

# Contrasting coordination of non-structural carbohydrates with leaf and root economic strategies of alpine coniferous forests

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## Summary

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- Non-structural carbohydrates (NSCs), as the labile fraction and dominant carbon currency, are essential mediators of plant adaptation to environments. However, whether and how NSC coordinates with plant economic strategy frameworks, particularly the well-recognized leaf economics spectrums (LES) and root economics space (RES), remains unclear.
- We examined the relationships between NSC and key plant economics traits in leaves and fine roots across 90 alpine coniferous populations on the Tibetan Plateau, China.
- We observed contrasting coordination of NSC with economics traits in leaves and roots. Leaf total NSC and soluble sugar aligned with the leaf economic spectrum, conveying a trade-off between growth and storage in leaves. However, NSC in roots was independent of the root economic spectrum, but highly coordinated with root foraging, with more starch and less sugar in forage-efficient, thinner roots. Further, NSC-trait coordination in leaves and roots was, respectively, driven by local temperature and precipitation.
- These findings highlight distinct roles of NSC in shaping the above- and belowground multi-dimensional economics trait space, and NSC-based carbon economics provides a mechanistic understanding of how plants adapt to heterogeneous habitats and respond to environmental changes.

## Introduction

The growth-survival trade-off is a fundamental framework by which we understand how plants respond and adapt to multiple biotic and abiotic stresses (Wright *et al.*, 2004; Stephenson *et al.*, 2011; Blumstein *et al.*, 2022). Carbon (C) allocation underpins this trade-off, as C provides the building block of life and is indispensable for multiple metabolic processes (García-Carreras *et al.*, 2018; Trugman *et al.*, 2018). Non-structural carbohydrates (NSCs), as the labile fraction and the dominant currency of C allocation, are of particular interest in understanding plant life-history strategy and modeling forest C cycles, due to their essential roles in mediating C source-sink balance (Martínez-Vilalta *et al.*, 2016; Hartmann *et al.*, 2020). Non-structural carbohydrates are stored in various organs over timescales spanning minutes to decades that can be reutilized to maintain vital tree function by providing C substrate for growth, fuel for respiration, and solutes for osmoregulation (Chapin *et al.*, 1990; Dietze *et al.*, 2014; Hartmann & Trumbore, 2016). Non-structural carbohydrate storage therefore serves as a buffer, allowing trees to

persist during periods of dormancy or environmental stress when C demand outstrips supply, such as under cold and drought (O'Brien *et al.*, 2014; Hoch, 2015). Considerable attention has been given to the potential role of stored NSC in mediating plant growth and tolerance to environmental change (McDowell *et al.*, 2008; Li *et al.*, 2018; Signori-Müller *et al.*, 2021), but it has not been routinely included in plant growth or life-history strategy schemes (Lubbe *et al.*, 2021; Piper, 2021).

Plant trait-based economic spectrums have hugely advanced our understanding of plant growth and life-history strategies. For example, the leaf economics spectrum (LES) eloquently displays the overarching trade-off between resource acquisition and conservation (Wright *et al.*, 2004; Díaz *et al.*, 2016). The LES trade-off is governed by plant C allocation along a continuum from enhancing productivity and competitiveness to promoting longevity and persistence (Shipley *et al.*, 2006; Reich, 2014). The C allocation for plant growth greatly affects NSC build-up and use, and will inevitably interact with NSC storage (Hartmann *et al.*, 2020). Leaf NSC, for example, might reserve passively as the consequence of a surplus of photosynthetic C supply exceeding demands in tissue respiration and growth (Le Roux *et al.*, 2001; Dietze *et al.*, 2014). It could also accumulate actively

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to become a competitive sink for leaf defense and tolerance at the expense of growth (Dietze *et al.*, 2014; Trumbore *et al.*, 2015). In this situation, NSC storage could be a heritable trait involving plant life-history or survival strategies to adapt to diverse environmental conditions. Several studies have observed a significant trade-off between growth and NSC storage across tree species (Blumstein *et al.*, 2022; Signori-Müller *et al.*, 2022). However, our current understanding is mostly based on woody organs or NSC roles as a response characteristic to environmental changes, lacking experimental investigation into whether and how leaf NSC coordinate with leaf traits in the context of LES.

The coordination of NSC with belowground traits may be more complex, as substantial evidence indicates the multidimensionality of root trait variation, also known as the root economics space (RES) (Weemstra *et al.*, 2016; Bergmann *et al.*, 2020; Weigelt *et al.*, 2021, 2023). Two orthogonal dimensions have been identified regarding RES (Ding *et al.*, 2020; Zhang *et al.*, 2024). One is the root economics spectrum, driven by the opposite change of root tissue density (RTD) and root nitrogen (N) concentration, conveying a trade-off between resource acquisition and conservation, and the other is related to resource foraging from the root itself, that is the 'do-it-yourself' strategy with thin, long roots, and larger surface areas to an 'outsourcing' strategy with mycorrhizal fungi (Kramer-Walter *et al.*, 2016; Bergmann *et al.*, 2020). Root NSC storage can be connected with both root dimensions, as it can not only provide substrates for root respiration, exudation, and cell wall construction associated with root N contents and RTD but also supply C for root elongation and colonization of symbiotic associations to expand resource foraging space (Jones *et al.*, 2009; Aubrey & Teskey, 2018). Specific root morphological traits may also contribute to NSC storage. For example, thicker absorptive roots typically have thicker sieves, allowing for higher sugar transport capacities; the larger parenchyma area in the thick roots could also provide more space to store NSC (Plavcová *et al.*, 2016; Kong *et al.*, 2021). Therefore, NSC storage in roots may follow the conservation-acquisition trade-off as it may occur in leaves, while also aligning with root diameter in the foraging dimension. However, direct evidence accounting for the coordination of NSC with root conservation or foraging dimensions is scarce, which hinders our understanding of the role of NSC in belowground resource acquisition and plant adaptation to changing environmental conditions.

Our limited knowledge on the relationship between NSC and plant economic strategies may arise mainly from the multifunctionality of various NSC compounds, specifically the two primary components, starch and soluble sugars (Dietze *et al.*, 2014; Hartmann & Trumbore, 2016). Starch is an osmotically inert polysaccharide used for energy storage and can be remobilized for future needs via degrading into sugars, presumably acting as a determinant of plant persistence and fitness (MacNeill *et al.*, 2017; Thalmann & Santelia, 2017). By contrast, soluble sugars are osmotically active and mediate plant metabolic rates and resistance to adverse conditions due to their immediate and direct involvement in osmoregulation, metabolism, and defense protection (Dietze *et al.*, 2014; O'Brien *et al.*, 2014). Discrepant responses and interconversion of starch and sugar have been

frequently observed under environmental change (Li *et al.*, 2018; Du *et al.*, 2020). Under prolonged water deficits, for example, soluble sugars tend to increase while starch tends to decrease (Dickman *et al.*, 2015; He *et al.*, 2020). Under extremely severe water stress, starch even becomes severely depleted, while soluble sugars remain above a threshold to maintain basic plant functions (Mitchell *et al.*, 2014; Sevanto *et al.*, 2014; Zhang *et al.*, 2021). These divergent functions (long-term storage vs immediate function) and responses to environmental change of sugar and starch highlight their distinct roles in plant growth or survival strategies. Plant comparative studies are an important way to clarify whether and how different NSC components are linked to above- and belowground plant strategies.

We developed a multisite dataset integrating leaf and root economics traits, total NSC (NSC<sub>T</sub>), and its component storage levels from 25 coniferous species across 90 populations of alpine forests on the eastern Tibetan Plateau (Fig. 1). The dataset encompasses a broad geographic scale, providing a unique opportunity to detect plant NSC variation across a dynamic landscape shaped by diverse climate and soil properties and across species that vary in life-history strategies. We hypothesized that NSC storage is coordinated with LES and RES. Specifically, plants with a conservative strategy would store more NSC both in leaves and fine roots, due to the potential C allocation trade-off between storage and growth or respiration. Moreover, compared with soluble sugars, starch storage is more closely linked to plant conservative strategies, given its long-term storage function in improving plant persistence under adverse conditions.

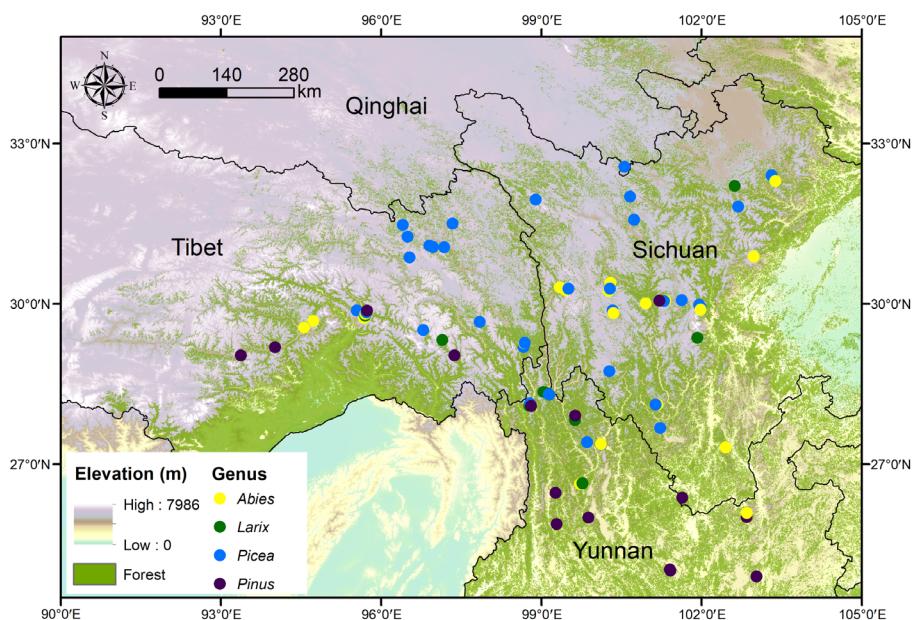
## Materials and Methods

### Study area

Our study was carried out in the alpine region of the eastern Tibetan Plateau in China, covering a wide geographic range of 27.37–35.27°N, 94.55–103.31°E, with altitudes of 2562.0–4351.0 m above sea level (Fig. 1). The study area falls within the temperate and subtropical climate zones, and encompasses a broad range of climate, soil conditions, and forest plant communities. The mean annual temperature (MAT) ranges from 0.32 to 15.64°C, and the mean annual precipitation (MAP) ranges from 494.99 to 1118.95 mm. Alpine coniferous forests account for the majority of the forested areas on the eastern Tibetan Plateau and are dominated by species from the genera *Pinus*, *Picea*, *Abies*, and *Larix*. These tree species are strongly associated with ectomycorrhizal (ECM) fungi and often form monodominant forests on the eastern Tibetan Plateau (Ding *et al.*, 2020).

### Field sampling

In July and August 2017–2018, sampling was performed at 90 coniferous forest stands distributed across the study area, including 26 *Abies* populations, 10 *Larix* populations, 37 *Picea* populations, and 17 *Pinus* populations. These stands were selected from well-identified distribution areas for each coniferous forest species, including 20 evergreen species belonging to the genera *Abies*, *Picea*,



**Fig. 1** Locations of the 90 coniferous populations in alpine forests on the eastern Tibetan Plateau, China, including the *Pinus*, *Picea*, *Abies*, and *Larix* forests.

and *Pinus*, and 5 deciduous species belonging to the *Larix* genera. At each stand, we established three to five 30 m × 40 m experimental plots separated by 50 m, and randomly sampled at least three healthy tree individuals of similar diameters at breast height. For each individual, three current-year twigs with needles from the sun-exposed mid-upper canopy were sampled using a pole pruner. Through excavating soil within a 2-m distance of the main trunk at 0–20 cm depth, roots with intact terminal branch orders were cut from the main lateral roots (Guo *et al.*, 2008). Five soil cores with diameters of 5 cm and at 0–20 cm depth were simultaneously collected by a soil auger in a plot. To minimize the possible effects of diurnal variation in tissue NSC, samples were always collected at midday (*c.* 10:00–14:00 h). Once collected, the samples from each plot were pooled by sample type (foliage, root, and soil) and immediately placed in a 0–4°C cooler with ice for transport.

#### Needle trait measurements

Current-year needles were detached from branches and pooled by plot for morphological and chemical analyses. We measured four leaf functional traits that defined the LES (Westoby, 1998; Wright *et al.*, 2004): leaf area (LA), leaf mass per area (LMA), leaf N concentrations (LN), and leaf  $\delta^{13}\text{C}$ . LA was obtained by scanning a needle subsample at 400 dpi using an Epson scanner (Epson Expression 11000XL; Seiko Epson Corp., Nagano, Japan) and analyzing it with the IMAGEJ software (v.1.52, Wayne Rasband-National Institute of Health, Bethesda, MD, USA). After scanning, the needles were oven-dried at 65°C to a constant mass and weighed, and LMA was calculated as dry mass divided by leaf area. Another subsample was oven-dried and ground into fine powders with a ball mill for chemical analysis. Leaf N concentrations were analyzed by an elemental analyzer (Vario Macro cube; Elementar, Hanau, Germany). Leaf  $\delta^{13}\text{C}$  values were obtained using an isotope mass spectrometer (MAT253; Finnigan MAT, Bremen, Germany).

#### Root trait measurements

The intact roots of 1–2 orders were carefully separated from rinsed root branches with fine forceps (Pregitzer *et al.*, 2002). Measurements for root morphological and chemical traits were taken on the distal two orders of roots, as they are predominantly responsible for resource acquisition (Guo *et al.*, 2008; McCormack *et al.*, 2015; Bergmann *et al.*, 2020). Six key functional traits directly involved in the RES were measured (Kramer-Walter *et al.*, 2016; Bergmann *et al.*, 2020; Ding *et al.*, 2020), including root diameter (RD), specific root length (SRL), root tissue density (RTD), root N concentrations (RNC), branching intensity (BRI), and mycorrhizal colonization rate (MCR). A subsample of fresh fine roots was scanned at a resolution of 400 dpi and analyzed with the WINRHIZO software to obtain mean root diameter, root length, and root surface area. The scanned fine roots were dried at 65°C to a constant mass and weighed, and then ground into fine powders. Specific root length was calculated as root length divided by dry mass. Root tissue density was obtained as dry mass divided by total volume. Branching intensity was calculated from the tip counts divided by the total root length. Root N concentrations were analyzed using an elemental analyzer on ground dry samples. For each plot, a second subsample of 50 root tips was randomly chosen for MCR determination. Roots were identified as ectomycorrhiza according to their macroscopic features in color, branching pattern, and fungal mantles under a stereoscopic microscope. The ECM colonization ratio was calculated as the percentage of infected root tips out of the total observed root tips.

#### NSC analysis

Fresh subsamples of detached needles and the distal two orders of roots for NSC analysis were microwaved at 800 W for 90 s to stop enzymatic activity within 6 h after collection. The maximum

6 h for sample storage is well within the acceptable time limit of 48 h by Landhäuser *et al.* (2018). Upon arrival at the laboratory, these samples were oven-dried at 65°C and ground into fine powders for NSC determination. Non-structural carbohydrates are defined here as soluble, low-molecular-weight sugars plus starch, and quantified using a modified phenol-sulfuric method (Chow & Landhäuser, 2004; Zhang *et al.*, 2020). Briefly, the ground samples were extracted by 80% (v/v) ethanol for 24 h, and then the supernatants obtained by twice centrifugations were combined together and used for soluble sugar determination. Starch was released from the ethanol-insoluble residual separated after extraction by boiling in distilled water and was then successively digested with  $\alpha$  amylase and amyloglucosidase. The supernatants gained after centrifugation were used for starch determination. The concentrations of soluble sugars and starch were measured with a multimode microplate reader (Spark; Tecan, Männedorf, Switzerland) at a wavelength of 490 nm using the phenol-sulfuric method. Starch concentration was calculated by multiplying a reference concentration of glucose by the conversion factor of 0.9 (Sullivan, 1935). The concentrations of soluble sugars and starch were expressed as the percentage of dry mass (% DM). The  $NSC_T$  was calculated as the sum of starch and soluble sugar concentrations.

### Climatic data and soil properties

Climate variables, MAT and MAP, were obtained from gridded data with a spatial resolution of  $0.5^\circ \times 0.5^\circ$  over the period 1981–2015, which was downloaded from the China Meteorological Data Service Center (<http://data.cma.cn/en/>). The composited soil samples by a plot were air-dried and sieved ( $< 2$  mm) before soil property measurements. Soil C and N concentrations (SC and SN) were analyzed using an elemental analyzer on ground dry samples (Vario Macro cube; Elementar). Soil P concentrations (SP) were determined with an inductively coupled plasma-atomic emission spectrometer (ICP-OES) (Optima 5300 DV; Perkin Elmer, Waltham, MA, USA). Soil available P concentrations (AP) were determined colorimetrically through the molybdenum blue method after extraction with 0.5 M  $NaHCO_3$ .

### Statistics

The measured values were averaged within one forest stand for statistical analysis. Differences across genera in soluble sugars, starch, and  $NSC_T$  in leaves and roots, were tested using Tukey's HSD. To quantify the extent of intraspecific and interspecific variation in NSC, soluble sugars, starch, and sugar : starch ratios, we performed variance partitioning analysis using the function 'partvar' of R package CATI (Taudiere & Violle, 2016). The data were log-transformed to ensure normality before variance partitioning. The variance partitioning analysis fits a linear mixed-effects model on restricted maximum likelihood method, to assess variation in traits across different ecological scales, namely within species, between species, between genus, and between sites (Messier *et al.*, 2010).

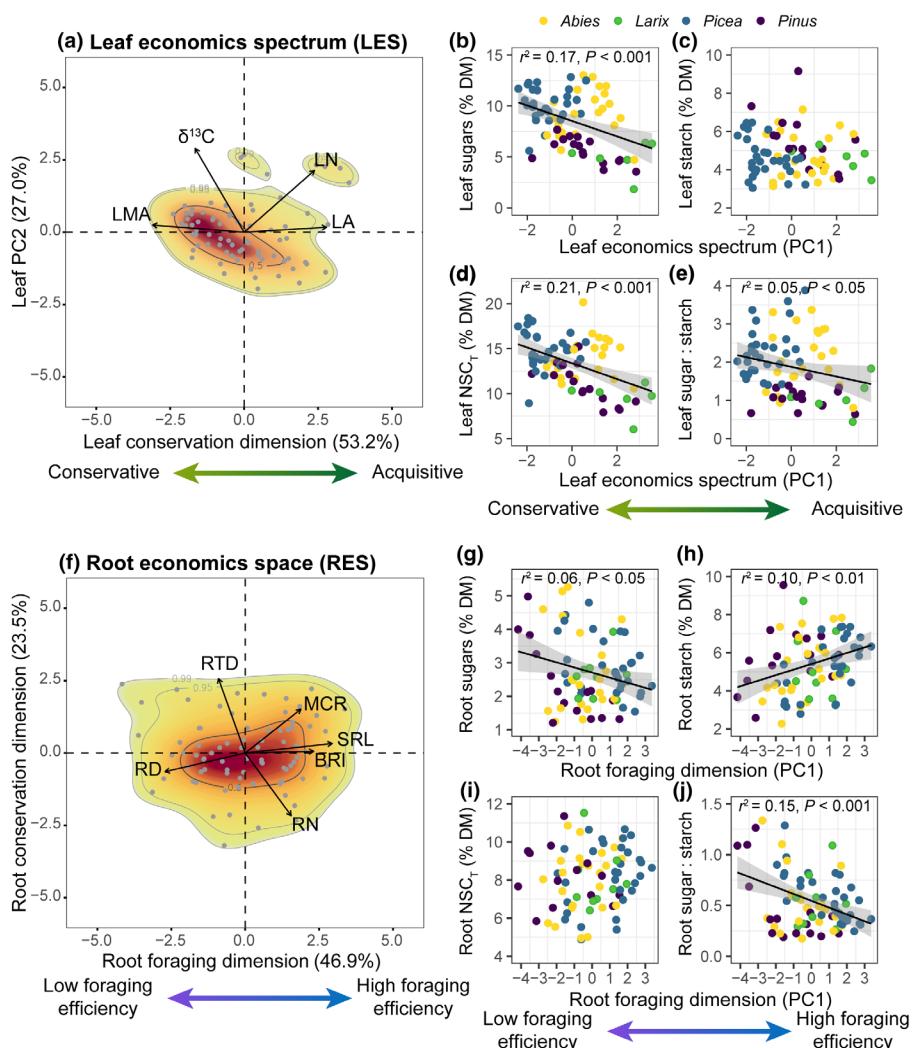
We first performed principal component analyses (PCA) using the matrix of site/population-level values of functional traits, which were LA, LMA, LN, and  $\delta^{13}C$  for leaves, and RD, SRL, RTD, RNC, BRI, and MCR for roots. We used the scores of the first axis dominated by LA, LMA, and LN to represent the continuum of the LES. As for fine roots, due to their multidimensional characteristics, we selected the scores of the first two axes, with the former dominated by RD, SRL, BRI, and MCR, and the latter dominated by RTD and RNC, as representatives of the root foraging and conservation dimensions, respectively. Pearson's correlations were done among functional traits, the concentrations of NSC and its components, and the scores of the first two axes (PC1 and PC2) extracted from the PCA. To visualize and identify the expression of NSC and its components in the LES and RES, we also conducted another PCA on NSC (and its two major components) concentrations and functional traits in leaves and roots. Afterwards, linear regression analyses were applied to NSC, soluble sugars, starch, and sugar : starch ratios as a function of the extracted PCA scores of selected PC axes, respectively, representing the LES and the root foraging dimension. As a robustness test, we also examined the carbohydrate-economics spectrum relationship at the species level through the PCA similar to those described above, using the species-averaged trait values.

We ran linear mixed-effect models using the R package LME4 to test the fixed effects of environmental factors MAP, MAT, SC, SN, SP, and AP on population-level variations in leaf and root PCA scores,  $NSC_T$  and its fractions, with tree species considered as a random effect. Hierarchical partitioning analysis to calculate the individual contributions of each predictor toward total (marginal)  $R^2$  was conducted with the R package GLMM.HP to determine the relative importance of each environmental factor (Lai *et al.*, 2022). We also performed linear regression analyses to evaluate the correlations of leaf and root trait dimensions, concentrations of  $NSC_T$  and its components with MAT and MAP. All statistical analyses were conducted with the R v.4.2.1 (R Core Team, 2022).

## Results

### Relationships between NSC and plant economic strategies

Across the coniferous forests, leaf sugar and  $NSC_T$  concentrations of the *Abies* and *Picea* genera were significantly higher than those of the *Larix* and *Pinus* genera (Supporting Information Fig. S1a,  $P < 0.01$ ), while leaf starch was at similar levels in all genera ( $P > 0.05$ ). Taxonomy including the genus and species accounted for a substantial portion of the total variation in leaf soluble sugars,  $NSC_T$  and sugar : starch ratios, respectively (Fig. S1b; Table S1). The contribution of taxonomy to these traits was much higher than that of sites and within-species. Leaf traits varied significantly across genera (Fig. S2a). Principal component analysis detected two major dimensions of leaf trait variation, similarly across both populations and species (Figs 2a, S3a,b). The first and second dimensions (PC1, PC2) explained 53.2% and 27.0% of the total variation, respectively, across the



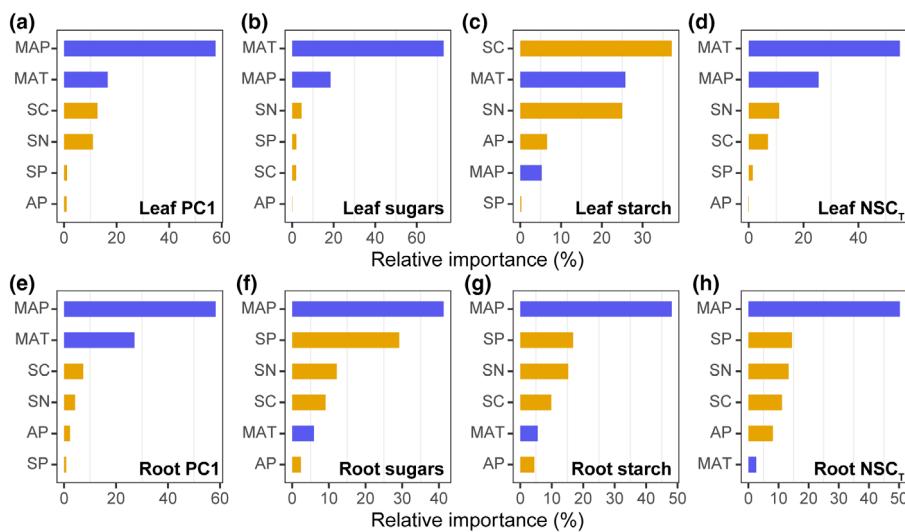
**Fig. 2** Relationships between non-structural carbohydrates (NSC) and the plant economics space. Principal component analysis (PCA) results for economics traits that respectively define the leaf economics spectrum (LES, a) and root economics space (RES, f), and the correlations of total NSC ( $NSC_T$ ), soluble sugars, starch, and sugar : starch in leaves (b–e) and roots (g–j) with the first PCA axis scores (PC1) depicting the LES and root foraging dimension, respectively. The regression line is shown when the relationship is significant ( $P < 0.05$ ). Shaded areas represent 95% confidence intervals. BRI, branching intensity; LA, leaf area; LMA, leaf mass per area; LN, leaf nitrogen concentrations; MCR, mycorrhizal colonization rates;  $NSC_T$ , total non-structural carbohydrate concentrations; RD, root diameter; RN, root nitrogen concentrations; RTD, root tissue density; SRL, specific root length.

populations. PC1 was contributed mainly by LA, LMA, and LN, and PC2 was closely associated with leaf  $\delta^{13}\text{C}$  (Fig. 2a). Leaf soluble sugars,  $NSC_T$  concentrations, and sugar : starch ratios were negatively correlated with leaf PC1 ( $r^2 = 0.17$ , 0.21, and 0.05, respectively,  $P < 0.05$ ). Both leaf soluble sugars and  $NSC_T$  concentrations were negatively correlated with LN (Fig. S4a;  $r^2 = 0.14$  and 0.15,  $P < 0.01$ ), and positively with LMA (Fig. S4a;  $r^2 = 0.18$  and 0.27, respectively,  $P < 0.001$ ). Leaf  $NSC_T$  was not correlated with leaf PC2 ( $P > 0.05$ ), while leaf starch had weak correlations with LMA and  $\delta^{13}\text{C}$  ( $r^2 = 0.07$  and 0.05, respectively,  $P < 0.05$ ). Leaf  $NSC_T$  and soluble sugars were also expressed on the first axis that aligned to LES across populations when key leaf traits and concentrations of leaf NSC and its components were put together (Fig. S5; 42.0% of the total variation explained).

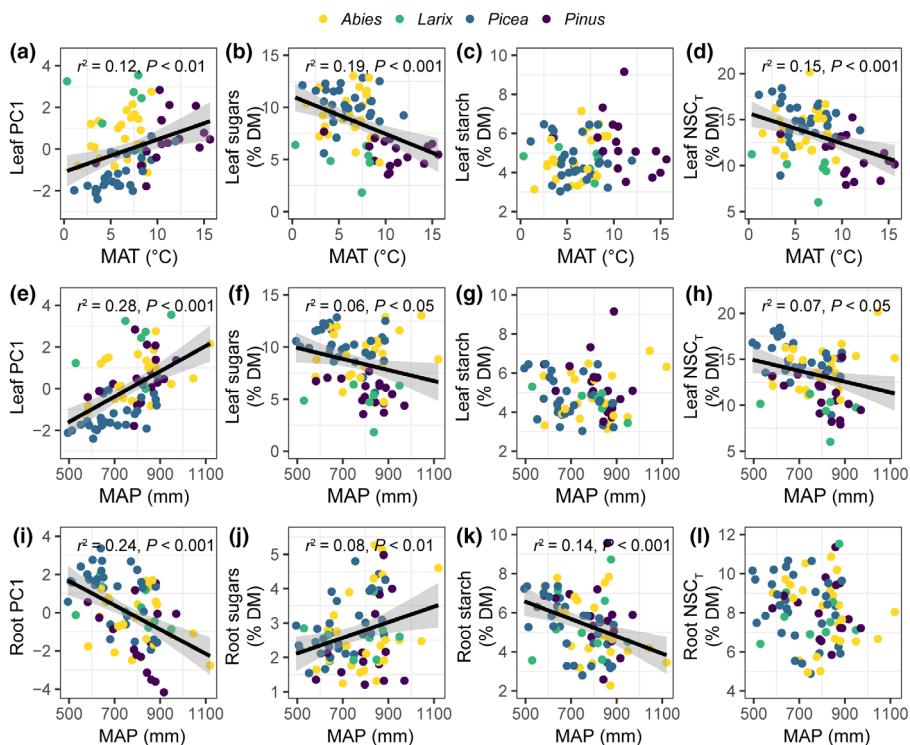
For carbohydrates in absorptive fine roots, little variation was observed across genera and species (Fig. S1c,  $P > 0.05$ ; Table S1). Root economics traits showed significant variation across genera (Fig. S2b). At both the population and species levels, two independent dimensions were detected (Figs 2f, S3c,d). Root PC1 was

mainly accounted for by negative relationships between RD and root foraging traits, including BRI, SRL, and MCR. Root PC2 was dominated by a negative correlation between RTD and RNC, corresponding to the root conservation dimension or the root economics spectrum. Root soluble sugars were negatively and root starch was positively correlated with root PC1 (Fig. 2g,h;  $r^2 = 0.06$  and 0.10, respectively,  $P < 0.05$ ; Fig. S4b), and hence a negative relationship between root sugar : starch ratio and root PC1 (Fig. 2j,  $r^2 = 0.15$ ,  $P < 0.001$ ). Root soluble sugar concentrations were positively correlated with RD but negatively with SRL (Fig. S4b; both  $r^2 = 0.06$ ,  $P < 0.05$ ), and root starch concentrations were positively correlated with SRL, BRI, and MCR (Fig. S4b;  $r^2 = 0.09$ , 0.06, and 0.08, respectively,  $P < 0.05$ ). However, no relationships were observed for  $NSC_T$  and its components with root PC2. Root soluble sugars, starch, and their ratios were expressed on the first axis aligned to the root foraging dimension, which together explained 38.8% of the total variation (PC1 of Fig. S6a).

As for the relationship of NSC between roots and leaves, only  $NSC_T$  instead of its components showed a significant correlation (Fig. S7;  $r^2 = 0.12$ ,  $P < 0.01$ ).



**Fig. 3** Relative importance of environmental factors to drive variations in plant economics strategies and non-structural carbohydrate concentrations in leaves (a–d) and roots (e–h). Leaf PC1 and root PC1 are the first principal component analysis axis scores, respectively, depicting the leaf economics spectrum and the root foraging dimension. AP, soil available phosphorus concentrations; MAP, mean annual precipitation; MAT, mean annual temperature; NSC<sub>T</sub>, total non-structural carbohydrate concentrations; SC, soil carbon concentrations; SN, soil nitrogen concentrations; SP, soil phosphorus concentrations.



**Fig. 4** Correlations of mean annual temperature (MAT) and mean annual precipitation (MAP) with plant economic strategies and non-structural carbohydrate concentrations in leaf (a–h) and root (i–l). Leaf PC1 and root PC1 are the first principal component analysis axis scores, respectively, depicting the leaf economics spectrum and root foraging dimension. The regression line is shown when the relationship is significant ( $P < 0.05$ ). Shaded areas represent 95% confidence intervals. NSC<sub>T</sub>, total non-structural carbohydrate concentrations.

## Environmental drivers for variations in NSC and plant economic strategies

Hierarchical partitioning analysis identified mean annual temperature (MAT) and mean annual precipitation (MAP) as the driving factors for variation of the leaf economics spectrum (LES, leaf PC1), soluble sugars, and NSC<sub>T</sub> concentrations (Fig. 3a,b, d). Specifically, trees tended to have conservative leaves with more storage of sugars and total NSC in cooler and drier sites (Fig. 4;  $P < 0.001$ ). By contrast, root foraging (root PC1), root soluble sugars, starch, and NSC<sub>T</sub> concentrations (Fig. 3e–h) were dominantly affected by MAP, with higher root foraging, more

starch, and less soluble sugars in drier conditions (Fig. 4;  $P < 0.01$ ).

## Discussion

### Contrasting coordination of NSC with economic strategies in leaves and roots

As expected, acquisitive plants characterized by high leaf area, high leaf N concentrations, and high LMA tended to accumulate lower amounts of NSC<sub>T</sub> and soluble sugar concentrations in leaves

(Figs 2a–e, S4a, S5a). This finding can be explained in light of the growth-storage trade-off theory, which suggests that NSC storage is a sink that competes with growth so that acquisitive plants allocate greater C investment to growth than to storage, while conservative plants store more C for environmental tolerance at the expense of growth and competitiveness (Grime, 2006; Piper, 2021; Signori-Müller *et al.*, 2022). Moreover, the association between NSC and sugar levels and plant growth strategies may stem from the feedback inhibition of photosynthetic efficiency by sugar accumulation. Reduced storage of sugar in leaves could facilitate rapid sugar unloading and export from leaves (McCormick *et al.*, 2008), thereby promoting efficient unloading and utilization of sink tissues such as roots in fast-growing plants. Recent evidence on a limited number of species, seedlings, or woody organs has suggested the existence of a growth-storage trade-off within and among species (O'Brien *et al.*, 2014; Blumstein *et al.*, 2022; Signori-Müller *et al.*, 2022). Allocation to storage could be prioritized over growth under severe C-limited conditions (Weber *et al.*, 2018; Reyes-Bahamonde *et al.*, 2021). Our finding of the close linkage between NSC storage and the LES provides evidence of the leaf-level growth-storage trade-off exhibited across populations and species.

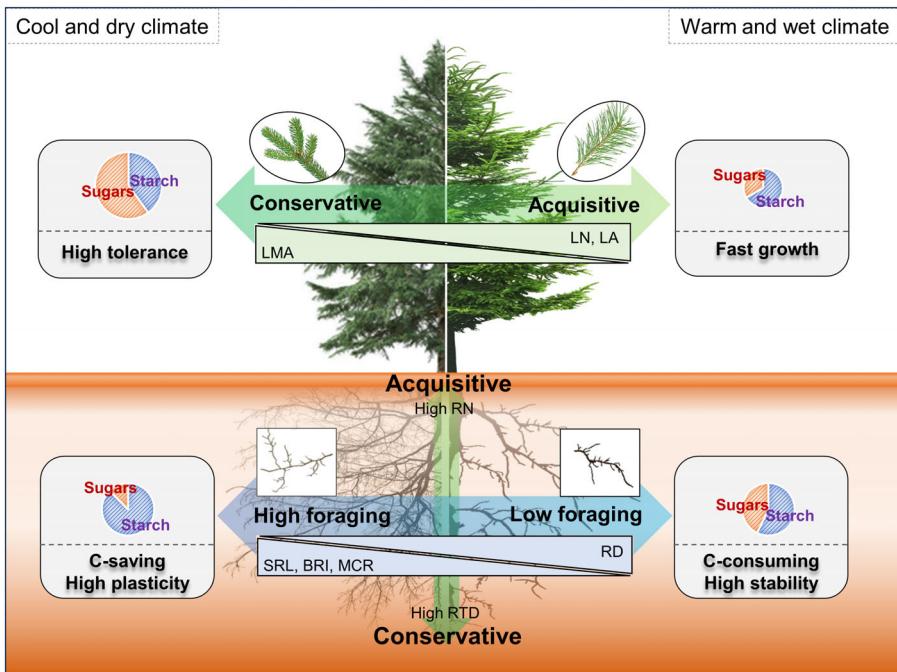
In fine roots, however, NSC component storage concentrations were strongly associated with the foraging dimension but not the conservation-acquisition trade-off across populations and species. Contrary to the complementary interaction observed in arbuscular mycorrhizal plants (Bergmann *et al.*, 2020), we observed a synergistic foraging relationship between roots and mycorrhizal fungi, as thinner and more branched roots exhibited a higher degree of ECM colonization (Fig. 2f). This result is in line with previous studies on ECM species and likely stems from the dependence of ECM colonization on root branching (Yan *et al.*, 2022; Ding *et al.*, 2023). Together, the thinner, longer, more branched, and intensely mycorrhizal-colonized characteristics confer a higher foraging efficiency on the roots. Interestingly, such forage-efficient roots tended to accumulate more starch but less soluble sugars (Figs 2f–j, S4b, S6). This finding was against previous observations that root NSC storage levels were positively associated with root acquisitive traits such as fine root respiration and tissue N concentrations (Rothstein *et al.*, 2000; Desrochers *et al.*, 2002; Zhu *et al.*, 2022). It suggests that the trade-off between growth/respiration and storage does not exist in fine roots, emphasizing the relevance of NSC fractions in mediating fine root foraging efficiency. Such contrasting coordination of NSC with the economics space in leaves and roots suggests distinct NSC functions between the above- and belowground organs within a given life-history strategy.

#### Leaf soluble sugars and root sugar : starch ratios coupled to plant economics traits

In contrast to our second hypothesis that starch is more closely linked to plant conservative strategies than sugars, we found that the linkage of NSC with LES was largely attributed to variation in soluble sugar rather than starch. Leaf starch concentrations were independent of the conservation-acquisition trade-off

(Fig. 2c), but appeared to be relevant to photosynthetic capacity as indexed by leaf  $\delta^{13}\text{C}$  (Figs S4a, S5a). By contrast, trees with traits aligned more with the conservative end of the spectrum tended to store higher concentrations of soluble sugars. Moreover, such coordination between leaf sugar storage and leaf conservative strategy was largely driven by local temperature and precipitation (Fig. 4), implying the importance of the immediate function of sugar over the future use of starch in conferring a fitness benefit. This is in line with previous reports that plants growing under cold or water deficits often have higher leaf sugar storage (Thalmann & Santelia, 2017; Signori-Müller *et al.*, 2021). This result may be attributed to the essential function of sugars in enhancing plant resistance or tolerance via osmoregulation, phloem loading, membrane protection, and the sustained maintenance of metabolism (O'Brien *et al.*, 2014; Lintunen *et al.*, 2016). Leaves in a cooler and drier environment would have greater sugar demands for osmotic homeostasis and membrane stabilization to support leaf stress tolerance (Saddhe *et al.*, 2021). However, starch in leaves serves as a temporal storage form of photosynthesis products, which is highly dynamic and related to the circadian clock, and daily to seasonal photosynthesis fluctuation (Smith & Zeeman, 2020; Wang *et al.*, 2022). As a result, compared with starch, the closer coordination of leaf soluble sugar with the conservative-acquisitive strategies indicated a trade-off between growth rates and leaf stress tolerance, which might ultimately be an important clue to understanding forest resistance and adaptation to future climate changes.

In fine roots, sugar and starch concentrations exhibit inverse correlations with root foraging efficiencies (Fig. 2g,h), and their variation was largely driven by stand precipitation (Fig. 4). In drier climates, fine roots became thinner and stored more starch but less soluble sugars, implying that a shift in C storage preference from readily to long-term accessible C may mediate fine root foraging and adaptation to water availability. The negative correlation observed between root soluble sugar storage and foraging efficiency may be intrinsically attributed to the strong dependence of fine root metabolism on recently assimilated photosynthates (Högberg *et al.*, 2001; Lynch *et al.*, 2013). In the examined coniferous trees, thinner roots often have more branches, higher specific surface areas, higher root respiration, and rapid turnover (Ding *et al.*, 2020). Besides, the greater branching in thinner roots allows for more intense ECM colonization (Fig. 2f), due to the heavy dependence of ECM fungi on the branching structure for symbiosis (Brundrett, 2002; Comas & Eissenstat, 2009; Yan *et al.*, 2022). Soluble sugars, as the direct substrates for metabolism, may be more rapidly consumed in thinner roots via processes such as greater root respiration, C-nutrient exchange with ectomycorrhizal fungi, proliferation, and exudation. Moreover, limited C transport capacity resulting from smaller phloem sizes in thinner roots, combined with decreased photosynthetic C supply under water stress, would also lead to diminished C flow toward fine roots (Kong *et al.*, 2021). This lower supply of recently assimilated photosynthate and rapid C consumption might together contribute to lower sugar concentrations in thin roots. Conversely, thicker roots would favor more



**Fig. 5** Conceptual framework illustrating the contrasting coordination of non-structural carbohydrate (NSC) and its components with economics spectrums in leaves and roots. Leaf total NSC and soluble sugar storage levels align with the leaf economics spectrum, ranging from high tolerance in cool and dry conditions to fast growth in warm and wet conditions. In fine roots, however, total NSC and its component storage are decoupled from the root economics spectrum. Storage preference (sugar or starch) is intimately related to root foraging traits, with foraging-efficient thin roots preferentially accumulating starch (C-saving) to enhance forage plasticity in drier conditions, and forage-inefficient thick roots prioritizing sugar (C-consuming) to increase stability in wetter conditions. BRI, branching intensity; LA, leaf area; LMA, leaf mass per area; LN, leaf nitrogen concentrations; MCR, mycorrhizal colonization rates; RD, root diameter; RN, root nitrogen concentrations; RTD, root tissue density; SRL, specific root length.

sugar reserve through enhanced phloem transport, creating greater water potential gradients from the root cells to the soil that facilitate water and nutrient absorption. The higher sugar storage would also support the longer longevity of the thick roots by supplying readily available C for metabolism and resource uptake.

Root starch was found to be positively correlated with root foraging efficiency. The thinner the roots and the higher the BRI, the higher the starch concentrations (Figs 2h, S3c). This positive correlation may stem from the role of starch in mediating fine root proliferation for soil resource exploration. Starch is immobile and metabolically inert, so storing more starch rather than sugars can reduce C loss for maintenance respiration in thinner fine roots that require a high C investment in resource foraging. Moreover, starch can provide labile and flexible C for transportation and utilization via degradation into soluble sugars (Di Iorio *et al.*, 2016). This dynamic C supply has been proven to play a major role in regulating fine root elongation and growth (Wang *et al.*, 2018; Tang *et al.*, 2022), particularly for short-lived thin roots that rely on root proliferation to generate more absorptive surfaces (Eissenstat *et al.*, 2015; Liu *et al.*, 2015; Bergmann *et al.*, 2020). Additionally, the proliferation of mycorrhizal hyphae also constitutes a vital strategy for nutrient foraging, especially in ECM-dominated trees (Chen *et al.*, 2016). Higher starch storage in thinner roots may ensure their greater plasticity and adaptability to heterogeneous environments, by supplying a C source for new root growth, rapid turnover, and symbiotic mycelial expansion, thereby facilitating efficient resource acquisition from the soil.

Further, the dominant role of precipitation in driving both carbohydrate storage and root foraging suggests a coupled C storage-resource foraging role in regulating tree adaptation to water availability. Numerous studies have shown consistent results that

climatic dryness shapes thinner and deeper root systems of trees to improve soil water and nutrient acquisition (Chapman *et al.*, 2012; Zhou *et al.*, 2018). Studies on fine root NSC dynamics showed that starch deposition occurred in very fine roots under drought and could be remobilized for recovery (Di Iorio *et al.*, 2016; Kannenberg *et al.*, 2018). One drought modulation study also found that starch accumulation co-occurred with decreasing RD and increasing SRL as drought intensity increased (Ji *et al.*, 2020). Our finding of the diametrically opposed changes in starch and sugars with root foraging efficiency along precipitation gradients, indicates a shift in C allocation strategy for adapting to varying water conditions. This involves the adoption of a 'C-saving' strategy via starch accumulation by thin roots, allowing for flexible C supply that enables efficient resource foraging under water deficiency, as opposed to a 'C-consuming' strategy by thick roots that retain soluble sugars for immediate function and stable C utilization to enhance root longevity in wetter conditions (Fig. 5). Such a shift in C storage modes contributes to the trade-off between resource foraging efficiency and root life span, which has great impacts on plant tolerance and adaptation to various environments. Moreover, it is worth noting that coarse roots, as critical organs for storing NSCs, may significantly contribute to plant foraging and survival through mobilizing reserves to absorptive roots (Aubrey & Teskey, 2018; Kannenberg *et al.*, 2018). Further research is warranted to fully grasp the coordination of NSC storage across various root types in relation to tree foraging and survival strategies.

## Conclusion and implications

Across 90 alpine coniferous populations, we observed strong coordination between NSC storage and plant economic strategies with opposing coordination patterns between leaves and roots

(Fig. 5). Leaf NSC, particularly the storage of soluble sugar, aligned with a conservative strategy. This arises from the trade-off between growth rates and leaf sugar-triggered tolerance to cold and water deficiency. By contrast, root NSC was decoupled from the root conservation dimension, while its two major components, sugars and starch, were inversely related to the root foraging dimension. This coupling of root NSC storage modes with root foraging was mainly driven by stand precipitation, suggesting a trade-off in C investment for foraging plasticity against stability across precipitation gradients. These findings indicate NSC is utilized for distinct strategical syndromes in leaves and fine roots, with significant implications for our knowledge of plant carbon allocation mechanisms that underline plant life-history strategies. This is the first attempt to integrate plant carbohydrate storage into plant above- and belowground growth strategy frameworks. To establish the generalizability of our findings, more studies over a broader range of species, biomes, and evolutionary histories are warranted. Additionally, conducting common-garden experiments or environmental manipulations is crucial to ascertaining the influence of genetic vs environmental factors on the observed patterns. Given the projected significant atmospheric warming and precipitation pattern alternation on the Tibetan Plateau as well as globally (Chen *et al.*, 2022), incorporating the role of carbohydrate storage into plant ecological strategies will be an important future direction to adequately understand and predict forest persistence and vegetation dynamics under climate change.

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## Competing interests

None declared.

## Author contributions

PZ, JD, HY and DK conceived and designed the experiments. PZ, JD and QW conducted the fieldwork and laboratory analysis. PZ and JD contributed to data analysis and interpretation of results. PZ, JD, QW, NGM, YT, DK and HY wrote and revised the manuscript. PZ and JD contributed equally to this work.

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## Data availability

The data that support the findings of this study are openly available in figshare repository at doi: [10.6084/m9.figshare.25040669](https://doi.org/10.6084/m9.figshare.25040669).

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Density plot and variance partitions of the  $\text{NSC}_T$  and its component concentrations in leaves and roots.

**Fig. S2** Boxplots depicting the distribution of leaf and root economics traits.

**Fig. S3** Principal component analysis and variable contribution to the first five PC axes of the key economics traits,  $\text{NSC}_T$  and its components in leaves ( $n=17$ ) and roots ( $n=24$ ) across species.

**Fig. S4** Correlation matrix between key economics traits,  $\text{NSC}_T$  and its components, and plant trait dimensions.

**Fig. S5** Principal component analysis of the leaf traits, concentrations of  $\text{NSC}_T$ , soluble sugars, starch, and their ratios across populations.

**Fig. S6** Principal component analysis of the root traits, concentrations of soluble sugars and starch, and their ratios across populations.

**Fig. S7** Correlation matrix between leaf and root economic strategies,  $\text{NSC}_T$ , and its components.

**Table S1** Variance partitions of total non-structural carbohydrates and its component concentrations in leaves ( $n=74$ ) and roots ( $n=79$ ) across the *Pinus*, *Picea*, *Abies*, and *Larix* forests.

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