

Non-structural carbohydrate concentrations in woody organs, but not leaves, of temperate and tropical tree angiosperms are independent of the ‘fast-slow’ plant economic spectrum

Ramirez, J.A.^{1,2*}, Craven, D.^{3,4†}, Posada, J.M.⁵, Reu, B.⁶, Sierra, C.A.⁷, Hoch, G.⁸, Handa, I.T.^{2,‡}, and Messier, C.^{2,9,‡}

¹ Facultad de Ciencias Agrarias, Universidad del Cauca, Popayán, Colombia

² Centre d’Étude de la Forêt (CEF), Université du Québec à Montréal, Montréal, Canada

³ Centro de Modelación y Monitoreo de Ecosistemas, Facultad de Ciencias, Universidad Mayor, Santiago, Chile

⁴ Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

⁵ Department of Biology, Faculty of Natural Sciences, Universidad del Rosario, Bogotá, Colombia.

⁶ School of Biology, Universidad Industrial de Santander, Bucaramanga, Colombia

⁷ Max Planck Institute for Biogeochemistry, Jena, Germany

⁸ Department of Environmental Sciences – Botany, University of Basel, Basel, Switzerland

⁹ Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, Ripon, Canada

† Ramirez, J.A. and Craven, D. contributed equally to this work as first authors

‡ Shared senior authors

*Corresponding author (j.ramirez@unicauca.edu.co).

Running title: NSC - fast-slow relationships across biomes

Summary

Background and Aims Carbohydrate reserves play a vital role in plant survival during periods of negative carbon balance. Considering active storage of reserves, there is a trade-off between carbon allocation to growth and to reserves and defense. A resulting hypothesis is that allocation to reserves exhibits a coordinated variation with functional traits associated with the ‘fast-slow’ plant economics spectrum.

Methods We tested the relationship between non-structural carbohydrates (NSC) of tree organs and functional traits using 61 angiosperm tree species from temperate and tropical forests with phylogenetic hierarchical Bayesian models.

Key Results Our results provide evidence that NSC concentrations in woody organs and plant functional traits are largely decoupled, meaning that species’ resilience is unrelated to their position on the ‘fast-slow’ plant economics spectrum. In contrast, we found that variation between NSC concentrations in leaves and the fast-slow continuum was coordinated, as species with higher leaf NSC had traits values associated with resource conservative species such as lower SLA, lower Amax, and high wood density. We did not detect an influence of leaf habit on the variation of NSC concentrations in tree organs.

Conclusions Efforts to predict the response of ecosystems to global change will need to integrate a suite of plant traits, such as NSC concentrations in woody organs, that are independent of the ‘fast-slow’ spectrum and that capture how species respond to a broad range of global change factors.

Key words: carbohydrate reserves, trait syndromes, leaf habit, carbon investment strategies,

tropical trees, temperate trees

INTRODUCTION

Carbon allocation to growth is a fundamental process that underpins global variation in plant functional traits, which describes quantitative differences between resource acquisitive and resource conservative species (Grime et al., 1997, Diaz et al., 2004, Wright et al., 2004, Chave et al., 2009, Reich, 2014, Díaz et al., 2016). These trade-offs reflect variation among plant traits for species that differ in growth form, size, and evolutionary history (Díaz et al., 2016, Donovan et al., 2011, Reich, 2014, Reich et al., 1999, Wright et al., 2004, Reich et al., 1997). For example, fast-growing, resource-acquisitive species, typically have high specific leaf area (SLA), high leaf nutrient concentrations, and low wood density (hereafter ‘fast’ species). In contrast, slow-growing, resource-conservative species, are characterized by low SLA, low leaf-nutrient concentrations, and high wood density (hereafter ‘slow’ species). While ‘slow’ trait values imply high construction costs, they allow trees to enhance resilience to different biotic or abiotic stress factors (Coley et al., 1985, Poorter and Kitajima, 2007).

To increase recovery and survival following periods of negative carbon balance caused by the loss of tissues that reduce the capacity to photosynthesize and take up nutrients and water, trees store and mobilize carbohydrate reserves (Atkinson et al., 2014, Canham et al., 1999, Kobe, 1997, Myers and Kitajima, 2007, O’Brien et al., 2014, Poorter and Kitajima, 2007). Thus, a significant fraction of the carbon captured by photosynthesis (between 1 and 19%) is allocated to carbohydrate reserves in the form of non-structural carbohydrates (NSC) (Hoch and Körner,

2003, Hoch et al., 2003, Landhäusser and Lieffers, 2003, Martínez-Vilalta et al., 2016, Piper et al., 2009, Würth et al., 2005). In general, NSC are comprised of low weight sugars and starch (Hoch et al., 2003). Sugars are mobilized easily and used for short-term metabolism (i.e. within a growing season), while starch is stored in a more recalcitrant form for long-term use (up to several decades (Carbone et al., 2013)) during periods of severe stress (Chapin et al., 1990, Dietze et al., 2014, Hartmann and Trumbore, 2016, Martínez-Vilalta et al., 2016).

In contrast to evergreen species that maintain photosynthetically active tissues that provide resources for plant functions all year (Fajardo et al., 2013), NSC support physiological activity during dormant periods and the flushing of new leaves of deciduous species (Fajardo et al., 2013, Gaucher et al., 2005, Gough et al., 2009, Klein et al., 2016, Messier et al., 2009, Newell et al., 2002, Würth et al., 2005). Additionally, NSC increase resilience to natural or anthropogenic disturbances providing the energy for the vital functions of plants (i.e. growth, defense, reproduction, resprouting, and survival) (Chapin et al., 1990, Kozłowski, 1992, Dietze et al., 2014, Powers, 2020). Availability of NSC may drastically reduce the risk of mortality through carbon supply to metabolism following drought periods (O'Brien et al., 2014, Doughty et al., 2015, Rowland et al., 2015, O'Brien et al., 2020, Piper and Paula, 2020, Signori-Müller et al., 2021) . For instance, droughts are common in regions like the northern tropical Andes during the El Niño phenomenon (Poveda et al., 2001, Pinilla Herrera and Pinzón Correa, 2016), which usually decrease NSC concentrations in tree organs (Piper and Paula, 2020). Additionally, although the incidence of fires is uncommon in high elevation Andean forests (unless caused by anthropogenic factors), recent increases in the strength of the El Niño phenomenon has led to more burned area (Armenteras-Pascual et al., 2011), where resprouting species may require

NSC as a pathway to regenerate (Poorter et al., 2010). In temperate forests of eastern North America, wind storms, ice storms, and insect outbreaks are the major natural drivers of forest dynamics (Runkle, 1982, Frelich and Lorimer, 1991). Thus, high concentrations of NSC may increase the probability of trees that restore their photosynthetic tissues and survive (Dietze et al., 2014, Hartmann and Trumbore, 2016, Martínez-Vilalta et al., 2016).

NSC concentrations increase via accumulation and reserve formation (Chapin et al., 1990). NSC accumulation is a passive process driven by the balance between photosynthesis supply and the demand of carbon for growth and respiration (Chapin et al., 1990, Sala et al., 2012, Dietze et al., 2014). Reserve formation can be also an active process in which NSC compete for carbon with plant growth and other physiological processes such as defense, even when carbon resources are limited (Chapin et al., 1990, Sala et al., 2012, Dietze et al., 2014, Weber et al., 2019). Active storage of NSC suggest an allocation-based trade-off between carbon allocated to growth and to reserves and defense (Kitajima, 1994, Kobe, 1997, Myers and Kitajima, 2007). Thus, tough leaves and dense woody organs suggest greater carbon investment in defense traits to resist and to recover from biotic and abiotic stress (Poorter and Kitajima, 2007, Poorter et al., 2010), which co-vary with carbon allocation to reserves, especially in roots (Kitajima, 1994, Myers and Kitajima, 2007). Also, since a higher SLA indicates a higher light capture potential, a higher net photosynthetic rate, and higher concentrations of foliar nutrients such as N (Wright et al., 2002, Wright et al., 2004), an increase in SLA may lead to an increase in the proportion of metabolically active carbon allocated to growth of woody organs (Shipley et al., 2006, Li et al., 2016), which may compete with storage in fast growing species. However, it remains uncertain

whether the ‘fast-slow’ plant economics spectrum (Reich, 2014), which captures variation in life-history strategies, varies in coordination with NSC concentrations in leaves and woody organs.

An alternative hypothesis is that NSC concentrations are decoupled from, or are orthogonal to, the ‘fast-slow’ plant economics spectrum. This pattern would suggest that variation in NSC concentrations is uncorrelated with ‘effect’ traits, which are associated with species’ effects on ecosystem functioning, but may form part of an independent axis of ecological variation including a broader suite of ‘response’ traits whose diversity may play a role in determining the resilience of ecosystems to global change (Suding et al., 2008, Mori et al., 2013). The extent to which a trait-based spectrum of ‘resilience’ is generalizable is of basic and applied importance as it will contribute towards improving predictions of how ecosystem functioning responds to global change.

We therefore examine how key functional traits associated with the ‘fast-slow’ plant economics spectrum, as well as biome and leaf habit, vary with NSC concentrations for each tree organ in angiosperm tree species, a central issue for predicting the role of NSC in the resilience of trees that differ in life strategies. We sampled 61 angiosperm tree species across tropical and temperate biomes. We test the hypothesis that, once accounting for phylogenetic relationships among species (Freckleton et al., 2002), NSC concentrations in woody organs and leaves will be coordinated with plant functional traits that underpin the ‘fast-slow’ plant economics spectrum. Further, we anticipate that species with ‘slow’ traits associated with greater carbon investment in defense and conservative ecological strategies, such as a low SLA, high tissue density, and low

concentrations of leaf nutrients will accumulate more NSC in woody organs (stem, branch and root) than species associated with acquisitive or ‘fast’ ecological strategies.

MATERIALS AND METHODS

Research sites

We performed this study in a deciduous temperate forest (DTF; Mont St-Hilaire, Quebec, Canada) and in an upper montane tropical forest (UMF) and a lowland tropical forest (LTF) in Colombia (Supplementary information, Table S1). These three sites were selected to generate contrasts in latitude, seasonality (temperate versus tropical), and elevation (lowland and upper montane forest (Colombia) (Fig. S1). Each study site within each biome had been protected and had not experienced recent anthropogenic disturbances (at least during the last 20 years). In the LTF, climate does not exhibit marked seasonality in terms of temperature and precipitation. The climate in the UMF exhibits a bimodal variation of precipitation between the rainy and dry seasons; the first dry period lasts from November to March, while the second one from June to August. In contrast, the climate in the DTF is characterized by strong intra-annual variation in temperature, with average sub-zero temperatures from November to March, mild and wet summers (June - September) and a growing season from May to October (Fig. S1).

Field sampling

We sampled a total of 61 mature native tree species (see species list and leaf habit in Table S2) across the three study sites in 2012. In the temperate forest site, samples were taken after bud break and leaf maturation (May) and at the end of the growing season (October) to capture seasonal dynamics in carbon reserves that are typical of northern temperate forests. Samples in the tropical forest sites were taken between January to May, which is mostly a rainy period in the LTF and coincides with the transition from the dry to the rainy season in the UMF. We sampled before the onset of the rainy season (i.e. before leaf out) to capture the previous year's carbon reserves. At each site, we selected abundant tree species for sampling. In Colombia, species were selected by consulting with researchers familiar with local ecosystems in order to have a representative sample of the plant communities since no biomass or abundance data were available. In Quebec, species were selected based on abundance data of Mont St. Hilaire (Maycock, 1961, Arian et al., 2005), which is why we did not sample evergreen tree species in the DTF. Botanical samples of all tropical species were verified and deposited at the Medellín Botanical Garden Herbarium Joaquin Antonio Uribe (JAUM).

At each study site, we selected the tallest trees of each species. Leaves and woody organs (branches, stems, and roots) were sampled from 3-5 individuals for each species. Current year leaves from adult plants without visible symptoms of pathogen or herbivore attack were sampled. To avoid possible effects of diurnal variation in NSC, leaf samples were collected in the early morning (Upmeyer and Koller, 1973). Leaf samples were taken from one sun-lit branch at the top of the canopy with a tree trimmer and then divided in two groups. One group was placed in paper bags for NSC measurements, while the second group was placed in plastic bags with damp tissue for measurement of leaf traits (see below). Stem samples were taken with a 4.3 mm

diameter increment borer. Stem cores were taken perpendicular to the slope to reduce variability in wood density due to compression or tension. Samples of sun-lit branches 2-3 cm in diameter were obtained by cutting them with a tree trimmer. Root samples were taken with an increment borer from large surface roots ca. 50 cm away from the base of the stem. In total, we collected and analyzed samples from 326 trees.

Non-structural carbohydrates (sugar, starch, and NSC, % of dry matter)

We placed leaf and wood samples for NSC analysis in paper bags and then in a cooler. These samples were then microwaved within 8 h after sampling to stop enzymatic activity (Popp et al., 1996). Leaf samples were ground using a ball mill and wood samples were ground using a coffee grinder with a mesh sieve. Due to the large number of samples, we selected a sub-sample of 180 samples (of a total of 1,271) using the Kennard–Stone algorithm (Kennard and Stone, 1969) for NSC analysis following (Hoch et al., 2002) based on variation in near-infrared spectra. Ground plant material was dissolved for 30 min in distilled water. Starch and sucrose were disaggregated in glucose and in glucose and fructose, respectively, with Clarase (*Aspergillus oryzae*, Enzyme Solutions Pty Ltd, Crydon South, Victoria, Australia) by incubation at 40°C for 15 h.

Phosphoglucose-isomerase was added to the solution and then the total amount of glucose (corresponding to total NSC) was quantified photo-metrically in a microplate photometer at 340 nm (Thermo Fisher Scientific, Waltham, USA) after conversion of glucose to gluconate-6-phosphate (hexokinase; Sigma-Aldrich, St. Louis, MO, USA). An aliquot of the original extract was treated with invertase and phosphoglucose-isomerase (both Sigma-Aldrich) to determine the amount of glucose, fructose, and sucrose using a glucose test. Starch was calculated as NSC

minus sugar. We used pure starch and solutions of glucose, fructose, sucrose, and plant powder (orchard leaves; Leco, St. Joseph, MI, USA) as standards and to control reproducibility of the extraction.

Using the same dataset, we extrapolated NSC values from the 180 sub-samples to all samples using near-infrared reflectance spectra (Ramirez et al., 2015). Reflectance spectra were measured using a FT-NIR spectrometer Analyzer (Bruker MPA Multi-Purpose FT-NIR Analyzer, Bruker Optik GmbH, Ettlingen, Germany) for all samples. The reflectance spectra were taken from 800 nm to 2780 nm with a mean spectral resolution of 1.7 nm on five scans per sample. The spectral data were recorded as absorbance ($\log(1/R)$, where R = reflectance). Then, we fitted regression models that predict NSC concentrations in different tree organs (leaves, stems, branches, and roots) from near-infrared reflectance spectra using partial least squares regression and competitive adaptive re-weighted sampling (Li et al., 2009). Across all tree organs, the model fit for NSC was $r^2 = 0.91$ (Ramirez et al., 2015). The NSC concentrations are reported here as the percentage of dry matter.

Because tree height may influence NSC allocation patterns (Sala and Hoch, 2009, Genet et al., 2009, Piper and Fajardo, 2011, Woodruff and Meinzer, 2011), we measured tree height of all sampled individuals (H, m). All sampled trees were at or close to their maximum height as they were sampled in mature forests. Tree height was measured with a TruPulse 360 laser with a resolution of 10 cm for linear lengths (Laser Technology, Inc., CO, USA).

Functional traits

We measured 11 traits that are associated with important ecological strategies for tree functioning, productivity, and survival (Table S3) following standard protocols (Pérez-Harguindeguy et al., 2013).

Leaf size (LS, mm²), leaf thickness (LT, mm), leaf dry matter content (LDMC, mg g⁻¹), and specific leaf area (SLA, mm² mg⁻¹): Eight completely expanded leaves were randomly collected from the leaves of a sampled branch of each individual. Leaves were placed in plastic bags in the field with damp paper to maintain humidity. After determining fresh leaf mass, we dried leaf samples in an oven at 60 °C until constant weight. LS was measured using WinFolia (*Regent Instruments, Toronto, Canada*). LT was measured on fresh leaves as the mean of four measurements with a digital micrometer (Mitutoyo Instruments, Singapore). LDMC was calculated as leaf dry mass divided by its fresh saturated mass. SLA was calculated as the area of the fresh lamina surface divided by its dry mass.

Photosynthetic capacity by mass (A_{mass}, nmol CO₂ g⁻¹ s⁻¹): Photosynthetic capacity was measured on six leaves from two sun-lit branches in both tropical forest sites using a LI-6400 portable photosynthetic system (LI-COR, Lincoln, NE, USA). Branches for photosynthesis determination were placed in a bucket of water during the measurements to avoid disruption of water transport within the xylem (Verryck et al., 2020). The photosynthetic capacity under saturating light (A_{max}) was measured at 2000 μmol m⁻² s⁻¹. Measurements were carried out under constant CO₂ concentration (390 ppm) and leaf temperature (set at 20 °C). Leaves were allowed to acclimate to 1000 μmol m⁻² s⁻¹ and then 2000 μmol m⁻² s⁻¹ for several minutes before

measurements. Photosynthetic capacity per leaf dry mass was calculated as the product of A_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and SLA^{-1} . Photosynthetic data for tree species in the DTF were obtained from (Marino et al., 2010), which were measured in a similar manner as described above.

Leaf nutrients (leaf N, % and leaf Ca, leaf Mg, and leaf P, mg kg⁻¹): About 20 g of leaf tissue per tree were dried and ground to a fine powder using a ball mill. Nitrogen concentrations were determined for all leaf samples with a CN elemental analyzer (Vario MAX, Elementar, Germany). Determination of Ca, Mg, and P was performed on 100 samples using the acid digest method (Allen et al., 1974), and these results were extrapolated to all leaf samples using FT-NIR reflectance spectroscopy as described for NSC (Ramirez et al., 2015). Model fit for leaf nutrients was (r^2) 0.93, 0.76 and 0.78 for Ca, Mg, and P, respectively (Fig. S2).

Wood density (stem density (SD) and branch density (BD), mg mm⁻³): Samples of stems and branches were placed in plastic bags in the field with damp paper to maintain humidity, and then were soaked in water in the lab for 48 hours. Fresh wood volume was measured without bark by water displacement, and wood mass was determined after drying samples at 60 °C, and then again at 100 °C, to a constant weight (Williamson and Wiemann, 2010).

Statistical analysis

Phylogeny: We used an updated version of the molecular phylogeny from Zanne *et al.* (2014) and Qian and Jin (2016) to build a phylogeny with the *congeneric.merge* function in the ‘pez’ R

package (Pearse et al., 2015), conservatively binding species into the backbone using dating information from congeners in the tree.

'Fast-slow' spectrum: Using gap-filled, individual-level data for all functional traits, we performed a principal components analysis using the PCA function in the R package “*FactoMineR*” (Lê et al., 2008) to represent the ‘fast-slow’ spectrum of plant form and function (Díaz et al., 2016). Prior to principal components analysis, leaf area, leaf thickness, SLA, Amass, and leaf Ca were natural log transformed to meet normality assumptions. Because the first two axes of the PCA explain a considerable amount of trait variation (57.4%), we decided to use both in subsequent analyses (see below) and hereon refer to them as fast-slow PC1 and fast-slow PC2. The PCA suggested that DTF species, all of which are deciduous, exhibit a restricted trait variation as compared to the trait space of the other species. For this reason, we included interactions between the first two axes of the ‘fast-slow’ spectrum with leaf habit and biome in the initial models described below.

Data analysis

Variance partitioning: To determine the relative contributions of biome, leaf habit, and species to variation in NSC for each tree organ, we fitted an intercept only linear mixed-effects model with a nested random effects structure ($\sim 1 | \text{Biome/Leaf habit/Species/Tree}$) using restricted maximum likelihood (REML) with the *lme* function in the R package “*nlme*” (Pinheiro et al., 2020). Variance partitioning was estimated using the *varcomp* function. The variance partitions represent the amount of variation within each level, i.e. the variance partition for “species” represents interspecific variation (Messier et al., 2010). Note that variation within the tree level

also includes residual variation, meaning that this partition captures intra-specific variation and error.

Phylogenetic signal: We estimated the phylogenetic signal of NSC concentrations of tree organs as lambda using the *phylosig* function in the R package “*phytools*” (Revell, 2012), incorporating sampling error following Ives, Midford and Garland (2007) to account for multiple observations per species. Lambda values close to 0 indicate no phylogenetic signal while values close to 1 indicate trait evolution according to the Brownian motion evolutionary model (Molina-Venegas and Rodríguez, 2017).

Phylogenetic hierarchical models: Because phylogenetically closely related species are likely to share similar trait values (Felsenstein, 1985, Freckleton et al., 2002), not accounting for phylogenetic relationships may reduce estimation accuracy and increase type I error rates (Li and Ives, 2017). Moreover, accounting for phylogenetic relationships in our analyses allow for direct comparisons across tree organs because different species were sampled for NSC across tree organs, and the phylogenetic signal of NSC varied markedly across tree organs (see Results). We therefore fitted separate phylogenetic multi-level Bayesian models to examine variation in root, stem, branch, and leaf NSC as a function of biome, leaf habit, the ‘fast-slow’ spectrum (fast-slow PC 1, fast-slow PC 2), and two-way interactions between biome, leaf habit, and both axes of the ‘fast-slow’ spectrum. Because we did not sample evergreen species in the deciduous temperate forest, we did not fit models with an interaction between biome and leaf habit. All interactions were initially included in all models; if the 95% credible intervals of interactions overlapped with zero, models were then re-fit without these interactions.

As sampled trees were likely to be at or close to their species' maximum height, we expected that the influence of tree height on NSC concentrations is similar across species. However, to account for the positive correlation between tree height and NSC concentrations within species (Sala and Hoch, 2009, Woodruff and Meinzer, 2011), we included tree height as a random slope in all models. To account for phylogenetic correlations among species, we included two random intercept terms for species: one term that models phylogenetic covariance and another term that accounts for repeated measurements and other effects that may be independent of phylogenetic relationships among species (Ives, 2018). The random effect structure allowed slope and intercept parameters to vary for each species. As NSC concentrations for roots, stems, branches, and leaves were not measured on all individuals, models were fit to subsets of data for each plant organ.

We fit all models using weakly informative priors, four chains, and 1,500 burn-in samples per chain, after which 4,500 samples per chain (total post-warmup samples = 18,000) were used to calculate posterior distributions of model parameters. To reduce the number of divergent transitions, we set the '*adapt_delta*' parameter within the '*brms*' function to 0.99 for all models (Bürkner, 2017). All fixed effects were standardized using a z-transformation to enable comparisons across models. Model convergence was evaluated visually and by estimating '*Rhat*' using the '*rhat*' function, where values considerably greater than 1 indicate that models have failed to converge. We selected the distribution family by fitting each model with a Gaussian or log-normal distribution, and assessed which fit better by comparing observed data to simulated data from the posterior predictive distribution (Fig. S3). Additionally, we estimated a Bayesian r^2

using the ‘*bayes_R2*’ function for each model to represent an estimate of the proportion of variation explained for new data.

As NSC from fall sampling may be a better overall indicator of current year growth-storage trade-offs in the Northern Hemisphere (Martínez-Vilalta et al., 2016), we used the fall NSC concentrations sampled in the deciduous temperate forest for all models. As a sensitivity test, we also examined if trait-NSC relationships varied across seasons within the DTF using a similar model structure as described above. All analyses were performed in R version 3.6.1 (R Core Team 2020).

RESULTS

Traits and NSC concentrations across biomes and leaf habit

Within each biome and leaf habit, tree species of the tropical biomes exhibited a broad range of variation in ecological strategies, in contrast to the DTF species, all of which are deciduous (Fig. 1, see Fig. S4 for individual functional traits). The first two axes of the PCA captured a total of 58.8% of variation among the 11 functional traits, the first axis capturing 34.3% of variation and the second capturing 23.1%. The first PCA axis represents traits associated with mechanical strength, defense and resource acquisition, from ‘slow’ species with high branch and stem density and LDMC, to fast species with high *A*_{mass}, leaf N, and leaf P. The second PCA axis represents traits related to resource acquisition and defense, from ‘slow’ species with high leaf thickness, leaf Mg and leaf area to fast species with high SLA and *A*_{mass} (Fig. 1).

Our analyses showed that NSC concentrations were similar across biomes for all tree organs except leaves, which were significantly higher in the DTF. However, NSC concentrations among organs were weakly correlated ($r < 0.4$, Fig. S5). Variance partitioning analysis showed that most of the variation in NSC in tree organs is explained by interspecific variation for roots, stems and branches and by among-biome variation for leaves (Fig. 2). There was a minimal influence of leaf habit on the variation of NSC concentrations for any tree organ (Fig. S6). We found broadly similar results when examining NSC concentrations in tree organs across seasons in the deciduous temperate forest (Fig. S7); only NSC in branches exhibited a higher concentration in the fall than in the spring (Fig. S7c).

The phylogenetic signal of NSC concentrations was greater than 0 for leaves, branches and stems, indicating a moderate amount of phylogenetic signal, but not as much as would be expected under Brownian movement (Table 1). In contrast, the phylogenetic signal of NSC concentrations for roots was close to zero (Table 1).

Relationships between carbohydrate concentrations and the fast-slow continuum across biomes and leaf habit

Our phylogenetic multi-level Bayesian models that examine variation in root, stem, branch, and leaf NSC as a function of biome, leaf habit, and the traits of the ‘fast-slow’ spectrum (fast-slow PC 1, fast-slow PC 2), explained a large amount of variation in NSC concentrations, ranging

from 53% to 72% across tree organs (mean Bayesian r^2 ; Table 1) and estimated NSC concentrations (Fig. 3).

Contrary to our expectations, the two dimensions of the ‘fast-slow’ spectrum (fast-slow PC1, fast-slow PC2) did not consistently predict variation in NSC concentrations of woody organs across biomes (Fig. 4, Table S4). Only fast-slow PC2 showed a marginally positive relationship with NSC concentrations in roots (80% credible intervals, Fig. 4a), indicating that more resource acquisitive species tend to have a higher concentration of reserves in roots. Fast-slow PC1 varied negatively with leaf NSC concentrations (Fig. 4d, Table S4), indicating that resource conservative species have higher concentrations of NSC in leaves.

Our analysis further showed context dependent effects of the ‘fast-slow’ spectrum on NSC concentrations in leaves (Figs. 4d, 5 and S8). Leaf NSC concentrations varied slightly along the fast-slow PC1 in the tropical biomes, while in the DTF leaf varied negatively with the fast-slow PC1 (Fig. 5). This result indicates that in the DTF ‘slow’ species along the first fast-slow dimension (PC1) have higher leaf NSC concentrations than fast species.

DISCUSSION

Our examination of the relationships between carbon reserve concentrations and functional traits of temperate and tropical angiosperm tree species revealed that variation between traits and NSC concentrations in woody organs was largely decoupled. Conversely, we found that leaves

exhibited coordinated variation between NSC concentrations and traits (fast-slow PC1), which varied in direction and strength among biomes (Fig. 4 and 5).

Coordination between carbohydrate concentrations and functional traits

In general, our results show that relationships between functional traits and carbohydrate concentrations in woody organs were not coordinated (Fig. 4). This suggests that the position of species along the ‘fast-slow’ plant economics spectrum is not predictive of NSC concentrations in woody organs, extending the findings from previous studies showing no trade-off between NSC concentrations and carbon investment (Lusk and Piper, 2007, Piper et al., 2009, Imaji and Seiwa, 2010, Piper, 2015) by considering species from multiple biomes.

A possible explanation for the lack of a consistent relationship between functional traits and NSC concentrations in woody tree organs may be that long-term allocation of carbohydrates to storage in stems or roots can take several growing seasons or years (Carbone et al., 2013, Richardson et al., 2015, Hartmann and Trumbore, 2016, Muhr et al., 2016), depending on the distance and the osmotic gradient between carbohydrate sources and sinks (Lacointe, 2000, Le Roux et al., 2001). If other trait values capture the current abiotic and biotic conditions to a greater extent than those present during the accumulation of NSC, the strength of their association with NSC concentrations may weaken with increasing age of stored NSC. Therefore, the age difference between NSC of leaves and woody organs may explain why variation in functional traits is largely decoupled from NSC of woody organs, but not from leaf NSC.

Among the studied traits included in fast-slow dimensions, it was surprising that variation in NSC in woody tissues was decoupled from wood density of stems and branches (SD and BD). Wood density has been suggested to be a proxy for both the amount of parenchyma (Ziemińska et al., 2015, Morris et al., 2016), and NSC concentrations (Plavcová and Jansen, 2015, Plavcová et al., 2016). However, parenchyma cells have multiple functional roles, e.g., acting as a water reservoir and contributing to different mechanical properties of wood (i.e., elasticity) that are independent of wood density and NSC concentrations (Ziemińska et al., 2015). Additionally, xylem structure – in order to enhance mechanical stability – places strong constraints on the storage capacity of tree stems (Plavcová et al., 2019), the dimension with which SD and BD are most strongly associated, and was decoupled from NSC concentrations in these tissues (Fig. 4).

In contrast with NSC concentrations of woody organs, we found evidence of coordination between leaf NSC concentrations and the fast-slow PC1 (Fig. 4d, Table S4). The decrease in leaf NSC with increasing leaf N, leaf P, SLA and Amax and the increase in leaf NSC with increasing SD and LT suggest that species with ‘slow’ ecological strategies accumulate more NSC in their leaves than those with ‘fast’ ecological strategies. Our results therefore suggest that acquisitive trait values of leaf N, leaf P, SLA and Amax may be associated with structural support traits such as leaf toughness and leaf lifespan (Osnas et al., 2018). Even though leaf N and P are strongly correlated with Amax (Reich and Schoettle, 1988), because physiologically they play a fundamental role in both photosynthesis and starch and sucrose synthesis (Rychter et al., 2016), they may not favor NSC accumulation in temperate and tropical biomes.

Thus, our results did not fully support our second hypothesis that species with ‘slow’ traits associated with greater carbon investment in defense and conservative ecological strategies accumulate more NSC in woody organs than species associated with acquisitive or ‘fast’ ecological strategies. Our results show that species with higher NSC concentrations in roots exhibit a weak, positive tendency (80% credible intervals) to have trait values associated with ‘fast’ ecological strategies. This finding may suggest that ‘fast’ species may allocate more carbohydrates to roots than ‘slow’ species as part of their response to mechanical damage to aboveground plant organs, which may enable them to persist in areas subjected to frequent disturbances, such as winds, low intensity fires (Poorter et al., 2010, Clarke et al., 2013), ice storms (Proulx and Greene, 2001), or in human-dominated ecosystems (Uhl, 1987, Jakovac et al., 2015). We found contrasting trends in trait-NSC relationships among biomes for leaves, where leaf NSC did not vary or increase with the fast-slow PC1 in the tropical biomes but decreased with increasing the fast-slow PC1 in the DTF (Fig. 5). Several studies on woody plants have reported contrasting patterns of plant functional strategies among biomes, which have been associated with phylogenetic constraints, or selective biogeographic processes, such as adaptation to different climatic regimes or physical barriers that generate different selective pressures within communities (Wright et al., 2005, Heberling and Fridley, 2012, Heberling and Fridley, 2013). Additionally, other abiotic factors, such as soil fertility and water availability, may mediate the growth-storage trade-off at the level of NSCs by either facilitating or constraining tree growth (Breugel et al., 2011).

Patterns of NSC storage across tree organs

While plants may remobilize nutrients and reserves between organs according to fluctuating resource availability (Maillard et al., 2015), our results show that trees accumulate large amounts of carbohydrate reserves over time in woody organs – especially in roots – regardless of their ecological strategy or species leaf habit (Fig. 2). The high NSC concentrations in roots observed in this study may indicate that roots serve as a long-term reservoir for responding to future disturbances (Clark and Clark, 1991, Poorter et al., 2010, Clarke et al., 2013), ensuring that resources are available for resprouting or leaf flush (Wiley, 2013). For example, different studies have shown that trees have sufficient reserves to rebuild the entire leaf canopy up to four times (Hoch et al., 2003, Körner, 2003, Würth et al., 2005), or even provide the carbon necessary for stem growth for up to 30 years (Klein et al., 2016). Thus, NSC stored in stems and roots probably remain stable or increase gradually over time, at least until a severe disturbance triggers an imbalance between carbon sources and sinks and initiates mobilization of reserves (e.g. Morales et al., 2020). The stability of root and stem NSC reserves is likely in contrast to the more labile, more recent NSC reserves stored in leaves and branches that support daily metabolism and annual growth (Martínez-Vilalta et al., 2016). We found lower branch NSC concentrations in the spring than in the fall of the deciduous temperate forest (Fig. S7), which suggests that carbohydrates used for leaf flush were supplied from the closest sources of reserves (branches) and not from the more distant ones (stems and roots) (Hoch, 2015, Klein et al., 2016).

Finally, NSC concentrations vary with the time of year, especially in trees subjected to strong seasonality, such as in temperate regions where carbohydrate reserves are necessary to survive the winter (Canham et al., 1999, Barbaroux et al., 2003, Li et al., 2002, Hoch and Körner, 2003, Körner, 2003, Genet et al., 2009, Carbone et al., 2013, Martínez-Vilalta et al., 2016). Thus, tree

species with contrasting ecological strategies may have similar fall carbohydrate concentrations but different spring concentrations (Hoch et al., 2003, Martínez-Vilalta et al., 2016). Here, we present results based on fall NSC concentrations in a deciduous temperate forest, since they may be a better indicator of current year growth-storage trade-offs in the Northern Hemisphere (Martínez-Vilalta et al., 2016). We also evaluated NSC concentrations based on mean NSC concentrations across seasons (spring and fall in the deciduous temperate forests) to examine seasonal remobilization of carbohydrates, and to test the sensitivity of our results to seasonal variation in NSC concentrations. We found broadly similar results when examining trait - NSC relationships across seasons in the deciduous temperate forest; only fast-slow dimensions and NSC in stem organs exhibited contrasting slopes across seasons (Figs. S7 and S8).

Conclusions

Our study tested the hypothesis that NSC concentrations in tree organs are associated with the ‘fast-slow’ spectrum of leaf and wood functional traits across biomes. In woody organs, we found that variation between NSC concentrations and functional traits were mostly decoupled, yet were strongly coordinated in leaves. Considering the concentrations of NSC in woody organs as a proxy for species’ capacity to respond to disturbances, our results imply that variation in species’ NSC concentrations is weakly associated with functional trait spectra that describe global variation in plant ecological strategies. Consequently, efforts to predict the response of ecosystems to global change will need to integrate a suite of plant traits, such as NSC concentrations, that are independent of the ‘fast-slow’ spectrum and that capture species’ resilience to a broad range of potential drivers.

ACKNOWLEDGEMENTS

The authors thank Milena Molina, Juan Carlos Medina, Luis Carlos Galeano, David Andres Herrera, Sergio Martinez, and Mathieu Messier for their help. We also thank Alfredo Navas (Hacienda Sabaneta Natural Reserve) and Alvaro Cogollo (Medellin Botanical Garden) for their logistical support, and Daijiang Li for his input on data analysis. This research was supported by the NSERC/Hydro-Quebec research chair on tree growth control and by a scholarship from the Quebec research fund for nature and technology. DC received support from Chile's National Fund for Scientific and Technological Development (FONDECYT No. 1201347).

AUTHOR CONTRIBUTIONS

JAR, DC, JP, ITH, and CM contributed to the design of the research. Fieldwork was carried out by JAR. Laboratory analysis of sugars and chemical elements were performed by JAR with the support of GH, BR, and CS. JAR and DC analyzed the data. JAR led the writing of the manuscript with substantial input from DC and ITH. All authors contributed critically to improve drafts and gave final approval for publication.

Tables and Figures

Table 1. Model fit and phylogenetic signal in NSC concentrations of organs of tropical and temperate tree species. Model convergence (Rhat) and Pagel's lambda were estimated directly by phylogenetic multi-level Bayesian models. 95% credible intervals are in parentheses.

Organ	r^2	Pagel's lambda	Rhat
Leaves	0.66 (0.57 – 0.72)	0.54	1.00014 (1.00011-1.00018)
Branches	0.53 (0.38 – 0.65)	0.12	1.00023 (1.00015-1.00030)
Stems	0.54 (0.34 – 0.70)	0.30	1.00016 (1.00011-1.00021)
Roots	0.72 (0.60 – 0.81)	0.00	1.00063 (1.00047-1.00079)

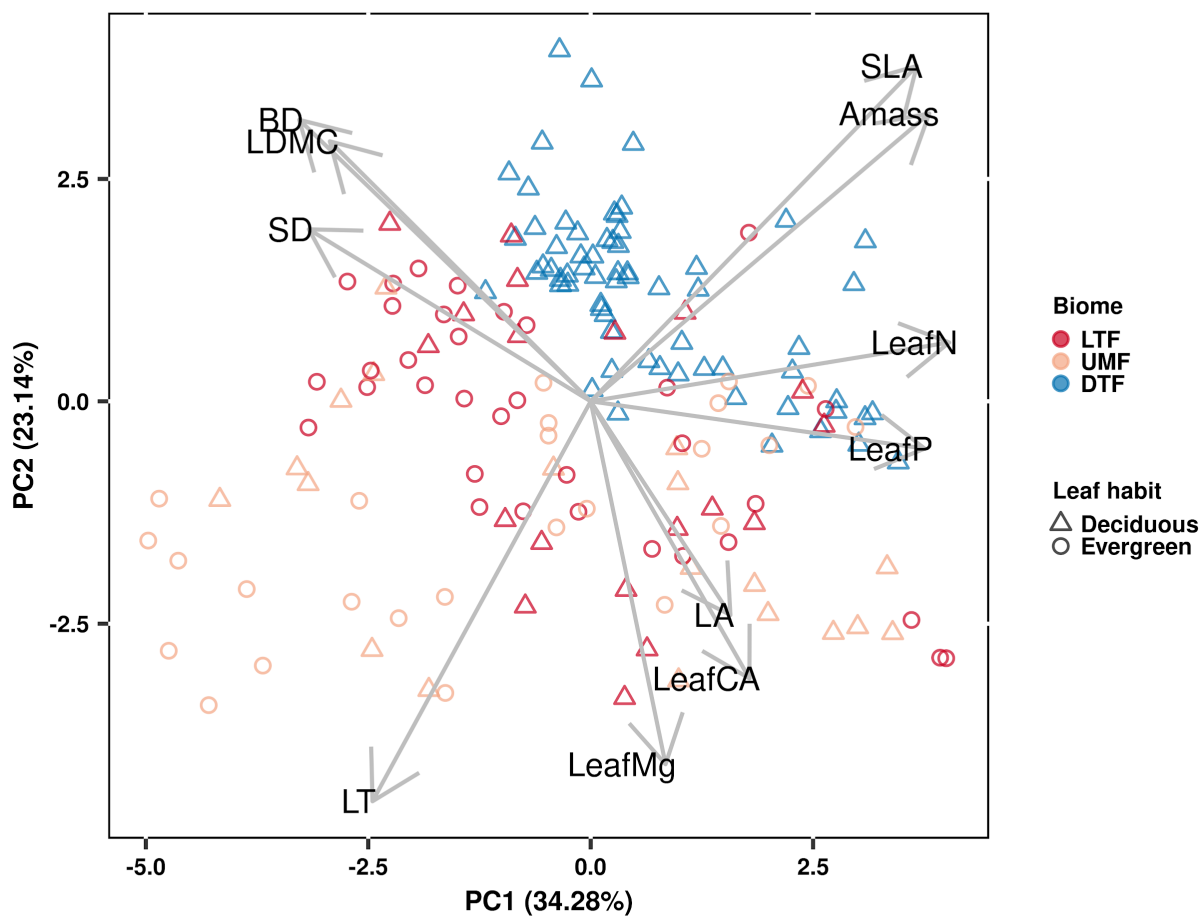


Fig. 1. Principal components analysis of plant functional traits across biomes ($n = 61$ species). LTF: lowland tropical rainforest, UMF: upper montane forest, and DTF: deciduous temperate forest. Table S3 shows trait abbreviations.

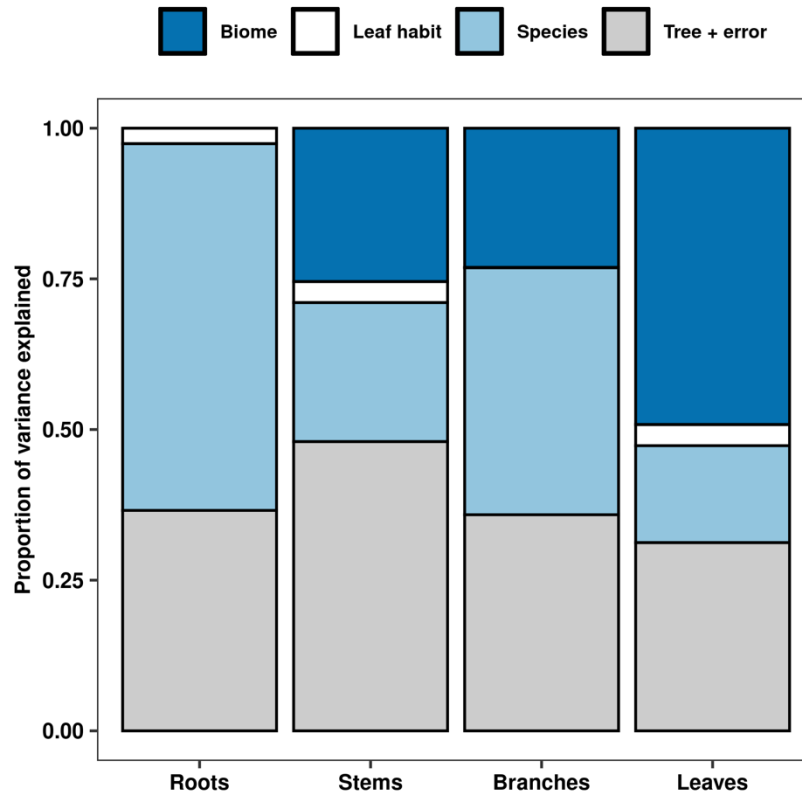


Fig. 2. Variance partitions of NSC concentrations for each tree organ across biome, leaf habit, and species. Variation within tree + error includes residual variation, meaning that this partition captures intra-specific variation and error.

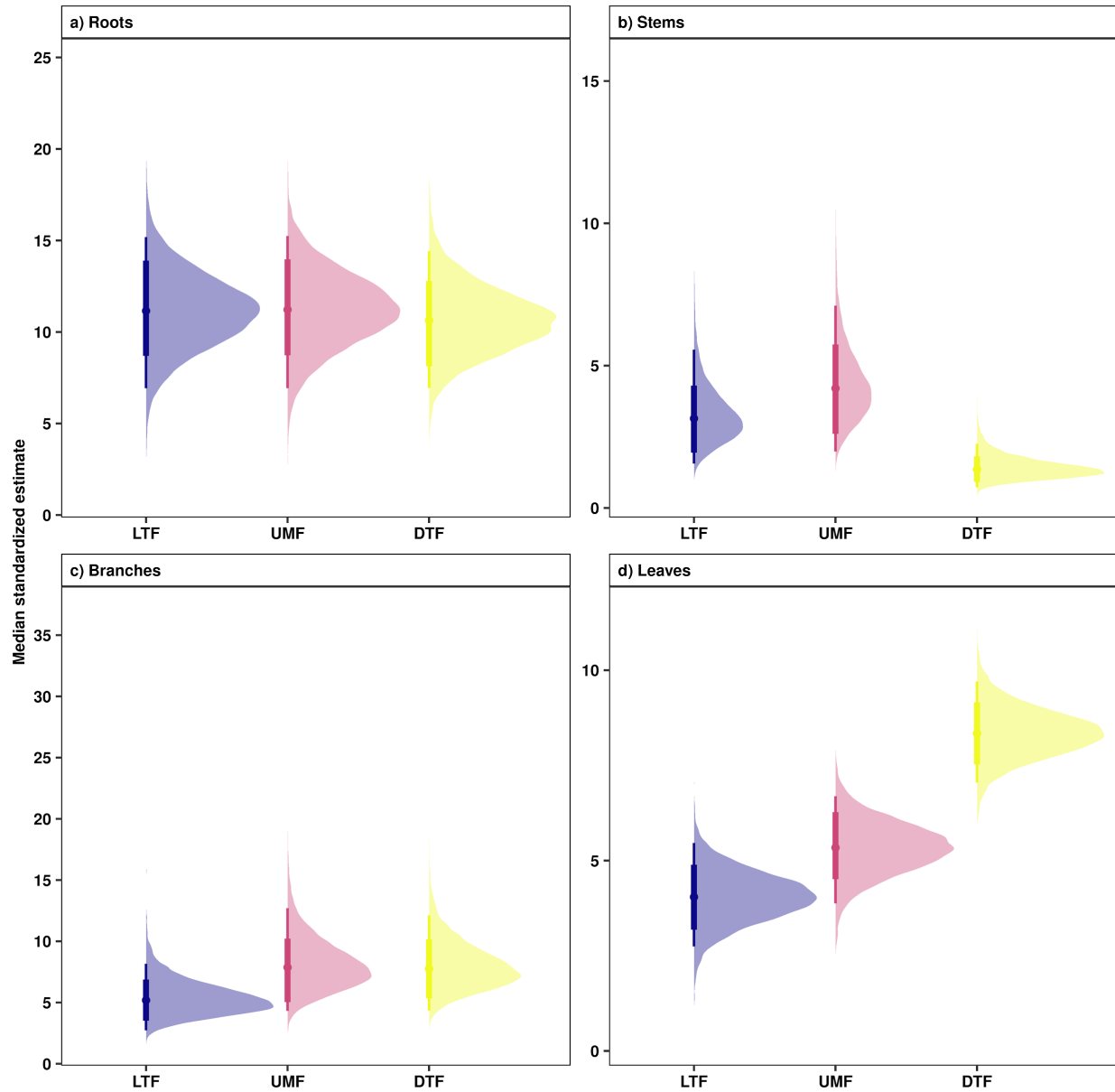


Fig. 3. Estimated fall NSC concentrations in **a)** root, **b)** stem, **c)** branch, and **d)** leaves across biomes. Points are medians and whisker bars are 80% and 95% credible intervals and were estimated using phylogenetic hierarchical Bayesian models. LTF: lowland tropical rainforest, UMF: upper montane forest, and DTF: deciduous temperate forest.

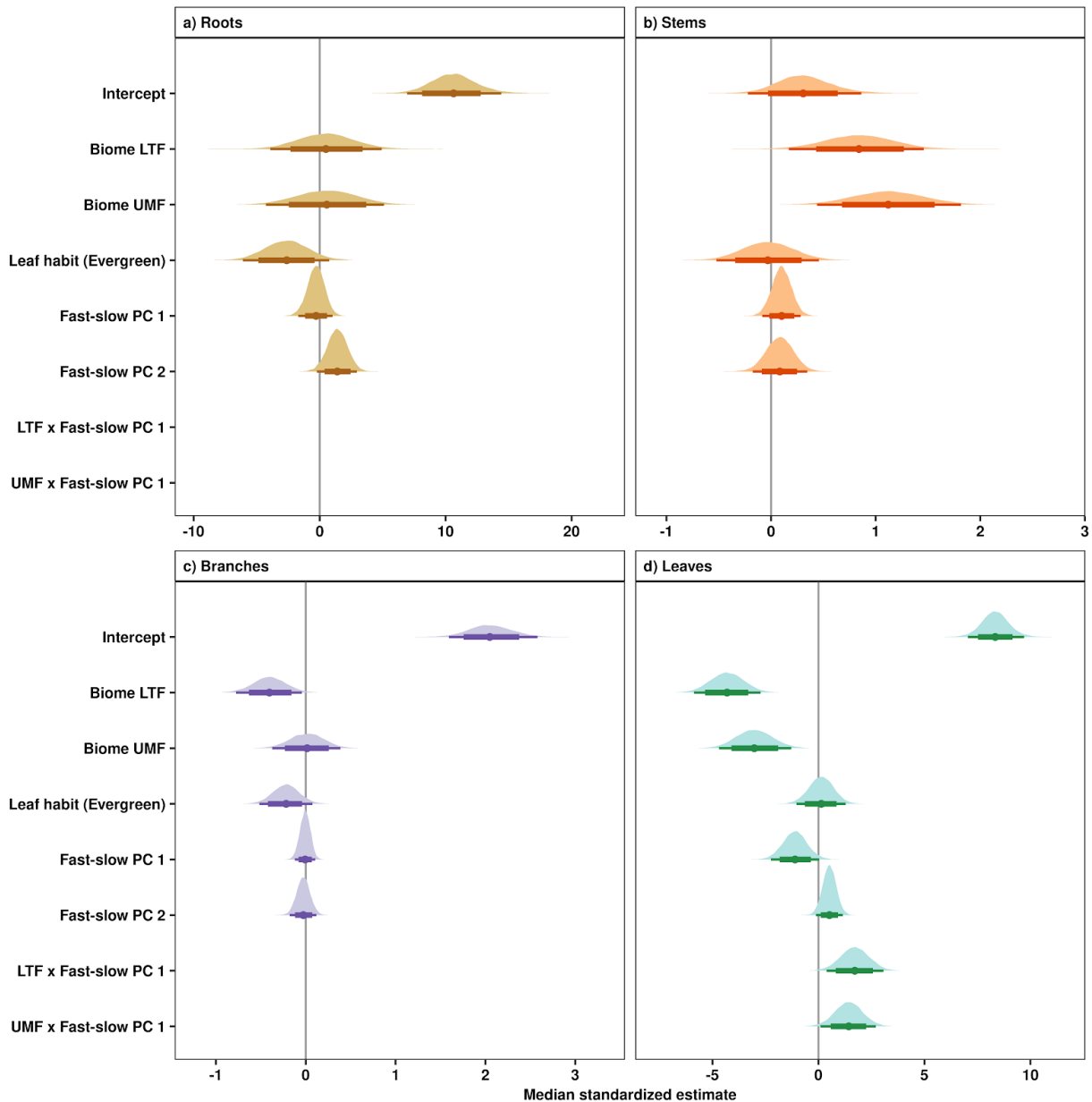


Fig. 4. Influence of the fast-slow continuum, biomes and leaf habit on NSC concentrations of **a)** roots, **b)** stems, **c)** branches, and **d)** leaves. Points are medians and whisker bars are 80% and 95% credible intervals estimated using phylogenetic hierarchical Bayesian models. Continuous variables were z-transformed prior to analysis to facilitate comparisons (within and across tree organs). Fast-slow PC1 and fast-slow PC2 are the first two axes of a principal component analysis of fast-slow plant functional traits. LTF: lowland tropical rainforest, UMF: upper montane forest, and DTF: deciduous temperate forest. Table S3 shows trait abbreviations.

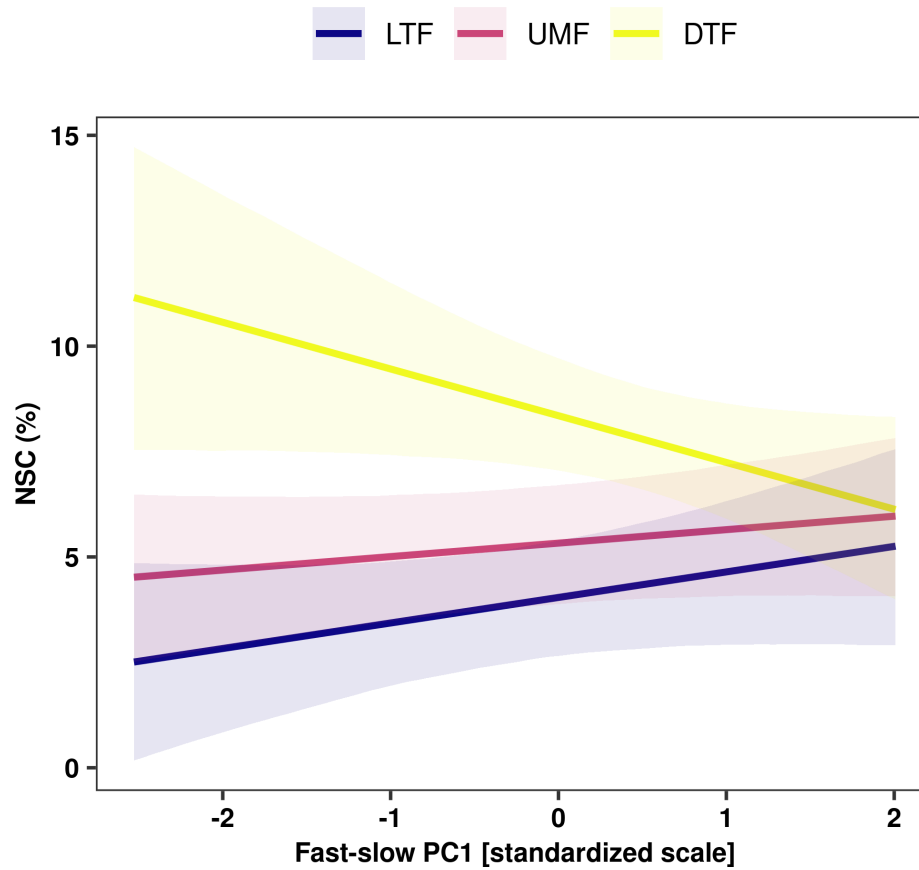


Fig. 5. Interactive effects of the fast-slow PC 1 and biome on NSC concentrations of leaves. Solid lines are predicted fitted values using phylogenetic hierarchical Bayesian models and shaded regions represent 95% credible intervals of fitted values. Plant functional traits were z-transformed prior to analysis. LTF: lowland tropical rainforest, UMF: upper montane forest, and DTF: deciduous temperate forest.

LITERATURE CITED

- Allen SE, Grimshaw HM, Parkinson JA, Quarmby C. 1974. *Chemical analysis of ecological materials*. Oxford: BlackwellScientific.
- Arii K, Hamel BR, Lechowicz MJ. 2005. Environmental correlates of canopy composition at Mont St. Hilaire, Quebec, Canada. *Journal of the Torrey Botanical Society*, **132**: 90-102.
- Armenteras-Pascual D, Retana-Alumbreros J, Molowny-Horas R, Roman-Cuesta RM, Gonzalez-Alonso F, Morales-Rivas M. 2011. Characterising fire spatial pattern interactions with climate and vegetation in Colombia. *Agricultural and Forest Meteorology*, **151**: 279-289.
- Atkinson RRL, Burrell MM, Rose KE, Osborne CP, Rees M. 2014. The dynamics of recovery and growth: how defoliation affects stored resources. *Proceedings of the Royal Society B*, **281**: 20133355.
- Baraloto C, Paine CET, Lourens P, Jacques B, Damien B, Anne-Marie D, Bruno H, Sandra p, Jean-Christophe R, Jerome C. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**: 1338-1347.
- Barbaroux C, Bréda N, Dufrêne E. 2003. Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). *New Phytologist*, **157**: 605-615.
- Breugel Mv, Hall JS, Craven DJ, Gregoire TG, Park A, Dent DH, Wishnie MH, Mariscal E, Deago J, Ibarra D, Cedeño N, Ashton MS. 2011. Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. *The Ecology and Ecosystem Services of Native Trees: Implications for Reforestation and Land Restoration in Mesoamerica*, **261**: 1580-1589.
- Bürkner PC. 2017. brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, **80**: 1-28.
- Canham CD, Kobe RK, Latty EF, Chazdon RL. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia*, **121**: 1-11.
- Carbone MS, Czimczik CI, Keenan TF, Murakami PF, Pederson N, Schaberg PG, Xu X, Richardson AD. 2013. Age, allocation and availability of nonstructural carbon in mature red maple trees. *New Phytologist*, **200**: 1145-1155.
- Chapin FS, Schulze ED, Mooney HA. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics*, **21**: 423-447.
- Chave J, David C, Steven J, Simon LL, Nathan GS, Amy EZ. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**: 351-366.
- Clark DB, Clark DA. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology*, **79**: 447-457.
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist*, **197**: 19-35.
- Coley PD, Bryant JP, Chapin FS. 1985. Resource availability and plant antiherbivore defense. *Science*, **230**: 895-899.
- Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Díez P, Funes G, Hamzehee B, Khoshnevi M, Pérez-Harguindeguy N, Pérez-Rontomé MC,

- Shirvany FA, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E, Kazemi-Saeed F, Maestro-Martínez M, Romo-Díez A, Shaw S, Siavash B, Villar-Salvador P, Zak MR. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, **15**: 295-304.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Joseph Wright S, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné LD. 2016. The global spectrum of plant form and function. *Nature*, **529**: 167-171.
- Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R. 2014. Nonstructural Carbon in Woody Plants. *Annual Review of Plant Biology*, **65**: 2.1-2.21.
- Donovan LA, Maherali H, Caruso CM, Huber H, de Kroon H. 2011. The evolution of the worldwide leaf economics spectrum. *Trends in Ecology & Evolution*, **26**: 88-95.
- Doughty CE, Metcalfe DB, Girardin CAJ, Amézquita FF, Cabrera DG, Huasco WH, Silva-Espejo JE, Araujo-Murakami A, da Costa MC, Rocha W, Feldpausch TR, Mendoza ALM, da Costa ACL, Meir P, Phillips OL, Malhi Y. 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, **519**: 78-82.
- Fajardo A, Piper FI, Hoch G. 2013. Similar variation in carbon storage between deciduous and evergreen treeline species across elevational gradients. *Annals of Botany*: 1-9.
- Felsenstein J. 1985. Phylogenies and the Comparative Method. *The American Naturalist*, **125**: 1-15.
- Fortunel C, Fine PVA, Baraloto C. 2012. Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology*, **26**: 1153-1161.
- Freckleton R, xa, P, Harvey P, xa, H, Pagel M, Associate Editor: Jonathan BL. 2002. Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. *The American Naturalist*, **160**: 712-726.
- Frelich LE, Lorimer CG. 1991. Natural Disturbance Regimes in Hemlock-Hardwood Forests of the Upper Great Lakes Region. *Ecological Monographs*, **61**: 145-164.
- Gaucher C, Gougeon S, Mauffette Y, Messier C. 2005. Seasonal variation in biomass and carbohydrate partitioning of understory sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) seedlings. *Tree Physiology*, **25**: 93-100.
- Genet H, Bréda N, Dufrêne E. 2009. Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology*, **30**: 177-192.
- Gough CM, Flower CE, Vogel CS, Dragoni D, Curtis PS. 2009. Whole-ecosystem labile carbon production in a north temperate deciduous forest. *Agricultural and Forest Meteorology*, **149**: 1531-1540.
- Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodgkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe

- PC, Whitehouse J. 1997.** Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**: 259-281.
- Harris I, Jones PD, Osborn TJ, Lister DH. 2014.** Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, **34**: 623-642.
- Hartmann H, Trumbore S. 2016.** Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. *New Phytologist*, **211**: 386-403.
- Heberling JM, Fridley JD. 2012.** Biogeographic constraints on the world-wide leaf economics spectrum. *Global Ecology and Biogeography*, **21**: 1137-1146.
- Heberling JM, Fridley JD. 2013.** Resource-use strategies of native and invasive plants in Eastern North American forests. *New Phytologist*, **200**: 523-533.
- Hoch G. 2015.** Carbon Reserves as Indicators for Carbon Limitation in Trees. In: Lüttge U, Beyschlag W, eds. *Progress in Botany: Vol. 76*. Cham: Springer International Publishing.
- Hoch G, Körner C. 2003.** The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia*, **135**: 10-21.
- 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**: 361-374.
- Hoch G, Richter A, Körner C. 2003.** Non-structural carbon compounds in temperate forest trees. *Plant, Cell and Environment*, **26**: 1067-1081.
- Imaji A, Seiwa K. 2010.** Carbon allocation to defense, storage, and growth in seedlings of two temperate broad-leaved tree species. *Oecologia*, **162**: 273-281.
- Ives AR. 2018.** *Mixed and Phylogenetic Models: A Conceptual Introduction to Correlated Data*: Leanpub.
- Ives AR, Midford PE, Garland T, Jr. 2007.** Within-species variation and measurement error in phylogenetic comparative methods. *Syst Biol*, **56**: 252-70.
- Jakovac CC, Peña-Claros M, Kuypers TW, Bongers F. 2015.** Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology*, **103**: 67-77.
- Kennard RW, Stone LA. 1969.** Computer aided design of experiments. *Technometrics*, **11**: 137-148.
- Kitajima K. 1994.** Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**: 419-428.
- Klein T, Vitasse Y, Hoch G. 2016.** Coordination between growth, phenology and carbon storage in three coexisting deciduous tree species in a temperate forest. *Tree Physiology*, **36**: 847-855.
- Kobe RK. 1997.** Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos*, **80**: 226-233.
- Körner C. 2003.** Carbon limitation in trees. *Journal of Ecology*, **91**: 4-17.
- Kozlowski TT. 1992.** Carbohydrate sources and sinks in woody plants. *Botanical Review*, **58**: 107-222.
- Kruschke JK. 2015.** Chapter 7 - Markov Chain Monte Carlo. In: Kruschke JK, ed. *Doing Bayesian Data Analysis (Second Edition)*. Boston: Academic Press.
- Lacointe A. 2000.** Carbon allocation among tree organs: A review of basic processes and representation in functional-structural tree models. *Annals of Forest Science*, **57**: 521-533.

- Landhäusser SM, Lieffers VJ. 2003.** Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. *Trees*, **17**: 471-476.
- Le Roux X, Lacoïnte A, Escobar-Gutiérrez A, Le Dizès S. 2001.** Carbon-based models of individual tree growth: a critical appraisal. *Annals of Forest Science*, **58**: 469-506.
- Lê S, Josse J, Husson F. 2008.** FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, **25**: 1-18.
- Li D, Ives AR. 2017.** The statistical need to include phylogeny in trait-based analyses of community composition. *Methods in Ecology and Evolution*, **8**: 1192-1199.
- Li H, Liang Y, Xu Q, Cao D. 2009.** Key wavelengths screening using competitive adaptive reweighted sampling method for multivariate calibration. *Analytica Chimica Acta*, **648**: 77-84.
- Li MH, Hoch G, Körner C. 2002.** Source/sink removal affects mobile carbohydrates in *Pinus cembra* at the Swiss treeline. *Trees-Structure and Function*, **16**: 331-337.
- Li N, He N, Yu G, Wang Q, Sun J. 2016.** Leaf non-structural carbohydrates regulated by plant functional groups and climate: Evidences from a tropical to cold-temperate forest transect. *Ecological Indicators*, **62**: 22-31.
- Lusk CH, Piper FI. 2007.** Seedling size influences relationships of shade tolerance with carbohydrate-storage patterns in a temperate rainforest. *Functional Ecology*, **21**: 78-86.
- Maillard A, Diquélou S, Billard V, Laîné P, Garnica M, Prudent M, Garcia-Mina J-M, Yvin J-C, Ourry A. 2015.** Leaf mineral nutrient remobilization during leaf senescence and modulation by nutrient deficiency. *Frontiers in plant science*, **6**: 317-317.
- Marino G, Aqil M, Shipley B. 2010.** The leaf economics spectrum and the prediction of photosynthetic light-response curves. *Functional Ecology*, **24**: 263-272.
- Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F. 2016.** Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecological Monographs*, **86**: 495-516.
- Maycock PF. 1961.** Botanical studies on Mont St. Hilaire, Rouvillecounty, Quebec: General description of the area and a floristic survey. *Canadian Journal of Botany*, **39**: 1293-1325.
- Messier C, Posada J, Aubin I, Beaudet M. 2009.** Functional Relationships Between Old-Growth Forest Canopies, Understorey Light and Vegetation Dynamics. In: Wirth C, Gleixner G, Heimann M, eds. *Old Growth Forests: Function, Fate and Value, Ecological Studies 207*. Berlin: Springer-Verlag.
- Messier J, McGill BJ, Lechowicz MJ. 2010.** How do traits vary across ecological scales? A case for trait-based ecology. *Ecological Letters*, **13**: 838-848.
- Molina-Venegas R, Rodríguez MÁ. 2017.** Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? *BMC evolutionary biology*, **17**: 53.
- Morales MS, Cook ER, Barichivich J, Christie DA, Villalba R, LeQuesne C, Sruar AM, Ferrero ME, González-Reyes Á, Couvreur F, Matskovsky V, Aravena JC, Lara A, Mundo IA, Rojas F, Prieto MR, Smerdon JE, Bianchi LO, Masiokas MH, Urrutia-Jalabert R, Rodríguez-Catón M, Muñoz AA, Rojas-Badilla M, Alvarez C, Lopez L, Luckman BH, Lister D, Harris I, Jones PD, Williams AP, Velazquez G, Aliste D, Aguilera-Betti I, Marcotti E, Flores F, Muñoz T, Cuq E, Boninsegna JA. 2020.** Six hundred years of South American tree rings reveal an increase in severe hydroclimatic events since mid-20th century. *Proceedings of the National Academy of Sciences*, **117**: 16816.

- Mori AS, Furukawa T, Sasaki T. 2013.** Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, **88**: 349-364.
- Morris H, Plavcová L, Cvecko P, Fichtler E, Gillingham MA, Martínez-Cabrera HI, McGlenn DJ, Wheeler E, Zheng J, Ziemińska K, Jansen S. 2016.** A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytologist*, **209**: 1553-1565.
- Muhr J, Messier C, Delagrange S, Trumbore S, Xu X, Hartmann H. 2016.** How fresh is maple syrup? Sugar maple trees mobilize carbon stored several years previously during early springtime sap-ascent. *New Phytologist*, **209**: 1410-1416.
- Myers JA, Kitajima K. 2007.** Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. *Journal of Ecology*, **95**: 383-395.
- Newell EA, Mulkey SS, Wright SJ. 2002.** Seasonal patterns of carbohydrate storage in four tropical tree species. *Oecologia*, **131**: 333-342.
- O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014.** Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change*, **4**: 710-714.
- O'Brien MJ, Valtat A, Abiven S, Studer MS, Ong R, Schmid B. 2020.** The role of soluble sugars during drought in tropical tree seedlings with contrasting tolerances. *Journal of Plant Ecology*, **13**: 389-397.
- Osnas JLD, Katabuchi M, Kitajima K, Wright SJ, Reich PB, Van Bael SA, Kraft NJB, Samaniego MJ, Pacala SW, Lichstein JW. 2018.** Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proceedings of the National Academy of Sciences*, **115**: 5480.
- Pearse WD, Cadotte MW, Cavender-Bares J, Ives AR, Tucker CM, Walker SC, Helmus MR. 2015.** pez: phylogenetics for the environmental sciences. *Bioinformatics*, **31**: 2888-2890.
- Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC. 2013.** New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**: 167-234.
- Pinheiro J, Bates D, DebRoy S, Sarkar D. 2020.** nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-148.
- Pinilla Herrera MC, Pinzón Correa CA. 2016.** An assessment of El Niño and La Niña impacts focused on monthly and seasonal rainfall and extreme dry/precipitation events in mountain regions of Colombia and México. *Adv. Geosci.*, **42**: 23-33.
- Piper FI. 2015.** Patterns of carbon storage in relation to shade tolerance in southern South American species. *American Journal of Botany*, **102**: 1442-1452.
- Piper FI, Fajardo A. 2011.** No evidence of carbon limitation with tree age and height in *Nothofagus pumilio* under mediterranean and temperate climate conditions. *Annals of Botany*, **108**: 907-917.
- Piper FI, Paula S. 2020.** The Role of Nonstructural Carbohydrates Storage in Forest Resilience under Climate Change. *Current Forestry Reports*.

- Piper FI, Reyes-Díaz M, Corcuera LJ, Lusk CH. 2009.** Carbohydrate storage, survival, and growth of two evergreen *Nothofagus* species in two contrasting light environments. *Ecological Research*, **24**: 1233-1241.
- Plavcová L, Gallenmüller F, Morris H, Khatamirad M, Jansen S, Speck T. 2019.** Mechanical properties and structure–function trade-offs in secondary xylem of young roots and stems. *Journal of Experimental Botany*, **70**: 3679-3691.
- Plavcová L, Hoch G, Morris G, Ghiasi S, Jansen S. 2016.** The amount of parenchyma and living fibers affects storage of nonstructural carbohydrates in young stems and roots of temperate trees. *American Journal of Botany*, **103**: 603-612.
- Plavcová L, Jansen S. 2015.** The role of xylem parenchyma in the storage and utilization of non-structural carbohydrates. In: Hacke UG, ed. *Functional and ecological xylem anatomy*. Heidelberg, Germany: Springer International.
- Poorter L, Kitajima K. 2007.** Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology*, **88**: 1000-1011.
- Poorter L, Kitajima K, Mercado P, Chubina J, Melgar I, Prins HHT. 2010.** Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology*, **91**: 2613-2627.
- Popp M, Wolfgang L, Andreas JM, Andreas R, Petra S, Hildegard S. 1996.** Sample preservation for determination of organic compounds: microwave versus freeze-drying. *Journal of Experimental Botany*, **47**: 1469-1473.
- Poveda G, Jaramillo A, Gil MM, Quiceno N, Mantilla RI. 2001.** Seasonally in ENSO-related precipitation, river discharges, soil moisture, and vegetation index in Colombia. *Water Resources Research*, **37**: 2169-2178.
- Powers JS. 2020.** A sweet new study: tropical forest species use nonstructural carbohydrates in different ways during drought. *Journal of Plant Ecology*, **13**: 387-388.
- Proulx OJ, Greene DF. 2001.** The relationship between ice thickness and northern hardwood tree damage during ice storms. *Canadian Journal of Forest Research*, **31**: 1758-1767.
- Qian H, Jin Y. 2016.** An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, **9**: 233-239.
- Ramirez JA, Posada JM, Handa IT, Hoch G, Vohland M, Messier C, Reu B. 2015.** Near-infrared spectroscopy (NIRS) predicts non-structural carbohydrate concentrations in different tissue types of a broad range of tree species. *Methods in Ecology and Evolution*, **6**: 1018-1025.
- Reich PB. 2014.** The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**: 275-301.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999.** Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**: 1955-1969.
- Reich PB, Schoettle AW. 1988.** Role of phosphorus and nitrogen in photosynthetic and whole plant carbon gain and nutrient use efficiency in eastern white pine. *Oecologia*, **77**: 25-33.
- Reich PB, Walters MB, Ellsworth DS. 1997.** From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, **94**: 13730.
- Revell LJ. 2012.** phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**: 217-223.

- Richardson AD, Carbone MS, Huggett BA, Furze ME, Czimczik CI, Walker JC, Xu X, Schaberg PG, Murakami P. 2015.** Distribution and mixing of old and new nonstructural carbon in two temperate trees. *New Phytologist*, **206**: 590-597.
- Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS, Ferreira LV, Malhi Y, Grace J, Mencuccini M, Meir P. 2015.** Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, **528**: 119-122.
- Runkle JR. 1982.** Patterns of Disturbance in Some Old-Growth Mesic Forests of Eastern North America. *Ecology*, **63**: 1533-1546.
- Rychter AM, Rao IM, Cardoso JA. 2016.** Role of phosphorus in photosynthetic carbon assimilation and partitioning. In: Pessarakli M, ed. *Handbook of Photosynthesis*. Boca Raton: CRC Press.
- Sala A, Hoch G. 2009.** Height-related growth declines in ponderosa pine are not due to carbon limitation. *Plant, Cell & Environment*, **32**: 22-30.
- Sala A, Woodruff DR, Meinzer F. 2012.** Carbon dynamics in trees: feast or famine? *Tree Physiology*, **32**: 764-775.
- Shipley B, Lechowicz MJ, Wright IJ, Reich PB. 2006.** Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, **87**: 535-541.
- Signori-Müller C, Oliveira RS, Barros FdV, Tavares JV, Gilpin M, Diniz FC, Zevallos MJM, Yupayccana CAS, Acosta M, Bacca J, Chino RSC, Cuellar GMA, Cumapa ERM, Martinez F, Mullisaca FMP, Nina A, Sanchez JMB, da Silva LF, Tello L, Tintaya JS, Ugarteche MTM, Baker TR, Bittencourt PRL, Borma LS, Brum M, Castro W, Coronado ENH, Cosio EG, Feldpausch TR, Fonseca LdAM, Gloor E, Llampazo GF, Malhi Y, Mendoza AM, Moscoso VC, Araujo-Murakami A, Phillips OL, Salinas N, Silveira M, Talbot J, Vasquez R, Mencuccini M, Galbraith D. 2021.** Non-structural carbohydrates mediate seasonal water stress across Amazon forests. *Nature Communications*, **12**: 2310.
- Suding KN, Lavorel S, Iii FSC, Cornelissen JHC, Díaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas ML. 2008.** Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**: 1125-1140.
- Uhl C. 1987.** Factors controlling succession following slash-and-burn agriculture in Amazonia. *Journal of Ecology*, **60**: 675-695.
- Upmeyer DJ, Koller HR. 1973.** Diurnal Trends in Net Photosynthetic Rate and Carbohydrate Levels of Soybean Leaves. *Plant Physiology*, **51**: 871-874.
- Verryckt LT, Van Langenhove L, Ciais P, Courtois EA, Vicca S, Peñuelas J, Stahl C, Coste S, Ellsworth DS, Posada JM, Obersteiner M, Chave J, Janssens IA. 2020.** Coping with branch excision when measuring leaf net photosynthetic rates in a lowland tropical forest. *Biotropica*, **52**: 608-615.
- Weber R, Gessler A, Hoch G. 2019.** High carbon storage in carbon-limited trees. *New Phytologist*.
- Wiley E. 2013.** *Towards a better understanding of nonstructural carbohydrate storage and carbon limitation in trees*, University of Pennsylvania.
- Williamson GB, Wiemann MC. 2010.** Measuring wood specific gravity... Correctly. *American Journal of Botany*, **97**: 519-524.

- Woodruff DR, Meinzer FC. 2011.** Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer. *Plant, Cell and Environment*, **34**: 1920-1930.
- Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Groom PK, Hikosaka K, Lee W, Lusk CH, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Warton DI, Westoby M. 2005.** Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, **14**: 411-421.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004.** The worldwide leaf economics spectrum. *Nature*, **428**: 821-827.
- Wright IJ, Westoby M, Reich PB. 2002.** Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology*, **90**: 534-543.
- Würth MKR, Peláez-Riedl S, Wright SJ, Körner C. 2005.** Non-structural carbohydrate pools in a tropical forest. *Oecologia*, **143**: 11-24.
- Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlenn DJ, O'Meara BC, Moles AT, Reich PB, Royer DL, Soltis DE, Stevens PF, Westoby M, Wright IJ, Aarssen L, Bertin RI, Calaminus A, Govaerts R, Hemmings F, Leishman MR, Oleksyn J, Soltis PS, Swenson NG, Warman L, Beaulieu JM. 2014.** Three keys to the radiation of angiosperms into freezing environments. *Nature*, **506**: 89-92.
- Ziemińska K, Westoby M, Wright IJ. 2015.** Broad Anatomical Variation within a Narrow Wood Density Range—A Study of Twig Wood across 69 Australian Angiosperms. *PLOS ONE*, **10**: e0124892.