

Functional Ecology

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

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Author contributions

CS-M, DG and RSO designed the study. CS-M led the data analysis. CS-M wrote the manuscript with significant inputs from DG, RSO, MM, MB, FVB, LR and OLP. CS-M and JVT led the field sampling. CS-M, JVT, MG, FCD, MJMZ, CASY and AN collected the samples. CS-M, FVB, and MG performed the NSC analysis. TRB, EGC, AMM, OLP, NS and RV led the ForestPlots.net field expeditions for data collection. LR and YM. provided the stem increment data from the two focal species. All authors critically revised the manuscript and gave final approval for publication.

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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.

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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 evaluate how stored non-structural carbohydrates (NSC) vary across adult trees spanning the fast-slow continuum in the Peruvian Amazon by: (i) analysing whole-tree NSC in two species of contrasting growth and (ii) 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. 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.
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

Resumo (Portuguese)**Variação das concentrações de carboidratos não estruturais ao longo do contínuo rápido-lento em espécies amazônicas de árvores de dossel**

1. Espécies de árvores tropicais possuem diferentes histórias de vida, que ocorrem ao longo de um contínuo 'rápido-lento' de estratégias de crescimento. Acredita-se que a posição de uma espécie dentro desse contínuo, reflita uma relação negativa entre crescimento e armazenamento, com espécies de crescimento rápido alocando mais carbono para o crescimento e espécies de crescimento lento investindo mais em armazenamento. Para espécies tropicais, a relação entre armazenamento e as estratégias ao longo do contínuo de histórias de vida tem sido amplamente estudada em plântulas, e menos em árvores adultas.
2. Neste trabalho avaliamos como os estoques de carbono (carboidratos não estruturais, CNE) variam entre árvores adultas ao longo do contínuo rápido-lento, coletadas na Amazônia Peruana (i) analisando as concentrações de CNE na árvore inteira em duas espécies com estratégias diferentes de crescimento e (ii) investigando as relações com as principais características da história de vida em um conjunto mais amplo de espécies.
3. Nossos resultados indicam que a alocação de carbono para crescimento ou estoque faz parte da estratégia das espécies. A análise de CNE em toda a árvore revelou que *Eschweilera coriacea* (crescimento lento), armazena cerca de 2,7 vezes mais CNE do que *Bixa arborea* (crescimento rápido). Essa diferença no tamanho dos estoques entre as espécies ocorre principalmente devido ao maior armazenamento de CNE em órgãos de reserva (tronco e raízes) da espécie lenta. Entre as duas espécies, *B. arborea* é a que apresenta maior variação nas concentrações de CNE entre as estações, refletindo sua forte sazonalidade no crescimento. Avaliando um conjunto maior de espécies, encontramos que o amido do tronco é negativamente relacionado à taxa de crescimento das espécies e positivamente relacionado à densidade da madeira.
4. Dado o papel do CNE na mediação da resposta ao estresse das plantas, nossos resultados sugerem que as espécies de crescimento lento, com maior densidade da

madeira e maiores estoques de CNE podem ser mais resistentes à seca do que as espécies de crescimento rápido e baixa densidade da madeira.

Palavras-chave: crescimento rápido; crescimento lento; açúcares solúveis, amido; tropical

Resumen (Spanish)**Variación en las concentraciones de carbohidratos no estructurales a lo largo del continuo rápido-lento en las especies de árboles del dosel de la Amazonía**

1. Las especies de árboles tropicales tienen diferentes ciclos vitales, que ocurren a lo largo de un continuo de estrategias de crecimiento de rápidas-lentas. Se cree que la posición de una especie dentro de este continuo refleja una relación negativa entre crecimiento y almacenamiento, las especies de crecimiento rápido invierten más carbono en crecimiento y las de crecimiento lento en almacenamiento. Para las especies tropicales, la relación entre el almacenamiento y las estrategias a lo largo de sus ciclos vitales se ha estudiado ampliamente en las plántulas y menos en los árboles adultos.
2. En este trabajo evaluamos cómo el almacenamiento de carbono (carbohidratos no estructurales, CNE) varían entre árboles adultos a lo largo del continuo rápido-lento, recogidos en la Amazonía Peruana (i) analizando las concentraciones de CNE en todo el árbol de dos especies de crecimiento contrastantes e (ii) investigando las relaciones con las características principales de los ciclos vitales en un conjunto más amplio de especies.
3. Nuestros resultados indican que la asignación de carbono al crecimiento o almacenamiento es parte de la estrategia de la especie. El análisis de CNE de todo el árbol reveló que *Eschweilera coriacea* (crecimiento lento) almacena aproximadamente 2,7 veces más CNE que *Bixa arborea* (crecimiento rápido). Esta diferencia en el tamaño de los reservorios entre especies se debe principalmente al mayor almacenamiento de NSC en los órganos de reserva (tronco y raíces) de las especies lentas. Entre las dos especies, *B. arborea* es la que presenta mayor variación en las concentraciones de CNE entre estaciones, lo que refleja su fuerte estacionalidad en el crecimiento. Al evaluar un conjunto más grande de especies, encontramos que el almidón del tronco está relacionado negativamente con la tasa de crecimiento de las especies y positivamente con la densidad de la madera.

4. Dado el papel de los CNE en la mediación de la respuesta al estrés de las plantas, nuestros resultados sugieren que las especies de crecimiento lento con mayor densidad de madera y mayores reservas de CNE pueden ser más resistentes a la sequía que las especies de crecimiento rápido y baja densidad de madera.

Palabras-clave: crecimiento rápido; crecimiento lento; azúcares solubles; almidón; tropical

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) (Oijen, Schapendonk, & Ho, 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, Davies, Tan, & Noor, 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, Leuzinger, Philipson, Tay, & Hector, 2014; Oliva, Stenlid, & Martínez-Vilalta, 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, Sperry, Wheeler, & Castro, 2006; Mcculloh et al., 2012; Oliveira et al., 2021) and may be associated with lower carbon storage, i.e. non-structural carbohydrates (Cherubini et al., 2017; Falchi et al., 2020; Herrera-Ramírez et

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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 (NSC) 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, Gear, Hultine, Koch, & Ogle, 2020; Liu, Su, Li, Lang, & Huang, 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, Richter, & Körner, 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 & 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, Peláez-Riedl, Wright, & Körner, 2005). 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 their growth in the wet season, compared to slow-growing species (Rowland et al., 2014).

In this study, we tested the hypotheses that i) slow growing species have higher NSC concentrations, especially in woody storage organs; ii) fast-growing species have greater seasonal variability in NSC content and iii) 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 southwestern Amazonia. To test hypotheses i and ii, 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 iii, we collected stem samples from eleven 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.

Methods

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, Ofício nº 334/2016/SSV-SP - MAPA.

This site has a mean annual precipitation of 2,451 mm/year and a dry season length, i.e. ≤ 100 mm/month of approximately three 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/yr) and high wood density (0.85 g/cm³) (Coelho de Souza et al., 2016a; Chave et al., 2009; Zanne et al., 2010). *B. arborea* is a light-demanding tree species with high diameter growth rates (mean basin-wide growth rate of 0.56 cm/yr) and low wood density (0.37 g/cm³) (Coelho de Souza et al., 2016a; Chave et al., 2009; Zanne et al., 2010). 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 (see Fig. 1).

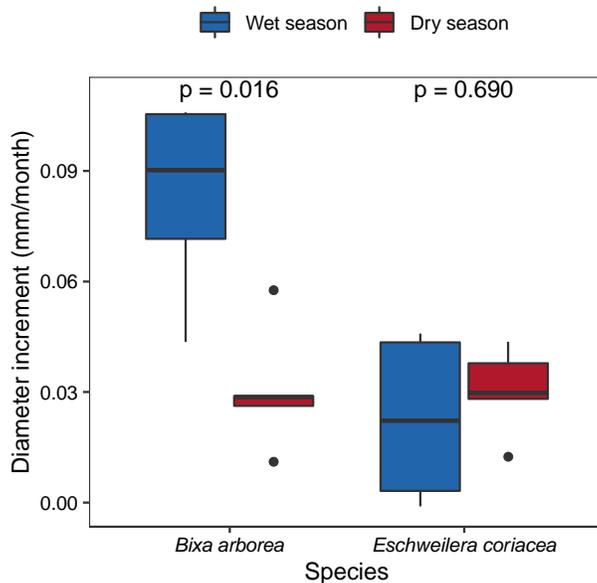


Fig. 1 – Mean increment in diameter (mm) during the wettest quarter (January to March) and driest quarter (July to August) for *Bixa arborea* and *Eschweilera coriacea*, measured with stem dendrometer bands from January 2006 to December 2010 in the Tambopata National Reserve (plot TAM-05). Data are from 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.

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 diameter at breast height between 20 cm and 30 cm, common diameters for adult trees of these species in our study plot (Rowland *et al.*, 2014; *B. arborea* mean \pm 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) season, and since NSC concentrations may vary depending on the time of the day, especially in leaves (Tixier, Orozco, Amico Roxas, Earles, & Zwieniecki, 2018), we standardized the sampling time to be between 08:30-10:00 am for both species. For each tree we sampled leaves, branches, stem wood,

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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 lab from the plot being approximately 45 minutes. Upon arrival at the laboratory, we microwaved the samples for 90 seconds at 700 W to stop enzymatic processes and oven-dried at $\sim 60^{\circ}\text{C}$ for at least 48 h or until they were completely dry (no more than 72 hours).

As there is no consensus about the within organ variability in NSC concentration across studies (Furze et al., 2018; Smith, Miller, Arndt, Kasel, & Bennett, 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: 1) sunlit, 2) partially shaded, and 3) fully-shaded. Sunlit was defined as the outermost branches of the top third of 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, Långsele, Sweden). 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 cm, 55 cm and 105 cm. At the deepest point we also collected fine roots (diameter $< 3\text{mm}$). 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: 1) close to the ground (5 cm height), 2) at breast height (1.30 m), 3) at approximately 10 m and 4) 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 center 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

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study plot (TAM-05) (ForestPlots.net; Lopez-Gonzalez, Lewis, Burkitt & Phillips 2011). The annual mean growth in diameter at breast height (1.3 cm) for the slow-growing *E. coriacea* in this site was 0.26 cm/yr, compared to 0.42 cm/yr 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 ~five-year growth increments ($0.26 \text{ cm} * 5 \text{ years} = 1.3 \text{ cm}$ for *E. coriacea* and $0.42 \text{ cm} * 5 \text{ years} = 2.1 \text{ cm}$ 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 (Fig 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: 1) sampled stem wood from nine additional species ($n = 11$ species; $n = 5$ to 6 trees per species, except for *B. arborea* and *E. coriacea* $n = 3$); and 2) made use of leaf and branch-level NSC data collected in Tambopata by Signori-Müller *et al.* (2021a,b) for 21 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 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 five years of growth.

The branch and leaf NSC data available in Signori-Müller et al. (2021a,b) were collected earlier in the morning (before 6:00 am) than the *B. arborea* and *E. coriacea* samples collected specifically for this study (08:30-10:00 am). 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,b) to test for relationships with life history attributes across the broader spectrum of species.

Branch wood density

To estimate in situ branch wood density, we sampled three individuals of each species, we used fully sun-exposed top canopy branches. 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 horas. Subsequently with 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 cm³). Samples were then oven dried for 48-72 hours at ~60 °C. After dried 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/cm³).

Table 1 – Sampled species and their traits.

Species	WD _{branch} ¹	WD _{stem} ²	Meangr ³	Mort ⁴	Sampled
<i>Bertholletia excelsa</i>	0.66	0.62	0.637	0.225	Leaf, Branch
<i>Bixa arborea</i>	0.52	0.37	0.568	-	Whole tree
<i>Brosimum guianense</i>	0.64	0.84	0.186	0.357	Leaf, Branch
<i>Brosimum rubescens</i>	-	0.82	0.171	0.480	Leaf, Branch
<i>Calophyllum brasiliense</i>	0.61	0.58	0.500	-	Leaf, Branch, Stem wood
<i>Cedrelinga cateniformis</i>	0.73	0.50	0.724	-	Leaf, Branch, Stem wood
<i>Clarisia racemosa</i>	0.64	0.58	0.319	0.526	Leaf, Branch,
<i>Dialium guianense</i>	0.64	0.87	0.235	0.387	Leaf, Branch
<i>Eschweilera coriacea</i>	0.70	0.85	0.175	0.298	Whole tree
<i>Hebepetalum humiriifolium</i>	0.73	0.87	0.214	0.352	Leaf, Branch
<i>Hevea guianensis</i>	0.51	0.57	0.152	0.343	Leaf, Branch
<i>Hymenaea parvifolia</i>	-	0.87	0.267	-	Stem wood
<i>Leonia glycyarpa</i>	0.56	0.60	0.122	0.928	Leaf, Branch
<i>Licania heteromorpha</i>	0.80	0.81	0.198	0.704	Leaf, Branch, Stem wood
<i>Micropholis guyanensis</i>	-	0.65	0.224	0.615	Stem wood
<i>Minquartia guianensis</i>	0.69	0.78	0.188	0.457	Leaf, Branch
<i>Ocotea bofo</i>	0.61	-	0.294	-	Leaf, Branch
<i>Pourouma guianensis</i>	-	0.38	0.598	2.285	Stem wood
<i>Pourouma minor</i>	0.74	0.43	0.484	1.495	Leaf, Branch, Stem wood
<i>Pouteria torta</i>	0.74	0.76	0.155	0.385	Leaf, Branch, Stem wood
<i>Pseudolmedia laevigata</i>	0.60	0.62	0.169	0.573	Leaf, Branch
<i>Pseudolmedia macrophylla</i>	0.60	0.66	0.160	0.429	Leaf, Branch
<i>Tachigali poeppigiana</i>	0.70	-	0.588	2.147	Leaf, Branch
<i>Tetragastris altissima</i>	0.70	0.70	0.230	0.831	Leaf, Branch, Stem wood

¹WD_{branch}: wood density (g/cm³) measured in branches of trees from the Tambopata Nacional reserve.

²WD_{stem}: wood density (g/cm³) 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);

³Meangr: Mean growth rate (cm/yr). 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);

⁴Mort: Mortality rate per species in the Amazon Basin (% /year). Data from Coelho de Souza *et al.* (2016b).

Laboratory preparations and NSC analyses

Non-structural carbohydrates (NSC) are defined here as free, low molecular weight sugars (glucose, fructose and sucrose, etc) plus starch. NSC was analysed as described in Hoch, Popp & Korner (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 minutes 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, St. Louis, MO, USA) to break down sucrose and fructose to glucose. Additionally, for both reaction routines, we used GAHK (Glucose Assay Hexokinase Kit - Sigma-Aldrich, St. Louis, MO, USA) together with phosphoglucose isomerase from *Saccharomyces cerevisiae* (Sigma-Aldrich, St. Louis, MO, USA). The concentration of free glucose was measured photometrically in a 96-well microplate spectrophotometer at 340 nm (EPOCH - Biotek Instruments INC - Winooski, VT - USA). The aliquot that we initially separated was incubated overnight to react with Amyloglucosidase from *Aspergillus niger* (Sigma-Aldrich, St. Louis, MO, USA) 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.

Statistical analysis

We performed all statistical analysis using the R software (R Core Team, 2018; 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 $\log_{10} [y_i + 1]$ transformed prior to parametric analysis or used without transformation in non-parametric 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 \log_{10} transformation. As there were no

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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 sugars concentrations within species were tested separately for each organ using non-parametric paired-sample Wilcoxon tests. To evaluate differences between *E. coriacea* and *B. arborea*, we used the non-parametric 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 $\log_{10}p$ transformation for both NSC and traits. For all analyses, we assume a significance level of 0.05.

To calculate biomass-weighted whole tree mean NSC_T concentrations, we assumed that roots represented 21% of the total biomass for both species (Houghton et al., 2001). Aboveground 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 species. 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) see Table 1 in the support information.

Results

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, shaded) in leaves or branches for either of our focal species (Fig. 2; Fig. S1 & 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 cm, 55 cm and 105 cm). We found no difference across radial profile segments for both species in most NSC fractions evaluated, with the exception soluble sugar concentrations in *E. coriacea* were two times lower in the innermost segments compared to the outermost segments (Fig. S2; $p < 0.05$).

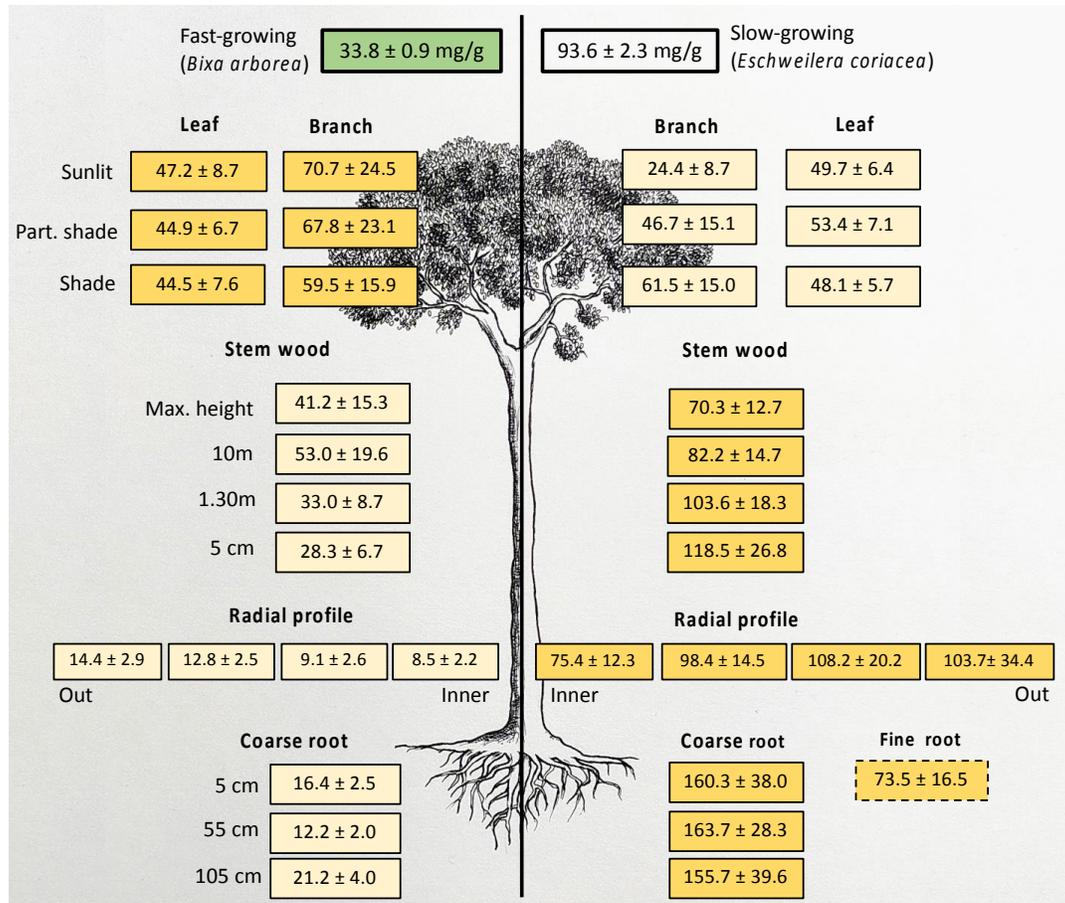


Fig. 2 – Whole tree NSC_T concentrations (mg/g, mean ± SE) in the fast-growing *Bixa arborea* (left) and in the slow-growing *Eschweilera coriacea* (right). The top box depicts the biomass-weighted mean whole-tree NSC_T concentrations for the fast (green box) and slow-growing species (purple box). Components 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).

Table 2 – Biomass-weighted whole-tree NSC concentrations, calculated from the mean NSC 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 (*B. arborea*), and for late-successional species (*E. coriacea*). The contribution of belowground biomass is based in the estimates of Houghton *et al.* (2001).

	Biomass allocation <i>B. arborea</i> (%)	NSC concentration <i>B. arborea</i> (mg/g)	Biomass allocation <i>E. coriacea</i> (%)	NSC concentration <i>E. coriacea</i> (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 <i>B. arborea</i>	33.8 ± 0.9 mg/g	Slow-growing <i>E. coriacea</i>	93.6 ± 2.3 mg/g

Patterns within organs revealed that NSC concentrations in the slow-growing species is less seasonal than in the fast-growing species (Fig. 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). In the fast-growing *B. arborea*, NSC in all organs displayed seasonality in at least one fraction (Fig. 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 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 sugars concentrations decreased by 51% (Fig. 3).

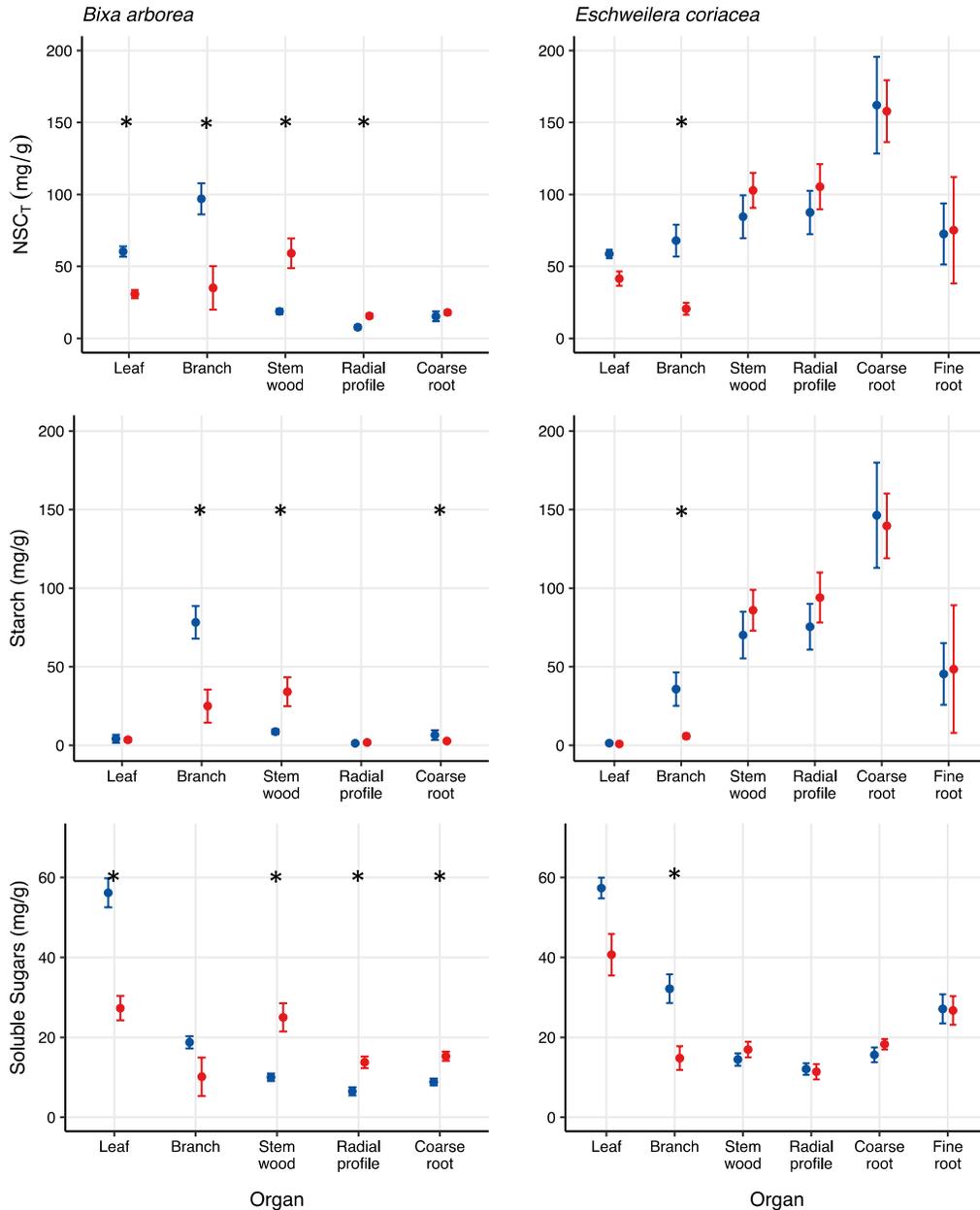
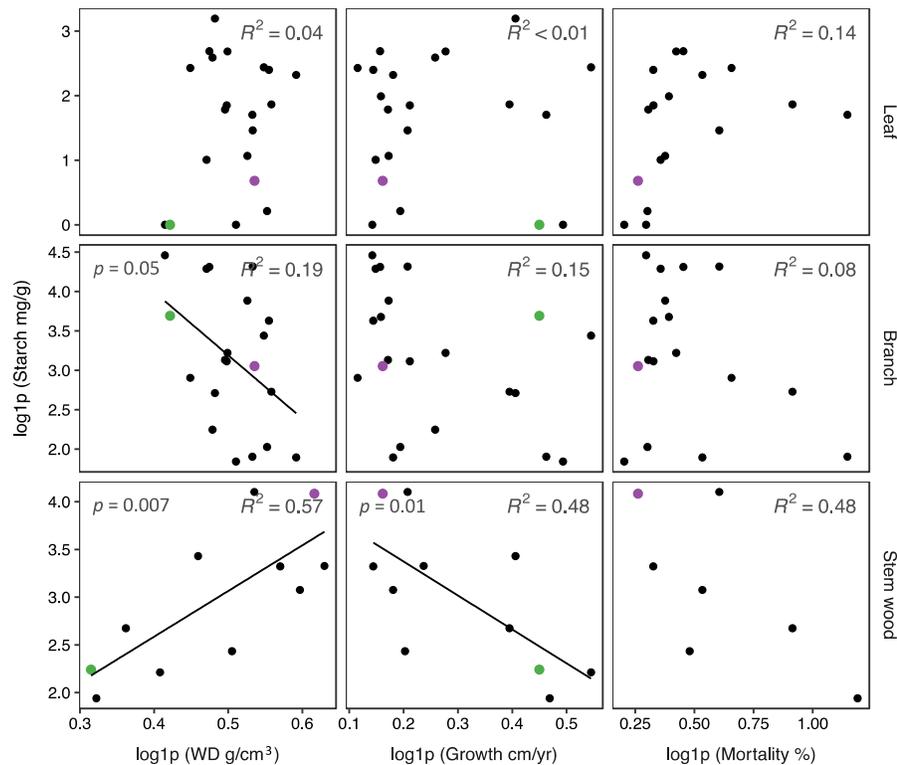


Fig. 3 – Seasonal differences in non-structural carbohydrates (NSC) for each species and organ. Total NSC (NSC_T), starch and soluble sugars concentrations in the fast-growing *Bixa arborea* (left) and slow-growing *Eschweilera coriacea* (right). Asterisks denote significant differences between concentrations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

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 with branch wood density, mean growth rate and mortality rate (Fig. 4, Fig. S4 & S5) across the locally-occurring species for which we had data. Branch starch concentrations are negatively related with branch wood density (Fig. 4; $p = 0.04$, $R^2 = 0.19$), but not with other traits or NSC fractions (Fig. S4 & S5). In contrast, stem starch concentrations across the 11 species for which we had data were positively related with stem wood density ($p = 0.007$; $R^2 = 0.57$) and negatively related with mean growth rate ($p = 0.001$; $R^2 = 0.48$).

Fig. 4 – Relationship between starch (mg/g) and wood density (WD g/cm³), mean growth rate



(Growth cm/yr) 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 wood density, and for relationships with leaf and branch starch, we used branch wood density. 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 the fast-growing *B. arborea*.

Discussion

Overall, our results provide support for our three overarching hypotheses as we found that: 1) 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, 2) NSC dynamics in *B. arborea* was markedly more seasonal than in *E. coriacea* and 3) 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; Oijen et al., 2010; Poorter & Kitajima, 2007).

Within-tree NSC concentrations

The apparent lack of variation in NSC within organs (Fig. 2, 1S & 2S) 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 – e.g. 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, Jain, & Jajoo, 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* (Fig.2; 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, Mulkey, & Wright, 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, it is unclear. However, many studies suggest that roots NSC have an important role in plant tolerance to stress (He, Marco, Soares, Yin, & Wiedenhoef, 2020; Kannenberg, Novick, & Phillips, 2018; Mei, Xiong, Gu, Wang, & Guo, 2015); and a study based on ¹⁴C isotopic analysis shows that relatively old carbon stores can be used to produce new fine roots after environmental disturbance in tropical species (Vargas, Trumbore, & Allen, 2009). This implies that long-term reserves, especially belowground 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 sugars 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, Woodruff, & Meinzer, 2012; Signori-Müller et al., 2021a).

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 (Fig. 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 (Fig. 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 – e.g. a greater requirement for osmoprotection. Branch NSC consumption is frequently reported in trees, both in temperate or tropical species (Furze, Trumbore, & Hartmann, 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 unfavorable 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 *E. coriacea* likely reflects the strong differences in the seasonality of growth between the two species (Fig. 1) (Martínez-Vilalta et al., 2016; Smith, Miller, Arndt, Kasel, & Bennett et al., 2018). Some studies have found that under water limitation conditions growth may cease before photosynthesis, leading to NSC accumulation (Fatichi, Leuzinger, & Körner, 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 C 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 (Fig. 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, Manzanares, De Andres, Tenorio, & Ayerbe, 1998). The reduction in starch could potentially also be associated with 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 unfavorable season may require consumption of root starch reserves. There have been very few studies to date examining seasonal patterns in root reserves in tropical

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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.

Relationship with species traits

Our analyses of NSC concentrations vs. 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 (Fig. 3). This is consistent with other studies that associate higher NSC storage to species that have lower growth and mortality rates (Herrera-Ramírez et al., 2021) and hardwooded 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, Savi, Trifilò, & Lo Gullo, 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, Orthen, & Franco, 2004; O'Brien et al., 2020; Poorter & Kitajima, 2007; Shibata et al., 2016; Smith, Arndt, Miller, Kasel, & Bennett, 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 are in line with a study from Panamá (Dickman et al., 2019), suggesting branches 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 & 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, Gessler, & Hoch, 2019). The lack of relationship between branch NSC and its components with mean stem growth rate (Fig. 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 is missing, see Tab. 1) is similar to that of growth, as species with higher baseline mortality rates had lower NSC storage (Fig 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., 2011; McDowell et al., 2008; Sala, Piper, & Hoch, 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 current and future compositional shifts in Amazon forests.

Data accessibility

The non-structural carbohydrates 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).

Author contributions

CS-M, DG and RSO designed the study. CS-M led the data analysis. CS-M wrote the manuscript with significant inputs from DG, RSO, MM, MB, FVB, LR and OLP. CS-M and JVT led the field sampling. CS-M, JVT, MG, FCD, MJMZ, CASY and AN collected the samples. CS-M, FVB, and MG performed the NSC analysis. TRB, EGC, AMM, OLP, NS and RV led the ForestPlots.net field expeditions for data collection. LR and YM. provided the stem increment data from the two focal species. All authors critically revised the manuscript and gave final approval for publication.

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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.

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