Check for updates

Received: 8 June 2021 | Accepted: 24 October 2021

DOI: 10.1111/1365-2435.13971

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Variation of non-structural carbohydrates across the fast–slow continuum in Amazon Forest canopy trees

Caroline Signori-Müller[1,2,3] | Rafael S. Oliveira[4] | Julia Valentim Tavares[3] | Francisco Carvalho Diniz[3] | Martin Gilpin[3] | Fernanda de V. Barros[1,5] | Manuel J. Marca Zevallos[6,7] | Carlos A. Salas Yupayccana[7] | Alex Nina[7] | Mauro Brum[8,5] | Timothy R. Baker[3] | Eric G. Cosio[9] | Yadvinder Malhi[10] | Abel Monteagudo Mendoza[6] | Oliver L. Phillips[3] | Lucy Rowland[1] | Norma Salinas[9,10] | Rodolfo Vasquez[11] | Maurizio Mencuccini[12,13] | David Galbraith[3]

[1]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK; [2]Department of Plant Biology, Institute of Biology, Programa de Pós Graduação em Biologia Vegetal, University of Campinas, Campinas, Brazil; [3]School of Geography, University of Leeds, Leeds, UK; [4]Department of Plant Biology, Institute of Biology, University of Campinas, Campinas, Brazil; [5]Department of Plant Biology, Institute of Biology, Programa de Pós Graduação em Ecologia, University of Campinas, Campinas, Brazil; [6]Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru; [7]Pontificia Universidad Católica del Perú, Lima, Perú; [8]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA; [9]Sección Química, Pontificia Universidad Católica del Perú, Lima, Peru; [10]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK; [11]Jardín Botánico de Missouri, Pasco, Peru; [12]CREAF, Campus UAB, Cerdanyola del Vallés, Spain and [13]ICREA, Barcelona, Spain

Correspondence
Caroline Signori-Müller
Email: c.signori-muller@exeter.ac.uk

Funding information
Natural Environment Research Council, Grant/Award Number: NE/N004655/1 and NE/S011811/1; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 140353/2017-8; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior

Handling Editor: C. E. Timothy Paine

Abstract

1. Tropical tree species span a range of life-history strategies within a fast–slow continuum. The position of a species within this continuum is thought to reflect a negative relationship between growth and storage, with fast-growing species allocating more carbon to growth and slow-growing species investing more in storage. For tropical species, the relationship between storage and life-history strategies has been largely studied on seedlings and less so in adult trees.
2. We evaluated how stored non-structural carbohydrates (NSC) vary across adult trees spanning the fast–slow continuum in the Peruvian Amazon by: (a) analysing whole-tree NSC in two species of contrasting growth and (b) investigating the relationships with key life-history traits across a broader set of species.
3. Our results are consistent with a growth–storage trade-off. The analysis of whole-tree NSC revealed that the slow-growing *Eschweilera coriacea* stored about 2.7 times as much NSC as the fast-growing *Bixa arborea* due to markedly higher storage in woody stems and roots. *B. arborea* also had higher seasonality in NSC, reflecting its strong seasonality in stem growth. Across a range of species, stem starch was negatively related to species growth rate and positively related to wood density.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2021 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

4. Given the role of NSC in mediating plants' response to stress, our results suggest that slow-growing species with greater storage reserves may be more resilient to drought than fast-growing species.

KEYWORDS
fast-growing, slow-growing, soluble sugars, starch, tropical

1 | INTRODUCTION

Amazon forest tree species vary markedly in their life-history strategies, exhibiting an approximately 50-fold variation in stem growth rates (Coelho de Souza et al., 2016a). This fast–slow growth continuum fundamentally shapes Amazon forest ecology, driving basin-wide patterns of tree mortality by means of a pervasive growth-survival trade-off (Esquivel-Muelbert et al., 2020), which in turn controls regional biomass storage (Johnson et al., 2016). The position of a species along the fast–slow growth continuum may have important consequences for resistance to climate stressors (Oliveira et al., 2021) and to disease (Fine et al., 2006), but the underlying mechanisms which underpin different life-history strategies remain unclear. Photosynthetic assimilate is predominantly used for respiration, growth or storage. Whereas the respiration:photosynthesis ratio is narrowly constrained across species, growth rate and storage vary more freely, giving rise to a trade-off between carbon allocation to growth on the one hand (fast-growing species), and carbon allocation to storage and defence on the other hand (slow-growing species; King et al., 2006; Van Oijen et al., 2010). This trade-off has been postulated to drive differences in life-history strategies of tropical trees (Kitajima, 1996; Poorter & Kitajima, 2007).

Combinations of plant functional traits result in particular life-history strategies (Salguero-Gómez et al., 2016). For example, hard-wooded species which invest in wood of high mechanical strength have slow growth rates and are expected to have increased investment in storage (Herrera-Ramírez et al., 2021; King et al., 2006). This is often an advantageous strategy in habitats with low nutrient availability and other environmental stress, as it enhances plant capacity to survive pathogen attack, biomass loss or abiotic stress (Aleixo et al., 2019; O'Brien et al., 2014; Oliva et al., 2014; Quentin et al., 2015). In contrast, soft-wooded fast-growing species have high water demand and photosynthetic rates, enabling faster growth, but reducing resistance to drought-induced embolism (Chave et al., 2009; Hacke et al., 2006; Mcculloh et al., 2012; Oliveira et al., 2021) and may be associated with lower carbon storage, that is non-structural carbohydrates (NSC; Falchi et al., 2020; Herrera-Ramírez et al., 2021; Poorter & Kitajima, 2007). However, there have been very few empirical studies exploring the relationship between storage and life-history strategies, particularly in adult tropical trees.

Non-structural carbohydrates are the major form of energy storage in many plant species and have been shown to play a critical role in maintaining hydraulic function and enhancing survival during drought (Guo et al., 2020; Liu et al., 2018; O'Brien et al., 2014; Tomasella et al., 2017). Starch and soluble sugars comprise the most significant portions of NSC reserves in most tree genera (Martínez-Vilalta et al., 2016), but other compounds such as lipids also play an important role as storage (Herrera-Ramírez et al., 2021; Hoch et al., 2003). Soluble sugars are involved in multiple functions such as supporting new growth, for respiration and defence, regulating stress-related genes and acting as osmoprotectants mitigating the negative effect caused by water stress (Krasensky & Jonak, 2012; MacNeill et al., 2017; Rosa et al., 2009; Sapes et al., 2019; Signori-Müller et al., 2021a). Starch is a storage compound for future use that under challenging environmental conditions can be remobilized to soluble sugars to sustain the necessary carbon supply for metabolic functions (Aubrey & Teskey, 2018; MacNeill et al., 2017; Signori-Müller et al., 2021a; Sulpice et al., 2009; Thalmann & Santelia, 2017).

Our current understanding of how NSC interacts with the fast–slow tree species continuum is fragmented and has largely been informed by studies on seedlings. Studying species with different life-history strategies, Poorter and Kitajima (2007) found that stem sugar concentrations and pools of seedlings of species occurring in moist tropical forests in Bolivia were positively correlated with survival but negatively correlated with stem growth. Recently, O'Brien et al. (2020) used ^{13}C pulse labelling to track sugar and starch movement through seedlings of two contrasting conservative and acquisitive species from Borneo. Their results showed clear differences in carbon allocation and dynamics between species under experimental drought, as the conservative species allocated more sugars to stems and roots. However, patterns observed in seedlings may not be readily extrapolated to mature trees (Hartmann et al., 2018). For example, Signori-Müller et al. (2021a) measured leaf and branch NSC concentrations in 82 Amazonian tree species and found no relationship between these and species-level growth and mortality rates. However, that study did not consider the major plant woody storage organs, including stems and coarse roots (Würth et al., 2005). The elucidation of the functional role of storage in the fast–slow continuum requires assessing NSC dynamics across multiple plant organs in adult trees of species with contrasting life-history strategies. A priori, slow-growing species would be expected to have greater NSC concentrations/pools in longer term storage tissues (e.g. stem, coarse roots) than fast-growing species which primarily allocate carbon to growth over storage (Herrera-Ramírez et al., 2021; Smith & Stitt, 2007). Fast-growing species may also have more seasonal NSC dynamics as these have been found to concentrate most of

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

their growth in the wet season, compared to slow-growing species (Rowland et al., 2014).

In this study, we tested the hypotheses that (a) slow-growing species have higher NSC concentrations, especially in woody storage organs; (b) fast-growing species have greater seasonal variability in NSC content; and (c) concentrations of NSC and its components are positively correlated with wood density but negatively correlated with growth and mortality rates. To address these hypotheses, we worked within a mature tropical moist forest in south-western Amazonia. To test hypotheses (a) and (b), we analysed total NSC concentrations (NSC_T) and its components (i.e. starch and soluble sugars) in 17 different tree compartments in two contrasting evergreen species over two seasons. We worked with the slow-growing, widespread Neotropical species *Eschweilera coriacea* (DC.) S. A. Mori, the most common non-palm Amazonian tree species, and the fast-growing widespread Neotropical species *Bixa arborea* Huber. To test hypothesis (c), we collected stem samples from 11 species and used available leaf and branch NSC data from 21 species in our study site spanning a broad range of wood density and growth rates.

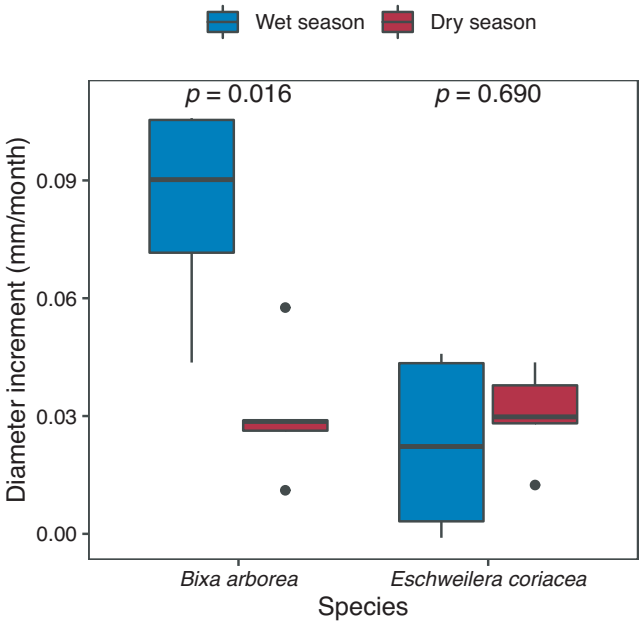


FIGURE 1 Mean increment in diameter (mm/month) during the wettest quarter (January to March) and driest quarter (July to August) for *Bixa arborea* and *Eschweilera coriacea*, measured with stem dendrometer bands from January 2006 to December 2010 in the Tambopata National Reserve (plot TAM-05). Data are from Rowland et al. (2014), *B. arborea* $n = 18$ trees and *E. coriacea* $n = 8$ trees. Each box encompasses the 25th to 75th percentiles; the median is indicated by the horizontal line within each box while external horizontal lines indicate the 10th and 90th percentiles; dots indicate outliers. To test for differences between seasons, we used paired-sample Wilcoxon tests

2 | MATERIALS AND METHODS

2.1 | Field collection and sampling strategy

We performed our sampling in the Tambopata National Reserve, in Madre de Dios, southern Peru (12°49′S, 69°16′W). Permit for sampling collection was granted for Dirección de Gestión de las Áreas Naturales Protegidas (SERNANP) no. 039-2016-SERNANP-RNTAMB-PRD, and permit to import samples from Peru to Brazil to carry out the NSC analysis was conceded by Ministério da Agricultura, Pecuária e Abastecimento, Oficio nº 334/2016/SSV-SP - MAPA.

This site has a mean annual precipitation of 2,451 mm/year and a dry season length, that is ≤100 mm/month of approximately 3 months, from June to August (Signori-Müller et al., 2021a). At this site we selected two contrasting evergreen canopy tree species, *Eschweilera coriacea* (Lecythidaceae) and *Bixa arborea* (Bixaceae). *E. coriacea* is one of the most dominant species in the Amazon Basin (Fauset et al., 2015) and is a shade-tolerant species with low mean diameter growth rate (mean basin-wide growth rate of 0.17 cm/year) and high wood density (0.85 g/cm^3; Chave et al., 2009; Coelho de Souza et al., 2016a; Zanne et al., 2009). *B. arborea* is a light-demanding tree species with high diameter growth rates (mean basin-wide growth rate of 0.56 cm/year) and low wood density (0.37 g/cm^3; Chave et al., 2009; Coelho de Souza et al., 2016a; Zanne et al., 2009). These species also differ in their seasonal stem growth patterns, with *B. arborea* exhibiting markedly higher growth rates in the wet season while *E. coriacea* does not display seasonality in growth (Figure 1).

We collected samples from three individuals per species, all mature trees with canopies exposed to full sunlight and without liana infestation or visible structural damage. For both species, all sampled trees have DBH between 20 and 30 cm, common diameters for adult trees of these species in our study plot [Rowland et al., 2014; *B. arborea* mean ± *SE* 18.87 ± 1.46 cm ($n = 18$); *E. coriacea* 19.36 ± 2.52 cm ($n = 8$)]. The selected trees were sampled in the wet (January 2017) and in the dry (July 2017) seasons, and since NSC concentrations may vary depending on the time of the day, especially in leaves (Tixier et al., 2018), we standardized the sampling time to be between 08:30 and 10:00 a.m. for both species. For each tree, we sampled leaves, branches, stem wood, coarse roots and fine roots, in different tree strata. In the field and during the transport to the laboratory, samples were kept on ice, with the time taken to the laboratory from the plot being approximately 45 min. Upon arrival at the laboratory, we microwaved the samples for 90 s at 700 W to stop enzymatic processes and oven-dried at ~60°C for at least 48 hr or until they were completely dry (no more than 72 hr).

As there is no consensus about the within-organ variability in NSC concentration across studies (Furze, Huggett, et al., 2018; Smith, Miller, et al., 2018; Würth et al., 2005), we performed a detailed sampling within organs to ensure that the within-organ variation in NSC concentrations was well-captured in the two contrasting species. We sampled leaves and branches from three different positions of the canopy: (a) sunlit, (b) partially shaded and (c) fully shaded. Sunlit was defined as the outermost branches of the top third of

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the canopy, partially sunlit was defined as the outer branches of the middle third of the canopy and shaded was defined as the most shaded branches found in the interior of the canopy. We used a 4.3-mm increment borer to sample coarse roots and stem wood (Haglöf Company Group). Roots were sampled by excavating close to the junction between the roots and the main trunk, and following and sampling the same coarse roots in three different depths: 5, 55 and 105 cm. At the deepest point, we also collected fine roots (diameter <3 mm). The fine-root sampling was performed only in the slow-growing *E. coriacea*, as in the fast-growing *B. arborea* we did not find fine roots at any depth up to 105 cm (the deepest point sampled). Stem wood samples were obtained at four different heights: (a) close to the ground (5 cm height), (b) at breast height (1.30 m), (c) at approximately 10 m and (d) at maximum stem height above the ground. The maximum height was defined as the highest point in the stem before forking was observable and thus varied from tree to tree. At 5 cm, 10 m and max. height, we cored the trees and took samples ~5 cm long; at breast height, we cored the trees to the centre of the stems.

As the two focal species have different growth rates, we did not use the same stem wood core length for the NSC analyses as this would represent a different number of growth years and environmental conditions for each species. As neither species produces annual growth rings, we calculated the growth rate of each species using inventory data from our study plot (TAM-05; ForestPlots.net; Lopez-Gonzalez et al., 2011). The annual mean growth in DBH (1.3 cm) for the slow-growing *E. coriacea* in this site was 0.26 cm/year, compared to 0.42 cm/year for the fast-growing *B. arborea* in our study plot. For NSC analysis, we removed the bark and phloem and used segment lengths corresponding to ~5-year growth increments (0.26 cm × 5 years = 1.3 cm for *E. coriacea* and 0.42 cm × 5 years = 2.1 cm for *B. arborea*). Stem wood cores obtained at breast height were divided into multiple 5-year growth segments (1.3 cm in length for *E. coriacea* and 2.1 cm in length for *B. arborea*). As DBH differed across individuals, the total number of radial segments (thereafter 'radial profile') varied among individuals. Therefore, we used only the first five segments (representing ~25 years of growth in total), which were common among all trees, to statistically evaluate radial variation in NSC storage (Figure 2).

2.2 | Stem, leaf and branch NSC from other local species

Logistical and financial constraints meant that it was not possible to conduct an intensive multi-compartment sampling of NSC across more than two species. To further investigate whether there is a relationship between NSC and life-history strategy in our study site, we: (a) sampled stem wood from nine additional species (n = 11 species; n = 5–6 trees per species, except for *B. arborea* and *E. coriacea* n = 3); and (b) made use of leaf and branch-level NSC data collected in Tambopata by Signori-Müller et al. (2021a, 2021b) for 21 species (n = 2–3 trees per species). Of the 11 species we sampled for stem wood NSC, eight were also sampled for leaf and branch NSC concentrations (Table 1).

We relate the NSC concentrations to species-level wood density, growth and mortality rates compiled in previous studies (Coelho de Souza et al., 2016b) and in situ branch wood density measurements. The species used for these analyses span a wide range of wood density, mean growth rates and mortality rates (Table 1). Species for

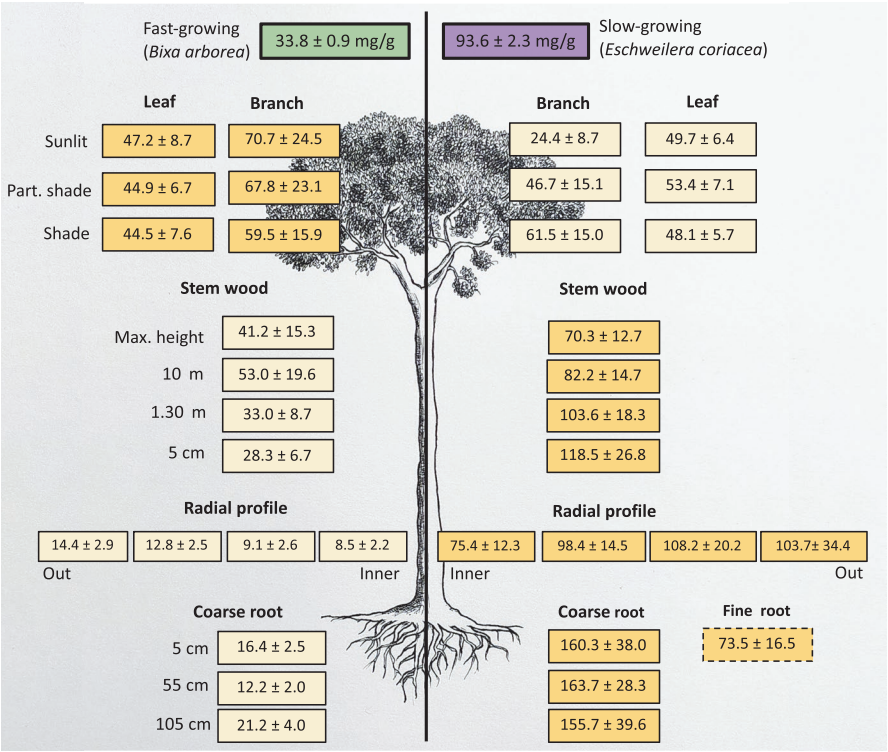


FIGURE 2 Whole-tree NSC_T concentrations (mg/g, mean ± *SE*) in the fast-growing *Bixa arborea* (left) and in the slow-growing *Eschweilera coriacea* (right). The top box depicts the biomass-weighted mean whole-tree NSC_T concentrations for the fast (green box) and slow-growing species (purple box). Components with relatively high storage in each species are shown in dark orange (canopy for *B. arborea* and stems and roots for *E. coriacea*). Mean NSC values were calculated using samples from both the dry and wet seasons (n = 3 trees per species)

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

which we have stem NSC concentration ($n = 11$) represent 30% of the total plot basal area while species sampled for leaf and branch NSC concentrations ($n = 21$) represent 47% of the total plot basal area. All stem wood, branch and leaf samples were collected within RAINFOR permanent plots in the Tambopata National Reserve (ForestPlots et al., 2021; Lopez-Gonzalez et al., 2011) during the wet season in January 2017.

Stem wood samples for the broader set of species were obtained at breast height (1.30 m). Unlike for *B. arborea* and *E. coriacea*, we did not core up to the centre of the tree but took cores of 3–6 cm in length. For these species, we used the same methodology as for *B. arborea* and *E. coriacea*, whereby we calculated the mean annual diameter growth of each species based on local inventory data and took cores corresponding to 5 years of growth.

The branch and leaf NSC data available in Signori-Müller et al. (2021a, 2021b) were collected earlier in the morning (before 6:00 a.m.) than the *B. arborea* and *E. coriacea* samples collected specifically for this study (08:30–10:00 a.m.). As leaves and branches may exhibit significant diurnal variation in NSC (Tixier et al., 2018), we only used the canopy NSC data from Signori-Müller et al. (2021a, 2021b) to test for relationships with life-history attributes across the broader spectrum of species.

2.3 | Branch wood density

To estimate in situ branch wood density, we sampled 2–3 individuals of each species, we used fully sun-exposed top canopy branches from the same trees NSC were analysed. Branch wood density was measured using the displacement method (Pérez-Harguindeguy et al., 2016). We first cut a branch segments of ~2.5 cm length and 1.2 cm diameter and removed the bark, then we placed the samples in a recipient with filtered water to rehydrate for 24 hr. Subsequently, with the help of a small needle we completely submerged the samples under filtered water in a recipient on a scale (three decimal) to register variations in the weight (volume cm^3). Samples were then oven-dried for 48–72 hr at ~60°C. After drying, we measured the segments' dry weight (g) with a scale (three decimal). Wood density is expressed as the ratio of wood dry mass and wood fresh volume (g/cm^3).

2.4 | Laboratory preparations and NSC analyses

Non-structural carbohydrates are defined here as free, low molecular weight sugars (glucose, fructose, sucrose, etc) plus starch. NSC was analysed as described in Hoch et al. (2002) with minor modifications, as in Rowland et al. (2015) and Signori-Müller et al. (2021a). First, we diluted 15 mg of the ground plant material with 1.6 ml of distilled water and then incubated in a water bath at 90–100°C for 60 min to solubilize sugars. Then we took an aliquot of 700 μl from each sample. We used the remaining aliquot volume (900 μl) to determine soluble sugar concentrations using invertase from *Saccharomyces cerevisiae* (Sigma-Aldrich) to break down sucrose and fructose to glucose. Additionally, for both reaction routines, we used GAHK (Glucose Assay Hexokinase Kit - Sigma-Aldrich) together with phosphoglucose isomerase from *Saccharomyces cerevisiae* (Sigma-Aldrich). The concentration of free glucose was measured photometrically in a 96-well microplate spectrophotometer at 340 mm (EPOCH - Biotek Instruments INC). The aliquot that we initially separated was incubated overnight to react with amyloglucosidase from *Aspergillus niger* (Sigma-Aldrich) to break down the total NSC to glucose. Thereafter total glucose (corresponding to NSC) was determined as described above and starch was calculated as total NSC minus soluble sugars. All NSC values are expressed in mg/g dry mass.

2.5 | Statistical analysis

We performed all statistical analysis using the R software (R Core Team, 2021; www.R-project.org; version 3.4.4) and its base packages. We tested for normality (Shapiro–Wilk) and homogeneity of variances (Fligner-Killeen) for each NSC fraction (NSC_T, soluble sugars and starch) and plant compartment. As NSC_T, starch and soluble sugars were not normally distributed and often contained values close or equal to zero, they were either *log1p* [$y_i = \log_e(x_i + 1)$] transformed prior to parametric analysis or used without transformation in nonparametric analyses, as described below.

To test for differences between different levels within specific organs (e.g. sunlit, partially shaded and shaded leaves or stem wood samples collected at 5 cm, 1.30 m, 10 m and maximum height), ANOVA was used following *log1p* transformation. As there were no differences between levels within organs, species differences and the seasonal variation were evaluated only at the organ scale (i.e. leaf, branch, stem wood, radial profile, root and fine roots) and not separately for each level within an organ (e.g. sunlit leaves). For these analyses, we used the mean organ concentrations across all levels for which we had data (e.g. stem wood samples at 5 cm, 1.30 m, 10 m and maximum height).

Seasonal changes in NSC_T, starch and soluble sugar concentrations within species were tested separately for each organ using nonparametric paired-sample Wilcoxon tests. To evaluate differences between *E. coriacea* and *B. arborea*, we used the nonparametric Kruskal–Wallis test. Relationships between NSC (NSC_T, starch and soluble sugars) and species traits (wood density, growth and mortality rates) were investigated using bivariate linear regression models *lm*() (R base function), following *log1p* transformation for both NSC and traits. For all analyses, we assume a significance level of 0.05.

To calculate whole-tree biomass-weighted mean NSC_T concentrations, we assumed that roots represented 21% of the total biomass for both species (Houghton et al., 2001). Above-ground biomass was allocated across branches, leaves and stems following Marra et al., 2016, who presented biomass allocation ratios separately for pioneer and late-successional Amazonian tree

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Sampled species and their traits

Species	WD_{branch} [a]	WD_{stem} [b]	Meangr[c]	Mort[d]	Sampled
Bertholletia excelsa	0.66	0.62	0.637	0.225	Leaf, Branch
Bixa arborea	0.52	0.37	0.568	—	Whole tree
Brosimum guianense	0.64	0.84	0.186	0.357	Leaf, Branch
Brosimum rubescens	—	0.82	0.171	0.480	Leaf, Branch
Calophyllum brasiliense	0.61	0.58	0.500	—	Leaf, Branch, Stem wood
Cedrelinga cateniformis	0.73	0.50	0.724	—	Leaf, Branch, Stem wood
Clarisia racemosa	0.64	0.58	0.319	0.526	Leaf, Branch
Dialium guianense	0.64	0.87	0.235	0.387	Leaf, Branch
Eschweilera coriacea	0.70	0.85	0.175	0.298	Whole tree
Hebepetalum humiriifolium	0.73	0.87	0.214	0.352	Leaf, Branch
Hevea guianensis	0.51	0.57	0.152	0.343	Leaf, Branch
Hymenaea parvifolia	—	0.87	0.267	—	Stem wood
Leonia glycycarpa	0.56	0.60	0.122	0.928	Leaf, Branch
Licania heteromorpha	0.80	0.81	0.198	0.704	Leaf, Branch, Stem wood
Micropholis guyanensis	—	0.65	0.224	0.615	Stem wood
Minquartia guianensis	0.69	0.78	0.188	0.457	Leaf, Branch
Ocotea bofo	0.61	—	0.294	—	Leaf, Branch
Pourouma guianensis	—	0.38	0.598	2.285	Stem wood
Pourouma minor	0.74	0.43	0.484	1.495	Leaf, Branch, Stem wood
Pouteria torta	0.74	0.76	0.155	0.385	Leaf, Branch, Stem wood
Pseudolmedia laevigata	0.60	0.62	0.169	0.573	Leaf, Branch
Pseudolmedia macrophylla	0.60	0.66	0.160	0.429	Leaf, Branch
Tachigali poeppigiana	0.70	—	0.588	2.147	Leaf, Branch
Tetragastris altissima	0.70	0.70	0.230	0.831	Leaf, Branch, Stem wood

[a] WD_{branch}: wood density (g/cm^3) measured in branches of trees from the Tambopata Nacional reserve.

[b] WD_{stem}: wood density (g/cm^3) measured in the stem. Data referred to the mean species WD for the Amazon Basin. Data from the Global Wood Density database (Chave et al., 2009; Zanne et al., 2009).

[c] Meangr: mean growth rate (cm/year). Species mean growth in the Amazon Basin, estimated as the average of mean growth per year across multiple censuses. Data from Coelho de Souza et al. (2016b).

[d] Mort: mortality rate per species in the Amazon Basin (%/year). Data from Coelho de Souza et al. (2016b).

species (Table 2). As we did not sample fine roots for *B. arborea*, we use only coarse root NSC_T data to scale up to the whole tree. For stem biomass concentrations, we took the mean of all sampled stem components (top to bottom and outer and inner stem segments). To assess the sensitivity of our whole-tree estimates, we also computed biomass-weighted mean NSC concentrations using the biomass distribution values assumed in Würth et al. (2005) (Table S1).

3 | RESULTS

3.1 | Whole-tree NSC patterns in *E. coriacea* and *B. arborea*

We did not find differences in NSC_T, starch and soluble sugar concentrations across light levels (sunlit, partially shaded and shaded) in leaves or branches for either of our focal species (Figure 2; Figures S1 and S2). Similarly, no differences were observed across stem samples obtained at different heights (close to the ground, 1.30 m, 10 m and max. height) or across coarse root samples obtained at different depths (5, 55 and 105 cm). We found no difference across radial profile segments for both species in most NSC fractions evaluated, with the exception that soluble sugar concentrations in *E. coriacea* were two times lower in the innermost segments compared to the outermost segments (Figure S2; $p < 0.05$).

Patterns within organs revealed that NSC concentrations in the slow-growing species are less seasonal than in the fast-growing species (Figure 3). In the slow-growing *E. coriacea*, only branch NSC varied seasonally, with all fractions decreasing considerably from wet to dry season (declines by 70%, 85% and 54% for NSC_T, starch and soluble sugars respectively). In the fast-growing *B. arborea*, NSC in all organs displayed seasonality in at least one fraction (Figure 3), with pronounced dry season decreases in NSC_T in leaves (−49%) and branches (−64%) but with increases in the stem wood (+216%) and in the stem radial profile (+101%). Starch concentration decreased

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

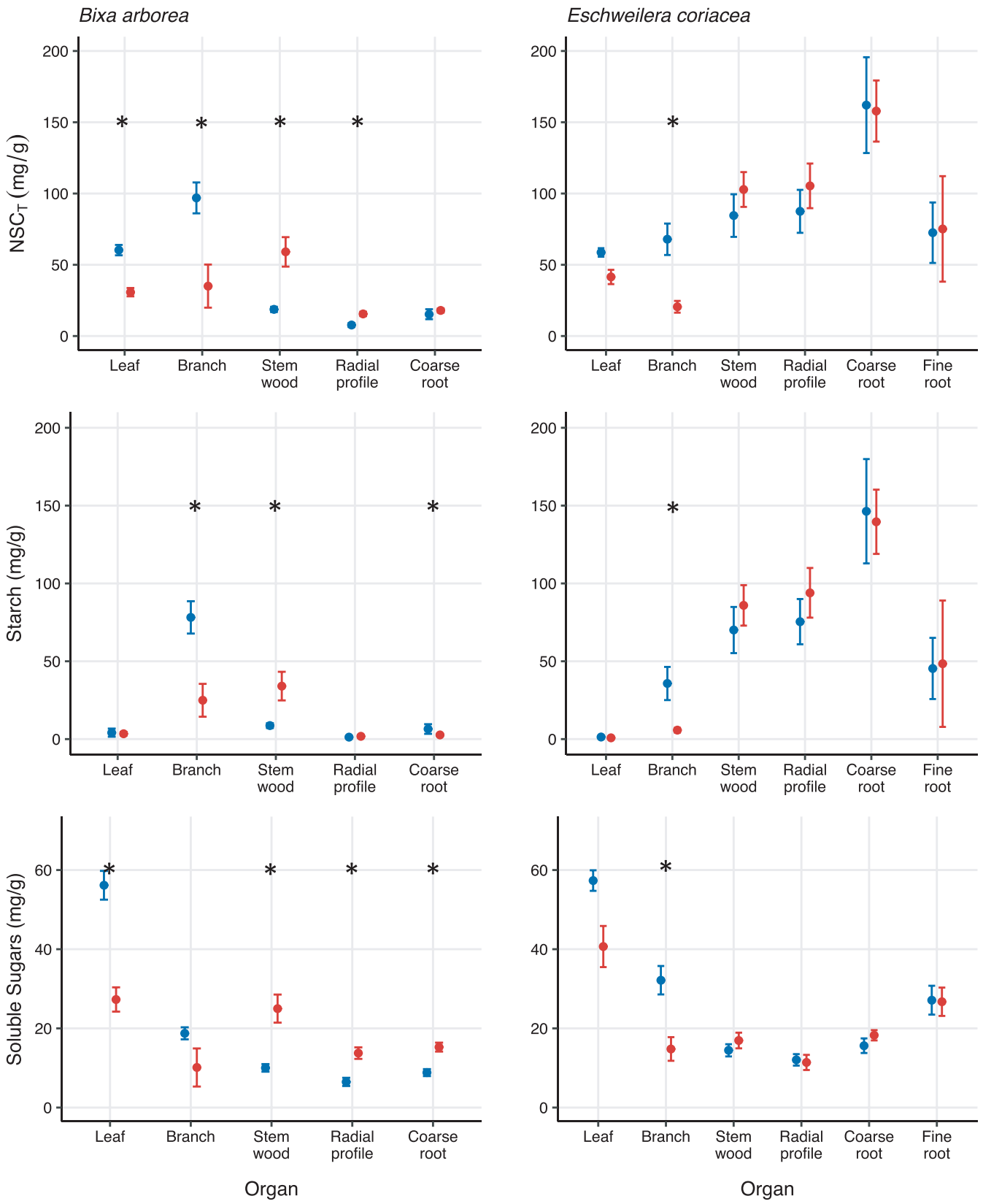


FIGURE 3 Seasonal differences in non-structural carbohydrates (NSC) for each species and organ. Total NSC (NSC$_T$), starch and soluble sugar concentrations in the fast-growing *Bixa arborea* (left) and slow-growing *Eschweilera coriacea* (right). Asterisks denote significant differences between concentrations in wet (blue) and dry (red) seasons calculated using a paired-sample Wilcoxon test. Vertical bars denote 1 standard error of the mean

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

from wet to dry season in branches (−68%) and roots (−59%), but increased in stem wood (+293%). Soluble sugars increased in coarse roots (+73%), stem wood (+149%) and in the stem radial profile (+112%) during the dry season, while in leaves soluble sugar concentrations decreased by 51% (Figure 3).

3.2 | Relationship between NSC and traits across a broader set of species

We found that leaf NSC_T, starch and soluble sugar concentrations are not significantly related to branch wood density, mean growth rate and mortality rate (Figure 4; Figures S4 and S5) across the locally occurring species for which we had data. Branch starch concentrations are negatively related to branch wood density (Figure 4; $p = 0.04$, $R^2 = 0.21$), but not with other traits or NSC fractions (Figures S4 and S5). In contrast, stem starch concentrations across the 11 species for which we had data were positively related to stem wood density ($p = 0.007$; $R^2 = 0.57$) and negatively related to mean growth rate ($p = 0.001$; $R^2 = 0.48$).

4 | DISCUSSION

Overall, our results provide support for our three overarching hypotheses as we found that: (a) mean organ-level NSC concentrations in the slow-growing *E. coriacea* was 2.7 times greater than in the fast-growing *B. arborea*, with much of the difference between them attributable to storage in woody stem and root organs (Table 2); (b) NSC dynamics in *B. arborea* was markedly more seasonal than in *E. coriacea*; and (c) stem NSC_T and starch were positively related to wood density but negatively related to growth rate across a broader set of species. Taken together, these findings are consistent with the alignment of NSC dynamics with life-history strategies and are in line with the existence of a growth–storage trade-off in adult tropical trees (Kitajima, 1996; O'Brien et al., 2020; Poorter & Kitajima, 2007; Van Oijen et al., 2010).

4.1 | Within-tree NSC concentrations

The apparent lack of variation in NSC within organs (Figure 2; Figures S1 and S2) is reassuring for future studies that seek to quantify community patterns in NSC storage, as it suggests that measurements for a single level of a given organ (e.g. the outer part of the stem or the uppermost coarse roots) represent overall organ NSC concentrations well. In the case of vertical profiles of roots and stems, the observed homogeneity with depth/height may indicate a uniform demand for NSC across the profile—for example through similar respiration requirements on a per mass basis throughout the profile. The lack of difference between sunlit and shaded leaves was more unexpected, given the differences in metabolic rates that have been observed between sunlit and shaded leaves (Mathur et al., 2018). However, our results are consistent with a previous assessment along an elevational transect which found that sunlit and shaded leaves differed in leaf mass per area and other leaf traits but not in foliar NSC concentrations (Martin et al., 2020).

The largest differences between species were in starch concentration in the roots and in the inner portions of the stem wood (radial profile), as these were 31 and 56 times higher in the slow-growing *E. coriacea* than in *B. arborea* (Figure 2; Figure S3). The high stem storage of NSC in slow-growing shade-tolerant species is consistent with previous work on seedlings in moist Amazon forests (Poorter & Kitajima, 2007), implying that a similar growth–storage trade-off axis also applies to adult trees within moist tropical forests. Slow-growing, shade-tolerant trees endure strong light limitation as they grow through the canopy and high NSC concentrations are needed to ensure survival during periods of low light (Poorter & Kitajima, 2007). Being longer lived, slow-growing species are also more likely to experience additional stress such as drought. Our results are consistent with a recent study in southern Amazonia which also found that stem NSC storage was higher in slow-growing species (Herrera-Ramírez et al., 2021). Interestingly, a previous study on a semi-deciduous forest in Panama (Würth et al., 2005) did not find a clear relationship between life-history strategy (early and mid-successional species) and NSC storage patterns. However, the differences in life-history strategy considered in that study were not as pronounced as between the two focal species in our study and the semi-deciduous nature of that Panamanian site (Kunert et al., 2021) may have made any growth–storage relationship more difficult to detect.

Very few studies in tropical forests have evaluated NSC concentrations in roots (Newell et al., 2002; Würth et al., 2005). We found that coarse root NSC and starch concentrations in *E. coriacea* were the highest recorded across any organ. Whether this is indicative of a specific life-history strategy or a passive consequence of the slow growth rates in this species is unclear. However, many studies suggest that roots NSC have an important role in plant tolerance to stress (Kannenberg et al., 2018; Mei et al., 2015); and a study based on ^{14}C isotopic analysis shows that relatively old carbon stores can be used to produce new fine roots after environmental disturbance in tropical species (Vargas et al., 2009). This implies that long-term reserves, especially below-ground storage of NSC, may be particularly important for plant survival of slow-growing, shade-tolerant species with significant NSC reserves. However, further sampling is needed to establish the generality of this finding across other species.

Despite the large differences in NSC and starch concentrations between species, soluble sugar concentrations during the dry season were similar between species. These results reinforce the view that soluble sugars, which are used for immediate metabolic activity and not as long-term stores, should be kept above certain thresholds for the maintenance of plant function (Sala et al., 2012; Signori-Müller et al., 2021a).

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

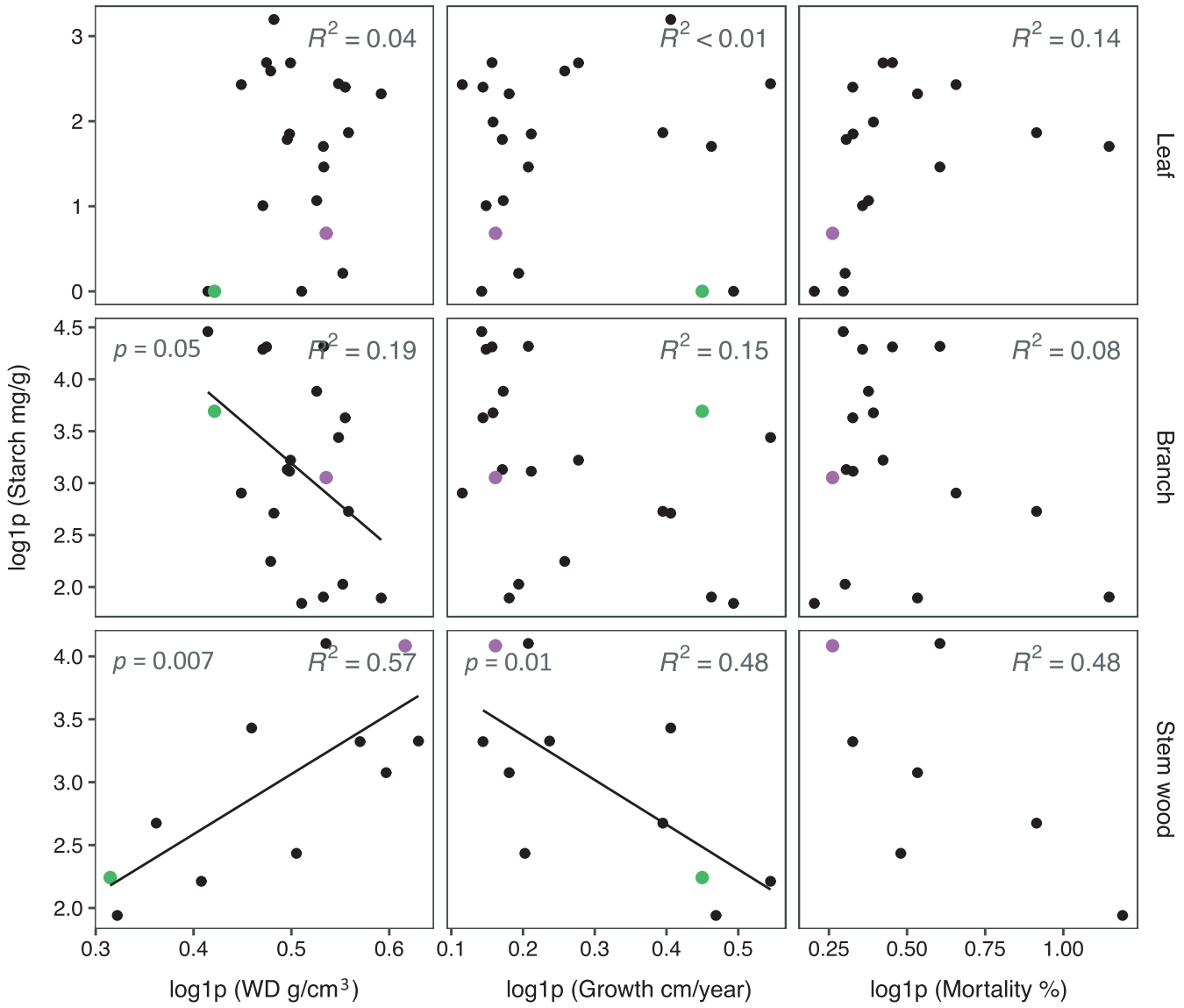


FIGURE 4 Relationship between starch (mg/g) and wood density (WD; g/cm^3), mean growth rate (Growth cm/year) and mortality rate (Mortality %). From top to bottom, relationships are presented for leaves, branches and stems. For relationships between stem starch and WD, we used stem WD, and for relationships with leaf and branch starch, we used branch WD. The R^2 values were calculated using ordinary linear regression. Best-fit lines and *p*-values are displayed only for significant relationships. The relationship between stem starch and mortality rate are marginally significant ($p = 0.08$). Purple dots represent the slow-growing *E. coriacea* and green dots represent the fast-growing *B. arborea*

TABLE 2 Biomass-weighted whole-tree NSC_T concentrations, calculated from the mean NSC_T concentrations in each organ and weighted by the fractional contribution of each organ to total plant biomass. Biomass allocations are obtained from Marra et al. (2016), for pioneer species (*Bixa arborea*) and for late-successional species (*Eschweilera coriacea*). The contribution of below-ground biomass is based on the estimates of Houghton et al. (2001)

	Biomass allocation *B. arborea* (%)	NSC_T concentration *B. arborea* (mg/g)	Biomass allocation *E. coriacea* (%)	NSC_T concentration *E. coriacea* (mg/g)
Leaf	3.8	45.5 ± 1.5	10.2	50 ± 3.4
Branch	23.3	66.0 ± 11.0	20.7	44.2 ± 3.8
Stem	51.8	25.3 ± 6.8	48.1	95.0 ± 14.9
Roots	21	16.3 ± 0.8	21	160.0 ± 47.2
Biomass-weighted mean	Fast-growing	33.8 ± 0.9 mg/g	Slow-growing	93.6 ± 2.3 mg/g

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

4.2 | Seasonal patterns

A previous study in our sampling site evaluated seasonal patterns of tree growth and found that dry season declines in precipitation and soil water content resulted in reduced tree growth, but that the seasonality of growth varied greatly across tree species (Rowland et al., 2014). Seasonality in growth was found to be most pronounced for fast-growing species, suggesting that while plants with a fast strategy have the capability for greater growth in wet season conditions, it is more constrained during the dry season (Rowland et al., 2014). Slow-growing species, on the other hand, were found to have less seasonal growth patterns (Rowland et al., 2014). The differences in seasonality of NSC concentrations between species reflect these contrasting growth patterns (Figure 1) as the fast-growing *B. arborea* was characterized by strong seasonality in almost all components while the slow-growing *E. coriacea* was characterized by an overall lack of seasonality in NSC, except in canopy organs (Figure 3).

Both species showed dry season decreases in NSC concentration in the canopy (leaves and branches). These results were especially consistent for branches, which presented a dry season decrease of ~65% in starch and soluble sugar concentrations in both fast- and slow-growing species. The consumption of branch NSC in the dry season in both species suggests that this may be a phenomenon that is independent of life-history strategy and may represent a mechanism to satisfy increased maintenance demands in the dry season—for example a greater requirement for osmoprotection. Branch NSC consumption is frequently reported in trees, both in temperate or tropical species (Furze, Trumbore, et al., 2018; Martínez-Vilalta et al., 2016; Newell et al., 2002; Würth et al., 2005), suggesting that canopy reserves act as an important carbon buffer during unfavourable periods. Indeed, Signori-Müller et al. (2021a) showed that in sites with more marked dry season almost all species exhibit declines in leaf and branch starch during the dry season, although this effect was less pronounced in more mesic sites such as Tambopata.

The strong depletion of stem starch and soluble sugar concentrations in the wet season in *B. arborea* and not in *E. coriacea* likely reflects the strong differences in the seasonality of growth between the two species (Figure 1; Martínez-Vilalta et al., 2016; Smith, Miller, et al., 2018). Some studies have found that under water limitation conditions growth may cease before photosynthesis, leading to NSC accumulation (Fatichi et al., 2014; Körner, 2003; Muller et al., 2011). The build-up of NSC in *B. arborea* stem wood in the dry season may therefore arise from decreases in carbon demand whereby photosynthate is not utilized for growth. On the other hand, the lack of seasonality in stem NSC observed in *E. coriacea* is consistent with the aseasonality in growth observed for that species. In a recent experimental study with seedlings of two tropical species of contrasting growth rates and drought sensitivity, O'Brien et al. (2020) found that growth of seedlings of the fast-growing species was more restricted under water stress and that this led to a passive accumulation of NSC in the stem. Our results suggest that such a mechanism may also play out in mature trees, but further studies investigating the seasonality of NSC in stem tissues across a spectrum of life-history strategies are needed to establish the generality of this pattern.

We found that root starch concentrations in the fast-growing *B. arborea* decreased by 59% during the dry season in synchrony with an accompanying increase in root-soluble sugars, thus suggesting starch to soluble sugar remobilization (Figure 2). This pattern may be associated with an increased requirement for regulation of osmotic potential and maintenance of water transport from the roots to the canopy (Sánchez et al., 1998). The reduction in starch could potentially also be associated with the production of new roots to enhance water absorption in the dry season or to sustain root respiratory demands. 'Fast' species have higher respiration rates than 'slow' species (Reich, 2014) and maintaining these rates during the unfavourable season may require consumption of root starch reserves. There have been very few studies to date examining seasonal patterns in root reserves in tropical trees. However, the limited number of studies to date has not found strong evidence of seasonal root starch consumption in mature tropical trees under baseline seasonality conditions (Newell et al., 2002; Würth et al., 2005), or during exceptionally dry years (Mauro Brum, personal communication). Further studies are needed to understand whether the dry season root starch consumption in *B. arborea* is also observed in other fast-growing species.

4.3 | Relationship with species traits

Our analyses of NSC concentrations versus species traits are consistent with the hypothesis of a growth–storage trade-off in adult tropical trees, as has been reported previously for seedlings (Poorter & Kitajima, 2007). As expected, we found a positive relationship between starch concentrations in the stem and wood density and a negative relationship with annual growth rates (Figure 4). This is consistent with other studies that associate higher NSC storage with species that have lower growth and mortality rates (Herrera-Ramírez et al., 2021) and hard-wooded tissue with greater resistance to attack by pathogens (Larjavaara & Muller-Landau, 2010). The maintenance of high stocks of starch may be part of a set of ecological strategies, such as high hydraulic safety (Anderegg et al., 2016) that confer lower mortality risks to slow-growing trees (Esquivel-Muelbert et al., 2020). The larger NSC storage in slow-growing trees could increase their ability to tolerate unusually stressful situations through osmoregulation or recovery after periods of water deficit (Nardini et al., 2017; Pagliarani et al., 2019; Savi et al., 2016; Tomasella et al., 2017) and enhance their chances of survival through resprouting, as has been broadly demonstrated to occur in species with high NSC content (Hoffmann et al., 2004; O'Brien et al., 2020; Poorter & Kitajima, 2007; Shibata et al., 2016; Smith, Arndt, et al., 2018).

Our results show that fast-growing species do not maintain sizeable long-term NSC stores in the stem but do maintain NSC reserves in the canopy (i.e. leaves and branches). The positive relationship between branch starch and branch wood density is in line with a study from Panamá (Dickman et al., 2019), suggesting branches

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

may act as an important carbon store for low wood density species. Maintaining starch stocks in the canopy is likely a mechanism that allows these species to quickly mobilize their carbon reserves to priority carbon sinks. Minchin and Thorpe (1996) suggested that sinks closer to sources (leaves) have higher priority in carbon allocation, thus the maintenance of respiration followed by canopy growth and fruit development is often assumed to have the highest carbon priority. Since fast-growing species allocate the assimilated carbon to growth rather than building up longer term stores of NSC, it is possible that they keep their starch reserves closer to the main carbon sinks to allow them to quickly use the reserves for growth, new leaf-flushing or for rapid repair of the hydraulic system in the case of species with low embolism resistance (Nardini et al., 2017; Stitt & Zeeman, 2012; Tomasella et al., 2017; Weber et al., 2019). The lack of relationship between branch NSC and its components with mean stem growth rate (Figure 3) is likely because growth measurements are taken in the stem, and therefore branch NSC storage may not be a good proxy for stem growth.

The relationship between stem NSC and mortality rates across species ($n = 7$, mortality data for four species are missing; Table 1) is similar to that of growth, as species with higher baseline mortality rates had lower NSC storage (Figure 2), although this result was not significant at a 0.05 confidence level ($p = 0.08$). Nonetheless, the general patterns are consistent with a trade-off between storage and survival and reflect the fact that growth and mortality rates are strongly coupled across Amazonian tree species (Esquivel-Muelbert et al., 2020). What remains unclear is the extent of the direct involvement of NSC stores in tree mortality in tropical trees across the life-history continuum. Many studies suggest that tree mortality is driven by the interconnection between water and carbon metabolism (McDowell et al., 2008, 2011; Sala et al., 2010). Understanding the physiological mechanisms associated with plant ecological strategies that can result in different responses to environmental stress is important for predicting changes in species composition and consequently, estimate how much carbon the forest is able to store (Dietze et al., 2014; Jones et al., 2020; Powers, 2020). Shifts in species composition have already been reported across Amazon forests (Esquivel-Muelbert et al., 2018) and future efforts should try to understand how these shifts are related to physiological properties such as NSC storage (Powers, 2020). Our results point to consistent differences in NSC storage between fast- and slow-growing Amazon species and strengthen the evidence of a growth–storage trade-off across Amazon tree species (Coelho de Souza et al., 2016a). Understanding these trade-offs in carbon allocation across species may help us to understand the current and future compositional shifts in Amazon forests.

ACKNOWLEDGEMENTS

Amazon fieldwork and laboratory analyses for this publication were supported by the UK Natural Environment Research Council project TREMOR (NE/N004655/1) to D.G. This paper is an outcome of C.S.-M.'s doctoral thesis in the Plant Biology Program at University of Campinas. C.S.-M., J.V.T., F.B.V., M.B. and R.S.O. were financed by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES Finance Code 001). C.S.-M. received a scholarship from the Brazilian National Council for Scientific and Technological Development (CNPq 140353/2017-8) and CAPES (science without borders 88881.135316/2016-01). D.G. acknowledges further support from the NERC-funded ARBOLES project (NE/S011811/1). R.S.O. acknowledge the São Paulo Research Foundation (FAPESP-Microsoft 11/52072-0). The Amazon forest plots in the RAINFOR network analysed here were established, identified and measured with support from many colleagues and grants mentioned elsewhere (Esquivel-Muelbert et al., 2020). This paper is an outcome of ForestPlots.net approved Research Project #18. The authors especially thank: Rakesh Tiwari for drawing the tree used in Figure 2; Vanessa Hilares and the Asociación para la Investigación y Desarrollo Integral (AIDER) for field campaign support; Hugo Ninantay and Alex Ninantay for sample collection; Fernanda Piccolo for laboratory support; and Grazielle S. Teodoro, Giuliano Locosselli and Peter Groenendyk for their comments on an early version of this manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest. Rafael S. Oliveira is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

C.S.-M., D.G. and R.S.O. designed the study; C.S.-M. led the data analysis; C.S.-M. wrote the manuscript with significant inputs from D.G., R.S.O., M.M., M.B., F.d.V.B., L.R. and O.L.P.; C.S.-M. and J.V.T. led the field sampling; C.S.-M., J.V.T., M.G., F.C.D., M.J.M.Z., C.A.S.Y. and A.N. collected the samples; C.S.-M., F.d.V.B. and M.G. performed the NSC analysis; T.R.B., E.G.C., A.M.M., O.L.P., N.S. and R.V. led the ForestPlots.net field expeditions for data collection; L.R. and Y.M. provided the stem increment data from the two focal species. All authors critically revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The non-structural carbohydrate concentration data are available as data packages via ForestPlots.net, the whole tree and stem data sampled for this study are from https://doi.org/10.5521/forestplots.net/2021_7 (Signori-Müller et al., 2021c), branch and leaf data are from https://doi.org/10.5521/forestplots.net/2021_3 (Signori-Müller et al., 2021b). The mean growth rate, potential tree size and mortality rate are available from https://doi.org/10.5521/FORESTPLOTS.NET/2016_4 (Coelho de Souza et al., 2016b). The inventory data to estimate species growth rate at the study site are from the RAINFOR network (Lopez-Gonzalez et al., 2011; Malhi et al., 2002), available upon request at ForestPlots.net. The increment growth measured with dendrometer bands presented in Figure 1 is from Rowland et al. (2014). All recorded species, genus and family names were checked and standardized using the Taxonomic Name Resolution Service (tnrs.biendata.org).

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ORCID

Caroline Signori-Müller https://orcid.org/0000-0003-1047-1896
Rafael S. Oliveira https://orcid.org/0000-0002-6392-2526
Julia Valentim Tavares https://orcid.org/0000-0003-3784-5720
Fernanda de V. Barros https://orcid.org/0000-0003-3835-2020
Mauro Brum https://orcid.org/0000-0002-9790-254X
Yadvinder Malhi https://orcid.org/0000-0002-3503-4783
Oliver L. Phillips https://orcid.org/0000-0002-8993-6168
Lucy Rowland https://orcid.org/0000-0002-0774-3216
David Galbraith https://orcid.org/0000-0002-5555-4823

REFERENCES

Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F., & Poorter, L. (2019). Amazonian rainforest tree mortality driven by climate and functional traits. *Nature Climate Change*, *9*(5), 384–388. https://doi.org/10.1038/s41558-019-0458-0

Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(18), 5024–5029. https://doi.org/10.1073/pnas.1525678113

Aubrey, D. P., & Teskey, R. O. (2018). Stored root carbohydrates can maintain root respiration for extended periods. *New Phytologist*, *218*(1), 142–152. https://doi.org/10.1111/nph.14972

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*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Coelho de Souza, F., Dexter, K. G., Phillips, O. L., Brienen, R. J. W., Chave, J., Galbraith, D. R., Lopez Gonzalez, G., Monteagudo Mendoza, A., Pennington, R. T., Poorter, L., Alexiades, M., Álvarez-Dávila, E., Andrade, A., Aragão, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Aymard, G. A., Baraloto, C., Barroso, J. G., … Baker, T. R. (2016a). Evolutionary heritage influences Amazon tree ecology. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 20161587. https://doi.org/10.1098/rspb.2016.1587

Coelho de Souza, F., Dexter, K. G., Phillips, O. L., Brienen, R. J. W., Chave, J., Galbraith, D. R., Lopez Gonzalez, G., Monteagudo Mendoza, A., Pennington, R. T., Poorter, L., Alexiades, M., Álvarez-Dávila, E., Andrade, A., Aragão, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Aymard C, G. A., Baraloto, C., Barroso, J. G., … Baker, T. R. (2016b). Trait data from: 'Evolutionary heritage influences Amazon tree ecology'. ForestPlots.Net. https://doi.org/10.5521/FORESTPLOTS.NET/2016_4

Dickman, L. T., McDowell, N. G., Grossiord, C., Collins, A. D., Wolfe, B. T., Detto, M., Wright, S. J., Medina-Vega, J. A., Goodsman, D., Rogers, A., Serbin, S. P., Wu, J., Ely, K. S., Michaletz, S. T., Xu, C., Kueppers, L., & Chambers, J. Q. (2019). Homoeostatic maintenance of nonstructural carbohydrates during the 2015–2016 El Niño drought across a tropical forest precipitation gradient. *Plant Cell and Environment*, *42*(5), 1705–1714. https://doi.org/10.1111/pce.13501

Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantooth, J. A., Richardson, A. D., & Vargas, R. (2014). Nonstructural carbon in woody plants. *Annual Review of Plant Biology*, *65*(1), 667–687. https://doi.org/10.1146/annurev-arplant-050213-040054

Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T. R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., … Phillips, O. L. (2018). Compositional response of Amazon forests to climate change. *Global Change Biology*, *25*(1), 39–56. https://doi.org/10.1111/gcb.14413

Esquivel-Muelbert, A., Phillips, O. L., Brienen, R. J. W., Fauset, S., Sullivan, M. J. P., Baker, T. R., Chao, K.-J., Feldpausch, T. R., Gloor, E., Higuchi, N., Houwing-Duistermaat, J., Lloyd, J., Liu, H., Malhi, Y., Marimon, B., Marimon Junior, B. H., Monteagudo-Mendoza, A., Poorter, L., Silveira, M., … Galbraith, D. (2020). Tree mode of death and mortality risk factors across Amazon forests. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-18996-3

Falchi, R., Petrussa, E., Braidot, E., Sivilotti, P., Boscutti, F., Vuerich, M., Calligaro, C., Filippi, A., Herrera, J. C., Sabbatini, P., Zancani, M., Nardini, A., Peterlunger, E., & Casolo, V. (2020). Analysis of non-structural carbohydrates and xylem anatomy of leaf petioles offers new insights in the drought response of two grapevine cultivars. *International Journal of Molecular Sciences*, *21*(February). https://doi.org/10.3390/ijms21041457

Fatichi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. *New Phytologist*, *201*(4), 1086–1095. https://doi.org/10.1111/nph.12614

Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo M., A., Brienen, R. J. W., Feldpausch, T. R., Lopez-Gonzalez, G., Malhi, Y., ter Steege, H., Pitman, N. C. A., Baraloto, C., Engel, J., Pétronelli, P., Andrade, A., Camargo, J. L. C., Laurance, S. G. W., Laurance, W. F., Chave, J., … Phillips, O. L. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, *6*, 1–9. https://doi.org/10.1038/ncomms7857

Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stevens, M. H. H., Sääksjärvi, I., Schultz, J. C., & Coley, P. D. (2006). The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, *87*(7 Suppl), 150–162. https://doi.org/10.1890/0012-9658(2006)87[150:tgtahs]2.0.co;2

ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., Osinaga-Acosta, O., Bird, M., Bradford, M., Catchpole, D., Ford, A., Graham, A., Hilbert, D., Kemp, J., Laurance, S., Laurance, W., Ishida, F. Y., Marshall, A., Waite, C., … Tran, H. D. (2021). Taking the pulse of Earth's tropical forests using networks of highly distributed plots. *Biological Conservation*, *260*(September 2020). https://doi.org/10.1016/j.biocon.2020.108849

Furze, M. E., Huggett, B. A., Aubrecht, D. M., Stolz, C. D., Carbone, M. S., & Richardson, A. D. (2018). *Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species*. https://doi.org/10.1111/nph.15462

Furze, M. E., Trumbore, S., & Hartmann, H. (2018). Detours on the phloem sugar highway: Stem carbon storage and remobilization. *Current Opinion in Plant Biology*, *43*, 89–95. https://doi.org/10.1016/j.pbi.2018.02.005

Guo, J. S., Gear, L., Hultine, K. R., Koch, G. W., & Ogle, K. (2020). Non-structural carbohydrate dynamics associated with antecedent stem water potential and air temperature in a dominant desert shrub. *Plant, Cell & Environment*, 1–17. https://doi.org/10.1111/pce.13749

Hacke, U. G., Sperry, J. S., Wheeler, J. K., & Castro, L. (2006). Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology*, *26*(6), 689–701. https://doi.org/10.1093/treephys/26.6.689

Hartmann, H., Adams, H. D., Hammond, W. M., Hoch, G., Landhäusser, S. M., Wiley, E., & Zaehle, S. (2018). Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests. *Environmental and Experimental Botany*, *152*, 7–18. https://doi.org/10.1016/j.envexpbot.2018.03.011

Herrera-Ramírez, D., Sierra, C. A., Römermann, C., Muhr, J., Trumbore, S., Silvério, D., Brando, P. M., & Hartmann, H. (2021). Starch and lipid storage strategies in tropical trees relate to growth

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and mortality. *New Phytologist*, *230*(1), 139–154. https://doi.org/10.1111/nph.17239

Hoch, G., Popp, M., & Körner, C. (2002). Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. *Oikos*, *98*(3), 361–374. https://doi.org/10.1034/j.1600-0706.2002.980301.x

Hoch, G., Richter, A., & Körner, C. H. (2003). Non-structural carbon compounds in temperate forest trees. *Plant, Cell & Environment*, *26*(7), 1067–1081. https://doi.org/10.1046/j.0016-8025.2003.01032.x

Hoffmann, W. A., Orthen, B., & Franco, A. C. (2004). Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. *Oecologia*, *140*(2), 252–260. https://doi.org/10.1007/s00442-004-1595-2

Houghton, R. A., Lawrence, K. T., Hackler, J. L., & Brown, S. (2001). The spatial distribution of forest biomass in the Brazilian Amazon: A comparison of estimates. *Global Change Biology*, *7*, 731–746. https://doi.org/10.1111/j.1365-2486.2001.00426.x

Johnson, M. O., Galbraith, D., Gloor, M., De Deurwaerder, H., Guimberteau, M., Rammig, A., Thonicke, K., Verbeeck, H., Randow, C., Monteagudo, A., Phillips, O. L., Brienen, R. J. W., Feldpausch, T. R., Lopez, G. G., Fauset, S., Quesada, C. A., Christoffersen, B., Ciais, P., Sampaio, G., & Baker, T. R. (2016). Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models. *Global Change Biology*, *22*(12), 3996–4013. https://doi.org/10.1111/gcb.13315

Jones, S., Rowland, L., Cox, P., Hemming, D., Wiltshire, A., Williams, K., Parazoo, N. C., Liu, J., da Costa, A. C. L., Meir, P., Mencuccini, M., & Harper, A. B. (2020). The impact of a simple representation of non-structural carbohydrates on the simulated response of tropical forests to drought. *Biogeosciences*, *17*(13), 3589–3612. https://doi.org/10.5194/bg-17-3589-2020

Kannenberg, S. A., Novick, K. A., & Phillips, R. P. (2018). Coarse roots prevent declines in whole-tree non-structural carbohydrate pools during drought in an isohydric and an anisohydric species. *Tree Physiology*, *38*(4), 582–590. https://doi.org/10.1093/treephys/tpx119

King, D. A., Davies, S. J., Tan, S., & Noor, N. S. M. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, *94*(3), 670–680. https://doi.org/10.1111/j.1365-2745.2006.01112.x

Kitajima, K. (1996). Ecophysiology of tropical tree seedlings. In S. S. Mulkey, R. L. Chazdon, & A. P. Smith (Eds.), *Tropical forest plant ecophysiology*. Springer. https://doi.org/10.1007/978-1-4613-1163-8_19

Körner, C. H. (2003). Carbon limitation in trees. *Journal of Ecology*, *91*(1), 4–17. https://doi.org/10.1046/j.1365-2745.2003.00742.x

Krasensky, J., & Jonak, C. (2012). Drought, salt, and temperature stress-induced metabolic rearrangements and regulatory networks. *Journal of Experimental Botany*, *63*, 1593–1608. https://doi.org/10.1093/jxb/err460

Kunert, N., Zailaa, J., Herrmann, V., Muller-Landau, H. C., Wright, S. J., Pérez, R., McMahon, S. M., Condit, R. C., Hubbell, S. P., Sack, L., Davies, S. J., … Anderson-Teixeira, K. J. (2021). Leaf turgor loss point shapes local and regional distributions of evergreen but not deciduous tropical trees. *New Phytologist*, *230*(2), 485–496. https://doi.org/10.1111/nph.17187

Larjavaara, M., & Muller-Landau, H. C. (2010). PERSPECTIVE: Rethinking the value of high wood density. *Functional Ecology*, *24*(4), 701–705. https://doi.org/10.1111/j.1365-2435.2010.01698.x

Liu, W., Su, J., Li, S., Lang, X., & Huang, X. (2018). Non-structural carbohydrates regulated by season and species in the subtropical monsoon broad-leaved evergreen forest of Yunnan Province, China. *Scientific Reports*, *8*(1), 1–10. https://doi.org/10.1038/s41598-018-19271-8

Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., & Phillips, O. L. (2011). ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science*, *22*(4), 610–613. https://doi.org/10.1111/j.1654-1103.2011.01312.x

MacNeill, G. J., Mehrpouyan, S., Minow, M. A. A., Patterson, J. A., Tetlow, I. J., & Emes, M. J. (2017). Starch as a source, starch as a sink: The bifunctional role of starch in carbon allocation. *Journal of Experimental Botany*, *68*(16), 4433–4453. https://doi.org/10.1093/jxb/erx291

Malhi, Y., Phillips, O. L., Lloyd, J., Baker, T., Wright, J., Almeida, S., Arroyo, L., Frederiksen, T., Grace, J., Higuchi, N., Killeen, T., Laurance, W. F., Leaño, C., Lewis, S., Meir, P., Monteagudo, A., Neill, D., Núñez, V. P., Panfil, S. N., … Vinceti, B. (2002). An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science*, *13*(3), 439–450. https://doi.org/10.1111/j.1654-1103.2002.tb02068.x

Magnabosco Marra, D., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., dos Santos, J., Carneiro, V. M. C., Lima, A. J. N., Chambers, J. Q., Negrón-Juárez, R. I., Holzwarth, F., Reu, B., & Wirth, C. (2016). Predicting biomass of hyperdiverse and structurally complex central Amazonian forests – A virtual approach using extensive field data. *Biogeosciences*, *13*(5), 1553–1570. https://doi.org/10.5194/bg-13-1553-2016

Martin, R. E., Asner, G. P., Bentley, L. P., Shenkin, A., Salinas, N., Huaypar, K. Q., Pillco, M. M., Ccori Álvarez, F. D., Enquist, B. J., Diaz, S., & Malhi, Y. (2020). Covariance of sun and shade leaf traits along a tropical forest elevation gradient. *Frontiers in Plant Science*, *10*(January), 1–13. https://doi.org/10.3389/fpls.2019.01810

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*(4), 495–516. https://doi.org/10.1002/ecm.1231

Mathur, S., Jain, L., & Jajoo, A. (2018). Photosynthetic efficiency in sun and shade plants. *Photosynthetica*, *56*(1), 354–365. https://doi.org/10.1007/s11099-018-0767-y

Mcculloh, K. A., Johnson, D. M., Meinzer, F. C., Voelker, S. L., Lachenbruch, B., & Domec, J. C. (2012). Hydraulic architecture of two species differing in wood density: Opposing strategies in co-occurring tropical pioneer trees. *Plant, Cell and Environment*, *35*(1), 116–125. https://doi.org/10.1111/j.1365-3040.2011.02421.x

McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution*, *26*(10), 523–532. https://doi.org/10.1016/j.tree.2011.06.003

Mcdowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., … Sperry, J. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739.

Mei, L., Xiong, Y., Gu, J., Wang, Z., & Guo, D. (2015). Whole-tree dynamics of non-structural carbohydrate and nitrogen pools across different seasons and in response to girdling in two temperate trees. *Oecologia*, *177*(2), 333–344. https://doi.org/10.1007/s00442-014-3186-1

Minchin, P. E. H., & Thorpe, M. R. (1996). What determines carbon partitioning between competing sinks? *Journal of Experimental Botany*, *47*, 1293–1296. https://doi.org/10.1093/jxb/47.special_issue.1293

Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M., & Gibon, Y. (2011). Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, *62*(6), 1715–1729. https://doi.org/10.1093/jxb/erq438

Nardini, A., Savi, T., Trifilò, P., & Lo Gullo, M. A. (2017). Drought stress and the recovery from xylem embolism in woody plants. In F. Cánovas, U. Lüttge, & R. Matyssek (Eds.), *Progress in botany* (Vol. 79). Springer. https://doi.org/10.1007/124_2017_11

Newell, E. A., Mulkey, S. S., & Wright, S. J. (2002). Seasonal patterns of carbohydrate storage in four tropical tree species. *Oecologia*, *131*(3), 333–342. https://doi.org/10.1007/s00442-002-0888-6

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J., & Hector, A. (2014). Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change*, *4*(8), 710–714. https://doi.org/10.1038/nclimate2281

O'Brien, M. J., Valtat, A., Abiven, S., Studer, M. S., Ong, R., & Schmid, B. (2020). The role of soluble sugars during drought in tropical tree seedlings with contrasting tolerances. *Journal of Plant Ecology*, *13*(4), 389–397. https://doi.org/10.1093/jpe/rtaa017

Oliva, J., Stenlid, J., & Martínez-Vilalta, J. (2014). The effect of fungal pathogens on the water and carbon economy of trees: Implications for drought-induced mortality. *New Phytologist*, *203*(4), 1028–1035. https://doi.org/10.1111/nph.12857

Oliveira, R. S., Eller, C. B., Barros, F. D. V., Hirota, M., Brum, M., & Bittencourt, P. (2021). Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist*, *230*(3), 904–923. https://doi.org/10.1111/nph.17266

Pagliarani, C., Casolo, V., Ashofteh Beiragi, M., Cavalletto, S., Siciliano, I., Schubert, A., Gullino, M. L., Zwieniecki, M. A., & Secchi, F. (2019). Priming xylem for stress recovery depends on coordinated activity of sugar metabolic pathways and changes in xylem sap pH. *Plant Cell and Environment*, *42*(6), 1775–1787. https://doi.org/10.1111/pce.13533

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *64*(8), 715. https://doi.org/10.1071/bt12225_co

Poorter, L., & Kitajima, K. (2007). Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology*, *88*(4), 1000–1011. https://doi.org/10.1890/06-0984

Powers, J. S. (2020). A sweet new study: tropical forest species use non-structural carbohydrates in different ways during drought. *Journal of Plant Ecology*, *13*(4), 387–388. https://doi.org/10.1093/jpe/rtaa020

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*(11), 1146–1165. https://doi.org/10.1109/IECON.2017.8217452

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Rosa, M., Prado, C., Podazza, G., Interdonato, R., González, J. A., Hilal, M., & Prado, F. E. (2009). Soluble sugars-metabolism, sensing and abiotic stress a complex network in the life of plants. *Plant Signaling and Behavior*, *4*(5), 388–393. https://doi.org/10.4161/psb.4.5.8294

Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. A. R., Pullen, A. M., Doughty, C. E., Metcalfe, D. B., Vasconcelos, S. S., Ferreira, L. V., Malhi, Y., Grace, J., Mencuccini, M., & Meir, P. (2015). Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, *528*(7580), 119–122. https://doi.org/10.1038/nature15539

Rowland, L., Malhi, Y., Silva-Espejo, J. E., Farfán-Amézquita, F., Halladay, K., Doughty, C. E., Meir, P., & Phillips, O. L. (2014). The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest. *Oecologia*, *174*(1), 295–306. https://doi.org/10.1007/s00442-013-2766-9

Sala, A., Piper, F., & Hoch, G. (2010). Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist*, *186*(2), 274–281. https://doi.org/10.1111/j.1469-8137.2009.03167.x

Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: Feast or famine? *Tree Physiology*, *32*(6), 764–775. https://doi.org/10.1093/treephys/tpr143

Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., Zuidema, P. A., de Kroon, H., & Buckley, Y. M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(1), 230–235. https://doi.org/10.1073/pnas.1506215112

Sánchez, F. J., Manzanares, M., de Andres, E. F., Tenorio, J. L., & Ayerbe, L. (1998). Turgor maintenance, osmotic adjustment and soluble sugar and proline accumulation in 49 pea cultivars in response to water stress. *Field Crops Research*, *59*(3), 225–235. https://doi.org/10.1016/s0378-4290(98)00125-7

Sapes, G., Roskilly, B., Dobrowski, S., Maneta, M., Anderegg, W. R. L., Martinez-Vilalta, J., & Sala, A. (2019). Plant water content integrates hydraulics and carbon depletion to predict drought-induced seedling mortality. *Tree Physiology*, *39*(8), 1300–1312. https://doi.org/10.1093/treephys/tpz062

Savi, T., Casolo, V., Luglio, J., Bertuzzi, S., Trifilo', P., Lo Gullo, M. A., & Nardini, A. (2016). Species-specific reversal of stem xylem embolism after a prolonged drought correlates to endpoint concentration of soluble sugars. *Plant Physiology and Biochemistry*, *106*, 198–207. https://doi.org/10.1016/j.plaphy.2016.04.051

Shibata, R., Kurokawa, H., Shibata, M., Tanaka, H., Iida, S., Masaki, T., & Nakashizuka, T. (2016). Relationships between resprouting ability, species traits and resource allocation patterns in woody species in a temperate forest. *Functional Ecology*, *30*(7), 1205–1215. https://doi.org/10.1111/1365-2435.12616

Signori-Müller, C., Oliveira, R. S., Barros, F. D. V., Tavares, J. V., Gilpin, M., Diniz, F. C., Zevallos, M. J. M., Yupayccana, C. A. S., Acosta, M., Bacca, J., Chino, R. S. C., Cuellar, G. M. A., Cumapa, E. R. M., Martinez, F., Mullisaca, F. M. P., Nina, A., Sanchez, J. M. B., da Silva, L. F., Tello, L., … Galbraith, D. (2021a). Non-structural carbohydrates mediate seasonal water stress across Amazon forests. *Nature Communications*, *12*(1), 2310. https://doi.org/10.1038/s41467-021-22378-8

Signori-Müller, C., Oliveira, R. S., Barros, F. D. V., Tavares, J. V., Gilpin, M., Diniz, F. C., Zevallos, M. J. M., Yupayccana, C. A. S., Acosta, M., Bacca, J., Chino, R. S. C., Cuellar, G. M. A., Cumapa, E. R. M., Martinez, F., Mullisaca, F. M. P., Nina, A., Sanchez, J. M. B., da Silva, L. F., Tello, L., … Galbraith, D. (2021b). Trait data from: Non-structural carbohydrates mediate seasonal water stress across Amazon forests. *ForestPlots.Net*. https://doi.org/10.5521/forestplots.net/2021_3

Signori-Müller, C., Oliveira, R. S., Valentim Tavares, J., Carvalho Diniz, F., Gilpin, M., de V. Barros, F., Marca Zevallos, M. J., Salas Yupayccana, C. A., Nina, A., Brum, M., Baker, T. R., Cosio, E. G., Malhi, Y., Monteagudo Mendoza, A., Phillips, O. L., Rowland, L., Salinas, N., Vasquez, R., Mencuccini, M., & Galbraith, D. (2021c). Trait data from: Variation of non-structural carbohydrates across the fast-slow continuum in Amazon forest canopy trees. *ForestPlots.Net*. https://doi.org/10.5521/forestplots.net/2021_7

Smith, A. M., & Stitt, M. (2007). Coordination of carbon supply and plant growth. *Plant, Cell & Environment*, *30*(9), 1126–1149. https://doi.org/10.1111/j.1365-3040.2007.01708.x

Smith, M. G., Arndt, S. K., Miller, R. E., Kasel, S., & Bennett, L. T. (2018). Trees use more non-structural carbohydrate reserves during epicormic than basal resprouting. *Tree Physiology*, *38*(12), 1779–1791. https://doi.org/10.1093/treephys/tpy099

Smith, M. G., Miller, R. E., Arndt, S. K., Kasel, S., & Bennett, L. T. (2018). Whole-tree distribution and temporal variation of non-structural

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

carbohydrates in broadleaf evergreen trees. *Tree Physiology*, *38*(4), 570–581. https://doi.org/10.1093/treephys/tpx141

Stitt, M., & Zeeman, S. C. (2012). Starch turnover: Pathways, regulation and role in growth. *Current Opinion in Plant Biology*, *15*(3), 282–292. https://doi.org/10.1016/j.pbi.2012.03.016

Sulpice, R., Pyl, E.-T., Ishihara, H., Trenkamp, S., Steinfath, M., Witucka-Wall, H., Gibon, Y., Usadel, B., Poree, F., Piques, M. C., Von Korff, M., Steinhauser, M. C., Keurentjes, J. J. B., Guenther, M., Hoehne, M., Selbig, J., Fernie, A. R., Altmann, T., & Stitt, M. (2009). Starch as a major integrator in the regulation of plant growth. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(25), 10348–10353. https://doi.org/10.1073/pnas.0903478106

Thalmann, M., & Santelia, D. (2017). Starch as a determinant of plant fitness under abiotic stress. *New Phytologist*, *214*(3), 943–951. https://doi.org/10.1111/nph.14491

Tixier, A., Orozco, J., Roxas, A. A., Earles, J. M., & Zwieniecki, M. A. (2018). Diurnal variation in nonstructural carbohydrate storage in trees: Remobilization and vertical mixing. *Plant Physiology*, *178*(4), 1602–1613. https://doi.org/10.1104/pp.18.00923

Tomasella, M., Häberle, K. H., Nardini, A., Hesse, B., Machlet, A., & Matyssek, R. (2017). Post-drought hydraulic recovery is accompanied by non-structural carbohydrate depletion in the stem wood of Norway spruce saplings. *Scientific Reports*, *7*(1), 1–13. https://doi.org/10.1038/s41598-017-14645-w

Van Oijen, M., Schapendonk, A., & Ho, M. (2010). On the relative magnitudes of photosynthesis, respiration, growth and carbon storage in vegetation. *Annals of Botany*, *105*(5), 793–797. https://doi.org/10.1093/aob/mcq039

Vargas, R., Trumbore, S. E., & Allen, M. F. (2009). Evidence of old carbon used to grow new fine roots in a tropical forest. *New Phytologist*, *182*(3), 710–718. https://doi.org/10.1111/j.1469-8137.2009.02789.x

Weber, R., Gessler, A., & Hoch, G. (2019). High carbon storage in carbon-limited trees. *New Phytologist*, *222*(1), 171–182. https://doi.org/10.1111/nph.15599

Würth, M. K. R., Peláez-Riedl, S., Wright, S. J., & Körner, C. (2005). Non-structural carbohydrate pools in a tropical forest. *Oecologia*, *143*(1), 11–24. https://doi.org/10.1007/s00442-004-1773-2

Zanne, A. E., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Chave, J. (2009). Data from: Towards a worldwide wood economics spectrum. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.234

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Signori-Müller, C., Oliveira, R. S., Valentim Tavares, J., Carvalho Diniz, F., Gilpin, M., de V. Barros, F., Marca Zevallos, M. J., Salas Yupayccana, C. A., Nina, A., Brum, M., Baker, T. R., Cosio, E. G., Malhi, Y., Monteagudo Mendoza, A., Phillips, O. L., Rowland, L., Salinas, N., Vasquez, R., Mencuccini, M., & Galbraith, D. (2022). Variation of non-structural carbohydrates across the fast–slow continuum in Amazon Forest canopy trees. *Functional Ecology*, 36, 341–355. https://doi.org/10.1111/1365-2435.13971

13652435, 2022, 2, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13971 by Osu Central Accounts Payable, Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License