B., Leclerc, R., Selli, L., Rey, H., Jourdan, C., & Stokes, A. (2018). Linking conifer root growth and production to soil temperature and carbon supply in temperate forests. *Plant and Soil*, 426, 33–50. https://doi.org/10.1007/s11104-018-3596-7

Warton, D. I., Wright, I. J., Falster, D. S., & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biological Reviews*, 81, 259–291. https://doi.org/10.1017/S1464793106007007

Weber, R., Gessler, A., & Hoch, G. (2019). High carbon storage in carbon-limited trees. *New Phytologist*, 222, 171–182. https://doi.org/10.1111/nph.15599

Williamson, G. B., & Wiemann, M. C. (2010). Measuring wood specific gravity… correctly. *American Journal of Botany*, 97, 519–524. https://doi.org/10.3732/ajb.0900243

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. https://doi.org/10.1038/nature02403

Wright, I. J., Westoby, M., & Reich, P. B. (2002). Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology*, 90, 534–543. https://doi.org/10.1046/j.1365-2745.2002.00689.x

Zhang, G. (2023). Tree economics spectrum dataset. *Recherche Data Gouv* https://doi.org/10.57745/C5BMMI

Zhang, G., Maillard, P., Mao, Z., Brancheriau, L., Engel, J., Gerard, B., Fortunel, C., Maeght, J. L., Martínez-Vilalta, J., Ramel, M., Nourissier-Mountou, S., Fourtier, S., & Stokes, A. (2022). Non-structural carbohydrates and morphological traits of leaves, stems and roots from tree species in different climates. *BMC Research Notes*, 15, 251. https://doi.org/10.1186/s13104-022-06136-7

Zhang, G., Mao, Z., Maillard, P., Brancheriau, L., Gerard, B., Engel, J., Fortunel, C., Heuret, P., Maeght, J. L., Martínez-Vilalta, J., & Stokes, A. (2023). Functional trade-offs are driven by coordinated changes among cell types in the wood of angiosperm trees from different climates. *New Phytologist*, 240, 1162–1176. https://doi.org/10.1111/nph.19132

Zhao, Y. T., Ali, A., & Yan, E. R. (2017). The plant economics spectrum is structured by leaf habits and growth forms across subtropical species. *Tree Physiology*, 37, 173–185. https://doi.org/10.1093/treephys/tpw098

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Boxplots of stem non-structural carbohydrates contents sampled in autumn and spring across 60 tree species from temperate and Mediterranean climates.

Figure S2. Phylogenetic tree of the 90 tree species measured in the study.

Figure S3. Principal component analysis of LMA, leaf nitrogen and leaf carbon across 90 species to show the classical leaf economics spectrum.

Figure S4. Standardized major axis regressions between LESPC1, stem RAP, VF and FFT for 90 species and between LESPC1, root RAP, VF and FFT for 60 tree species across climates.

Figure S5. Standardized major axis regressions between leaf N, LMA, leaf NSC and stem NSC for 90 species and between leaf N, LMA and root NSC for 60 tree species across climates.

Figure S6. Standardized major axis regressions between leaf N, LMA, stem N and wood density for 90 species and between leaf N, LMA, root N and wood density for 60 tree species across climates.

Figure S7. Standardized major axis regressions between leaf N, LMA, stem RAP and VF for 90 species and between leaf N, LMA, root RAP and VF for 60 tree species across climates.

Figure S8. Standardized major axis regressions between leaf, stem and root NSC and between stem and root structural traits for 60 tree species across climates.

Figure S9. Principal component analysis of functional traits with phylogenetically independent contrasts among 90 species for leaf and stem, and among 60 species for root and whole-tree.

Figure S10. Boxplots of leaf PC1, stem PC1 scores across 90 species and root PC1 and whole-tree PC1 scores across 60 tree species with different climates.

Table S1. List of 90 species from three climates.

Table S2. Model parameters of near-infrared spectroscopy calibration for soluble sugars and starch.

Table S3. Model parameters of near-infrared spectroscopy calibration for carbon and nitrogen.