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RESEARCH ARTICLE

Global variation in nonstructural carbohydrate stores in response to climate

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Abstract

Woody plant species store nonstructural carbohydrates (NSCs) for many functions. While known to buffer against fluctuations in photosynthetic supply, such as at night, NSC stores are also thought to buffer against environmental extremes, such as drought or freezing temperatures by serving as either back-up energy reserves or osmolytes. However, a clear picture of how NSCs are shaped by climate is still lacking. Here, we update and leverage a unique global database of seasonal NSC storage measurements to examine whether maximum total NSC stores and the amount of soluble sugars are associated with clinal patterns in low temperatures or aridity, indicating they may confer a benefit under freezing or drought conditions. We examine patterns using the average climate at each study site and the unique climatic conditions at the time and place in which the sample was taken. Altogether, our results support the idea that NSC stores act as critical osmolytes. Soluble Sugars increase with both colder and drier conditions in aboveground tissues, indicating they can plastically increase a plants' tolerance of cold or arid conditions. However, maximum total NSCs increased, rather than decreased, with average site temperature and had no relationship to average site aridity. This result suggests that the total amount of NSC a plant stores may be more strongly determined by its capacity to assimilate carbon than by environmental stress. Thus, NSCs are unlikely to serve as reservoir of energy. This study is the most comprehensive synthesis to date of global NSC variation in relation to climate and supports the idea that NSC stores likely serve as buffers against environmental stress. By clarifying their role in cold and drought tolerance, we improve our ability to predict plant response to environment.

KEYWORDS

climate, global, nonstructural carbohydrates (NSCs), soluble sugars, starch, storage

1 | INTRODUCTION

Plants fix carbon into carbohydrates via photosynthesis, which they then use for respiration, defense, growth, reproduction, or store for later use. Nonstructural carbohydrate (NSC) storage plays a critical role in supplying plants with energy reserves when photosynthesis

cannot occur—such as at night, during the dormant season, or during periods of environmental stress (Chapin et al., 1990; Hartmann & Trumbore, 2016). These NSC stores are generally measured as soluble sugars and insoluble starches. Some plants, however, also store other compounds such as sugar alcohols and neutral lipids (Hoch et al., 2003). Starch serves as a long-term carbon storage molecule

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and takes a compact, insoluble form, allowing plants to store carbohydrates while conditions allow high photosynthetic rates (Jang & Sheen, 1994). In contrast, soluble sugars (SS) provide energy and substrate for various carbon sinks within the plant and can also serve as intermediary metabolites, signaling molecules or osmolytes (Hartmann & Trumbore, 2016). Thus, both the total amount of carbon residing in plant stores as well as the degree to which NSC is split between sugars and starches is critical for understanding the function of NSC stores in plants.

NSC stores buffer against carbon supply deficits in plants and they can vary with seasonal cycles (Furze et al., 2019; Martínez-Vilalta et al., 2016), in response to abiotic and biotic stressors (e.g., Adams et al., 2017; Barker Plotkin et al., 2021; Landhüsser & Liefers, 2011; Sevanto et al., 2014), and based on the genetic background (Blumstein & Hopkins, 2021; Blumstein et al., 2020). Given predictions of more extreme climates and pest/pathogen outbreaks in the future, a renewed interest in the role of NSC stores in buffering plants against environmental stress has arisen (e.g., McDowell, 2011; Sala et al., 2012; Wiley & Helliker, 2012). Indeed, when plants living under the same conditions have higher stores than their counterparts, they can survive longer under environmental stress, indicating that increased NSC stores can be an adaptive strategy (Myers & Kitajima, 2007; O'Brien et al., 2017). Thus, studies of NSC variation over the past decade have examined many environmental stressors, including how NSC stores vary in response to drought (i.e., low water availability and/or high temperatures; e.g., Adams et al., 2013; He et al., 2020), freezing stress (Yano et al., 2005), and along environmental gradients (Fajardo et al., 2012; Piper et al., 2017).

In the case of drought, NSC stores have been hypothesized to play two different roles. The first is as a buffer against “carbon starvation,” in which photosynthesis is hampered by drought conditions and plants slowly burn-through their stored reserves until death (McDowell et al., 2008). Thus, plants that live in hotter and drier climates have been hypothesized to allocate more of their carbon to storage than those from wetter climates as a conservative buffer against drought stress (e.g., Wiley & Helliker, 2012). The build-up of stores could be achieved via evolution for some plants to inherently store more (Blumstein et al., 2020; Long et al., 2021) or by a plastic increase in NSC (as shown in Piper et al., 2017). This increase can result from greater growth sensitivity to environmental stress relative to photosynthesis (sink limitation hypothesis; Körner, 2003), or it could be a selected strategy due to an upregulation of carbohydrate accumulation in cells and/or a downregulation of growth or other carbon sinks, sometimes referred to as “quasi-active storage” (Dietze et al., 2014; Sala et al., 2012). Regardless of the drivers, increased stores are thought to result in a higher tolerance of plants to drought conditions (O'Brien et al., 2014).

The second hypothesized role of NSC in droughted plants is as an osmotic buffer. Plants can convert insoluble starch back into soluble sugars when water stress activates starch-degrading enzymes (Thalman & Santelia, 2017). This conversion from starch to sugar can decrease plants' osmotic potentials to maintain cell turgor during drought (Blum, 2017; Guo et al., 2020). While the role of soluble

sugars in osmoregulation is well known in plants, it is unclear if plants from drier environments can allocate more carbon to storage or maintain higher levels of soluble sugars for this purpose, as the few studies on this topic have produced mixed results (Blumstein et al., 2020; Piper et al., 2017; Reyes-Bahamonde et al., 2021). Thus it has been hypothesized that plants that have evolved in or are grown in drier environments will maintain higher stores and a greater fraction of their stores as soluble sugars so as to decrease the water potential at which turgor loss occurs and live longer under drought (Bartlett et al., 2012; Dickman et al., 2019; O'Brien et al., 2014, 2017). Emerging from both hypotheses is the prediction that individuals from drier climates will exhibit higher maximum stores (i.e., greater storage capacity) and/or maintain a greater proportion of their stores as soluble sugars, a pattern that may result from plant storage evolving in response to environment over time or from individual plasticity to environment.

Similar to the case of drought, NSC stores are also known to serve as osmolytes that protect plant tissues from freezing in winter by lowering the freezing temperature of water (Thalman & Santelia, 2017; Thomashow, 1999). Thus, plants living in colder environments are hypothesized to, either plastically or heritably, invest more in total NSC storage and/or maintain a higher fraction of those stores as soluble sugars than plants growing in more moderate climates (e.g., Chapin et al., 1990; Reyes-Bahamonde et al., 2021). Most studies examining NSC concentrations in reference to freezing temperatures have examined altitudinal clines. These studies have found that plants growing at higher elevations have higher NSC concentrations, likely as a result of plastic processes (Fajardo et al., 2012; Hoch et al., 2002; Shi et al., 2008). Studies, largely conducted in temperate and boreal environments, have also found that soluble sugar fractions increase with latitude in the northern hemisphere (Kreyling et al., 2014; Lintunen et al., 2016), with elevation (Hoch et al., 2002; Long et al., 2021), and with experimentally induced cold shock (Hoermler et al., 2017; Kaplan & Guy, 2005; Nagao et al., 2005). In addition, evidence of a heritable investment in NSC has been demonstrated in a common garden in *Tamarix chinensis* X *ramosissima*, where genotypes from higher elevations stored more NSC than those from lower elevations and exhibited a higher degree of freeze tolerance (Long et al., 2021). These studies suggest that NSC concentrations increase with freezing temperatures, either upregulated as a form of cryoprotection or are the result of the build-up of sugars due to physiological limitations in growth at low temperatures (i.e., sink-limitation hypothesis) (Körner, 2003, 2015), or some combination of the two.

While much work has been done on the topic of NSC variation in response to environmental extremes, no study to date has examined data across biomes to understand global patterns of NSC investment and whether they are consistent with the predominant hypotheses of the field. Here we present an updated global database of seasonal dynamics in NSC storage in trees (Martínez-Vilalta et al., 2016) to examine patterns between the total amount of storage and soluble sugar and climate. We specifically test the following hypotheses:

1. If NSC stores confer drought resistance as back-up energy reserves or osmolytes, then we would expect the maximum investment capacity for total NSC and SS stores, or % SS to increase with climatic aridity. If stores are mostly conferring a benefit as back-up energy reserves, we would expect total NSC storage capacity to increase with aridity, but not necessarily an increase in SS storage capacity and % SS. If stores mostly confer a benefit as osmolytes, then we would expect a concomitant increase in the seasonal maximum of total SS and the % SS with aridity, but not necessarily total NSC storage capacity.
2. Similarly, if NSC stores confer freezing resistance as osmolytes, then we would expect investment in NSC and SS storage capacity, or % SS to increase as temperatures decrease. In this case, we would expect higher SS under cold temperatures, either through higher NSC, higher %SS or both. All indicate an investment of SS, whether via upregulation or accumulation, which can serve as a cryoprotectant.

For this study, we examined the major organs of branches, stems, and roots independently. Prior work has demonstrated that these organs behave differently through time and across species, where branches are most dynamic as they are proximal to sources and sinks, while roots, which are belowground and thus shielded from some climate variability, are more consistent through the year (e.g., Furze et al., 2019). We chose not to include leaves due to their high diurnal variation in NSC, making emergent patterns difficult to distinguish from background noise. Notably, in an attempt to tease-out short-term, plastic processes from longer-term, possibly evolved patterns, we compared climate trends of NSC using measurements from the month in which they were collected *and* the seasonal maximum NSC for each species, within each study. We would expect the seasonal maximum NSC for each species to reflect longer-term processes such as storage capacity, thus patterns like higher stores could reflect an evolved strategy to store more in response to climate, although transplant studies would be needed to confirm this. Conversely, the monthly NSC measurements likely reflect variation in plastic responses to short-term environmental perturbations, where NSC/SS may increase via upregulation or passive accumulation due to sink limitations (Körner, 2003, 2015).

2 | METHODS

2.1 | Building/updating the database

The data used for our analysis were initially collected in a database of NSC measurements, published in 2016 (Martínez-Vilalta et al., 2016), then updated by us to include articles through April 2020. To begin, we conducted a search on Web of Science (accessed April 6, 2020) for the following word combinations in any field of the articles "(NSC OR TNC OR starch OR carbohydrate*) AND (plant* OR shrub* OR tree* OR seedling* OR sapling*) AND (seasonal* OR temporal*)". Our search yielded 1040 articles, of which we reviewed the abstracts to further

only include measurements taken on wild species (none under cultivation) under natural, field conditions. Where a paper reported the results of a natural or under field conditions experiment, we only included the control samples in our analysis. We further only examined papers that took at least (1) three measurements over time of the same individuals or populations and (2) ran for at least 4 months or more. Finally, due to a lack of data in some categories and to keep comparisons consistent, we further limited studies to only those done on (3) woody land plants and (4) mature trees (as defined by the authors of each study) (5) where the tissue sampled was *not* bark, phloem, or cortex, and (6) the organ sampled was the branch, coarse root, or stem. The age of the tissue itself can also affect the amount of NSC stores (Carbone et al., 2013; Furze et al., 2019); in our database all stem results included are the sapwood, typically the outer 2 cm of the core, and only two studies that eventually made it to our final cut specified whether branches were current or previous years. Given these branch NSC concentration values of current versus older branches were all within 2–3 mg/g of each other, we averaged them together.

All data were taken from the text, tables, supplementary data repositories, or the figures. For figure data extraction, we employed the software WebPlotDigitizer (Rohatgi, 2021). NSC data were converted to standard units of milligrams NSC per gram dry weight (mg/g) and reported as soluble sugars and starch. The composition of soluble sugars may vary depending on method (Landhausser et al., 2018; Quentin et al., 2015), but they are largely composed of glucose, fructose, and sucrose (Hoch et al., 2003). Soluble sugars and starches were added to estimate total NSC (referred to throughout as NSC). For our following climate analyses, we examined NSC (SS+starch), SS, and % SS (SS / NSC).

Beyond collecting NSC data, we also included relevant information about each study and the samples collected such as location data (latitude, longitude, biome), the duration of the study, species, the organ (stem, root, branches, etc.), tissue (sapwood, heartwood, xylem, all), sampling month and year, measured NSC component (NSC, soluble sugars, starch, other compounds), and detailed methods used during the sample processing, extraction, and quantification. Our final database of NSC, SS, and % SS used for analysis contains 4676 unique measurements (1148 branches, 452 roots, and 3076 stems) which encompass 90 species from six biomes (Biome:# species; Boreal: 3, Desert: 1, Mediterranean: 30, Temperate: 85, Tropical: 22, Tundra: 3). Biomes were standardized using the Nature Conservancy's terrestrial ecoregion spatial layer (TN Conservancy, 2019). Note, unlike Martínez-Vilalta et al. (2016), we did not include herbaceous or shrub species, choosing to focus instead on tree species.

2.2 | Climate data

To examine how NSC stores vary with climate, we merged our database with climate variables based on the latitude and longitude provided by each study for the sample locations. Temperature, vapor pressure, and precipitation data were taken from the gridded Climate Research Unit (CRU) data v.4.01, which are high-resolution

(0.5×0.5-degree grids) month-to-month variations in climate over the period 1901–2016 (Harris et al., 2020). Data were provided as monthly minimum and maximum temperature (°C), total precipitation (mm), and vapor pressure deficit (VPa hPa). We then used the CRU data to calculate metrics that describe both the average annual conditions of each site as well as the conditions the month each sample was taken.

For the average annual metrics, we calculated the *average annual temperature* (°C) by taking the mean of the minimum and maximum temperatures over the entire time period (1901–2016) and *average annual precipitation* (cm) by summing across each year and then averaging across years. To complement our temperature metrics, we found the *maximum and minimum temperatures* in the record, representing the coldest and hottest months between 1901 and 2016 for each site. We then calculated the *average vapor pressure deficit* (VPD) over the data period by calculating the saturated vapor pressure as:

$$\text{Saturated vapor pressure} = 6.1078 \times e^{(17.269 \times \text{Average temperature})} / (237.3 + \text{Average Temperature}) \quad (1)$$

Then subtracting the actual vapor pressure provided by the CRU data from this calculated saturated vapor pressure (Equation 1). Finally, to better capture how dry each site is, we included an additional Global Aridity Index (30 arc second resolution) calculated using the WorldClim 2.0 (Fick & Hijmans, 2017; Harris et al., 2014), downscaled from CRU data 3.10 (Harris et al., 2014). These data are a summary of the rainfall (precipitation) versus potential evapotranspiration over the period 1970–2000.

In addition to annual summaries over the whole time period, we also examined what the weather was like in the month and year each sample was taken. To do so, we used the date taken (month and year) and latitude/longitude coordinates corresponding to each sample to retrieve the relevant weather information from the CRU data. For each sample, we calculated the *total precipitation* (cm), *minimum temperature* (°C), *maximum temperature* (°C), *average temperature* (°C), and *VPD* (hPa) for the month it was collected. We additionally added the metric of the standardized precipitation–evapotranspiration index (SPEI), averaged over the 3 months prior to sample collection. SPEI was calculated using the CRU climate records at a 0.5° spatial and monthly temporal resolution.

Finally, we summarized climate to winter and summer seasonal periods. Winter is defined as December, January, and February above 0° Latitude and June, July, and August below 0° Latitude. Summer was defined as the reverse. We averaged across winter and summer months using the CRU data for the period 1901–2016 to get seasonal estimates for average monthly precipitation (cm), average temperature (°C), and VPD (hPa).

2.3 | Climate PCA

Using the programming language R v 4.1.3, we checked the collinearity among our climate variables via a Pearson's correlation

analysis (Tables S1 and S2). Given the high correlations between many climate variables, we chose to utilize a principal component analysis (PCA) to identify major axes of climate variation in our data, using the *vegan* 2.5-7 package in R (Oksanen et al., 2018; Figure S1). PC1 explains 55% of the variation in our annual climate data and 53% in our monthly climate data and describes a cline from hotter temperatures to colder temperatures. PC2 explains 30% of the variation in our annual climate data and 19% in our monthly climate data and describes a cline from wet to dry.

2.4 | Models

To test how NCSs, SS, and % SS varied with climate, we formulated linear mixed models using the programming language R (Team, 2022) and package *lme4* (Bates et al., 2015). All of our mixed models had the following general formulation

$$Y = \alpha_0 + \alpha_1 X_{PC1} + \alpha_2 X_{PC2} + \beta_{\text{species}} + \beta_{\text{MethodSS}} + \beta_{\text{MethodSSstarch}} + \epsilon \quad (2)$$

where alphas are fixed effects, beta random effects, and epsilon is the residual variance. We included the method of soluble sugar and starch extraction and quantification to account for variability associated with using different methods for each (Landhausser et al., 2018; Quentin et al., 2015). Method is a three-part variable which reflects the extraction, processing, and reading portions of the laboratory protocol. For example, for soluble sugars "ETHA_H2SO4_SPEC" would indicate a method that used ethanol for extraction, sulfuric acid for processing, and read results on a spectrophotometer. For sugars we had 14 unique methodological combinations and 17 for starch. We additionally ran each model with study, rather than sugar and starch methods, as the random effect for comparison, as study may also capture similar variation between laboratories. We found that the substitution of study for method did not significantly alter results, thus we kept method as our random effect.

For each comparison, we ran the three organs (branches, stems, and roots) in our database as separate models. In all, we tested each of the following against both average climate and the conditions in the month the sample was taken; NSC_{stems}, NSC_{branches}, NSC_{roots}, SS_{stems}, SS_{branches}, SS_{roots}, % SS_{stems}, % SS_{branches}, and % SS_{oots}. % SS was approximately normally distributed, while both NSC and SS were logged to normalize (Figure S2). For the conditions in the month the sample was taken, we averaged across any replicates in the study for that time point and organ, but otherwise used the raw values from our database. To aggregate NSC measures to annual timescales, we took the maximum value for each metric, for each species, in each study. Given that NSCs vary seasonally, we wanted to minimize error due to time of sampling by capturing the putative maxima for each species/site pairing and because the maximum reflects the storage capacity.

To evaluate the fit of the models, we calculated the *p*-value of each coefficient using the *lmerTest* package (Kuznetsova et al., 2017) and examined the marginal and conditional *R*² using the *MuMin* package (Barton, 2022). The marginal *R*² provides a measure of the

proportion of variation explained by fixed effects compared to the total variation, while the conditional R^2 additionally accounts for the variation explained by both fixed and random effects. Model fits displayed in text (Figures 2–5) show a given climate variable conditional on the average of the others from the model. For example, Figure 2a–c show PC1 conditional on the average PC2 across all samples.

3 | RESULTS

3.1 | Annual climate versus NSC, SS, and %SS

For analyses of NSC and SS trends with long-term climate, NSC and SS value refer to maximum values. Total NSC is significantly negatively associated with annual climate PC1 in branches and stems, implying lower NSC concentrations under colder conditions, but not roots (Table 1, Figure 2a–c). Soluble sugars are only significantly negatively associated with PC1 in stems, implying lower SS amounts under colder conditions in stems only (Figure 2d–f). Conversely, the percent of NSC in SS is significantly positively associated with annual climate PC1 in branches, but not other organs, indicating that the percent of stores in SS in branches increases with colder environments (Table 1, Figure 2g–i). The NSC, SS, nor the percent of % SS is significantly associated with annual climate PC2 (aridity) for any organ (Table 1, Figure 3).

3.2 | Monthly weather versus NSC, SS, and % SS

Both total NSC and soluble sugars are significantly positively associated with colder monthly conditions (PC1) in stems, but not branches (Table 1, Figure 4a–f). In addition, total NSC is positively correlated with colder conditions (PC1) in roots (Table 1, Figure 4c). % SS is significantly positively associated with colder monthly conditions (PC1) in all organs (Table 1, Figure 4g–i).

Total NSC is not significantly associated with monthly aridity conditions (PC2) in any organ (Table 1, Figure 5a–c). In contrast, SS and % SS are both significantly positively associated with drier conditions (PC2) in branches and stems, but not roots (Table 1, Figure 5d–i).

4 | DISCUSSION

Altogether, our results support the idea that NSC stores may serve as buffers against environmental stress. Most likely these stores act as critical osmolytes, enabling plants to quickly respond to decreasing temperatures or increasing aridity. Our results demonstrate an increase in NSC, SS, and % SS in colder months and an increase in SS and % SS in more arid months (Figures 4 and 5). Conversely, our predictions that colder or more arid climates of origin would lead plants to store more NSC or maintain a higher proportion of those

stores as SS were unsupported. We found no relationship between our NSC metrics and how arid a climate of origin was and found the opposite of what we expected for increasingly cold climates—as average temperatures at a site increase, so does the NSC and SS within trees at those sites. Overall, our results shed light on long-standing hypotheses regarding the role of NSC storage in plants.

4.1 | Hypothesis 1: NSC stores confer drought resistance as back-up reserves or osmolytes

Our initial hypothesis regarding drought sought to tease out whether NSC stores serve as a back-up energy reserve or osmolytes for plants living in arid environments or subject to arid conditions. We further hypothesized that if total maximum NSCs were high, but maximum SS or % SS remained low or unchanged in arid conditions, then NSCs likely serve as evolved energy reservoirs for plants to draw on when photosynthesis is inhibited, preventing so-called carbon starvation (McDowell et al., 2008). In particular, we would expect plants that are growing in climates that are on average drier than others (i.e., our average climate analysis) to exhibit a conservative, bet-hedging strategy and have higher maximal stores of NSC (Wiley & Helliker, 2012). However, we found no evidence to support this idea, as total NSCs were not associated with aridity (given by PC2) when examined by annual climate of origin or monthly conditions. Our lack of pattern in the monthly weather conditions analysis also fits with a litany of studies which have found NSCs may increase, decrease, or not change at all following drought (Adams et al., 2013, 2017; Anderegg et al., 2012; Dickman et al., 2019; Galiano et al., 2012; Hartmann et al., 2013; O'Brien et al., 2014; Quirk et al., 2013; Sevanto et al., 2014). These results suggest that species likely have different strategies for coping with arid conditions, leading to high variation in our data, that seasonal fluctuations in NSC may mask clear patterns, or that differences in carbon accumulation among species may also mask patterns (Blumstein et al., 2022).

In contrast to maximum NSC and SS, and %SS, NSC, SS and %SS at the time of sampling, significantly increased with how dry the conditions were at that time, specifically in aboveground tissues (stems and branches). This indicates that, under drier conditions, plants plastically increase the amount of SS they have, either through up-regulation (increased rate of NSC conversion from starch to sugar) or passive accumulation due to growth-inhibition and preferential build-up of SS (e.g., Piper et al., 2017), or some combination of the both. The former argument is consistent with the wider plant literature, which reports starch degradation and a subsequent increase in sugars in leaves following drought stress, likely mediated by the hydrolytic enzymes BAM1, AMY3, and PHS1 (reviewed in: He et al., 2020; Thalmann & Santelia, 2017). This pattern supports the idea that NSCs play an important role as osmolytes to avoid desiccation by maintaining turgor in plant cells (Sala et al., 2012; Salmon et al., 2015; Sapes et al., 2021). Interestingly, only aboveground organs seem to respond to aridity. This is consistent with a recent review of the NSC experimental drought literature, which found that

TABLE 1 Linear mixed model regression results examining the natural log of maximum nonstructural carbohydrate (NSC) and the percent of NSC in soluble sugars against annual climate summary predictors for the period 1901–2016 and the conditions in the month each sample was taken (PCA, [Figure S1](#)).

Parameter	Branch				Stem				Root									
	In NSC (mg/g)		In soluble sugars (mg/g)		Percent SS (%)		In NSC (mg/g)		In Soluble Sugars (mg/g)		Percent SS (%)		In NSC (mg/g)		In soluble sugars (mg/g)		Percent SS (%)	
	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p
Average annual climate																		
(Intercept)	4.71 ± 0.13	<.01	3.92 ± 0.19	<.01	31.49 ± 3.54	<.01	3.83 ± 0.08	<.01	3.03 ± 0.13	<.01	32.03 ± 5.61	<.01	4.32 ± 0.15	<.01	3.17 ± 0.23	<.01	25.58 ± 3.61	<.01
PC1	-1.69 ± 0.77	0.03	0.39 ± 1.01	.70	58.33 ± 27.02	.04	-4.39 ± 0.69	<.01	-3.54 ± 1.01	<.01	41.59 ± 21.54	.06	-1.64 ± 1.21	.19	-1.44 ± 1.56	.37	22.52 ± 26.22	.40
PC2	-0.06 ± 0.73	.93	1.55 ± 1.06	.15	15.62 ± 27.7	.58	-0.76 ± 0.74	.30	-0.01 ± 1.1	1.00	3.71 ± 20.8	.86	-0.9 ± 1.19	.46	1.04 ± 1.73	.56	15.63 ± 32.88	.64
Species	0.15		0.17		150.47		0.22		0.33		21.77		0.37		0.3		0	
Method starch	0		0		0		0		0.07		181.07		0		0		0	
Method soluble sugars	0.05		0.09		13.43		0.01		0		152.67		0.01		0.08		0	
Residual	0.15		0.23		146.11		0.15		0.26		88		0.2		0.22		202.09	
Marginal R ² / Conditional R ²	0.08/0.6		0.05/0.56		0.09/0.57		0.3/0.72		0.12/0.65		0.02/0.81		0.08/0.68		0.05/0.65		0.05/0.05	
N Observations	67		53		51		120		111		105		38		28		25	
Month sample was taken																		
(Intercept)	4.35 ± 0.14	<.01	3.68 ± 0.25	<.01	44.93 ± 5.01	<.01	3.61 ± 0.2	<.01	2.77 ± 0.2	<.01	52.83 ± 6.94	<.01	3.75 ± 0.26	<.01	2.54 ± 0.29	<.01	34.06 ± 7.53	<.01
PC1	-1.35 ± 0.85	0.12	0.97 ± 1.07	.36	161.07 ± 29.44	<.01	2.72 ± 0.37	<.01	5.79 ± 0.46	<.01	136.84 ± 13.04	<.01	2.8 ± 1.11	.01	2.55 ± 2.07	.22	141.37 ± 41.05	<.01
PC2	1.11 ± 0.84	.19	4.64 ± 1.05	<.01	148.02 ± 30.53	<.01	0.25 ± 0.43	.57	4.36 ± 0.53	<.01	153.2 ± 15.14	<.01	0.57 ± 0.96	.55	0.48 ± 1.61	.77	6.36 ± 32.06	.84
Species	0.28		0.19		264.43		0.47		0.57		128.56		0.6		0.48		289.33	
Method starch	0		0.01		0		0.14		0.13		171.41		0.04		0		0	
Method soluble sugars	0.07		0.32		77.23		0.19		0.16		315.07		0.12		0.23		180.09	
Residual	0.19		0.29		201.51		0.13		0.19		152.59		0.13		0.34		124.68	
Marginal R ² / Conditional R ²	0/0.65		0.03/0.65		0.11/0.67		0.01/0.86		0.04/0.83		0.04/0.81		0.01/0.85		0.01/0.68		0.04/0.8	
N Observations	460		406		380		1455		1409		1350		251		200		179	

Note: Each organ examined separately. Estimates for PC1 and PC2 are fixed effects slopes and random effects variance for species and sugar/starch method. Significant results ($p \leq .05$) bolded.

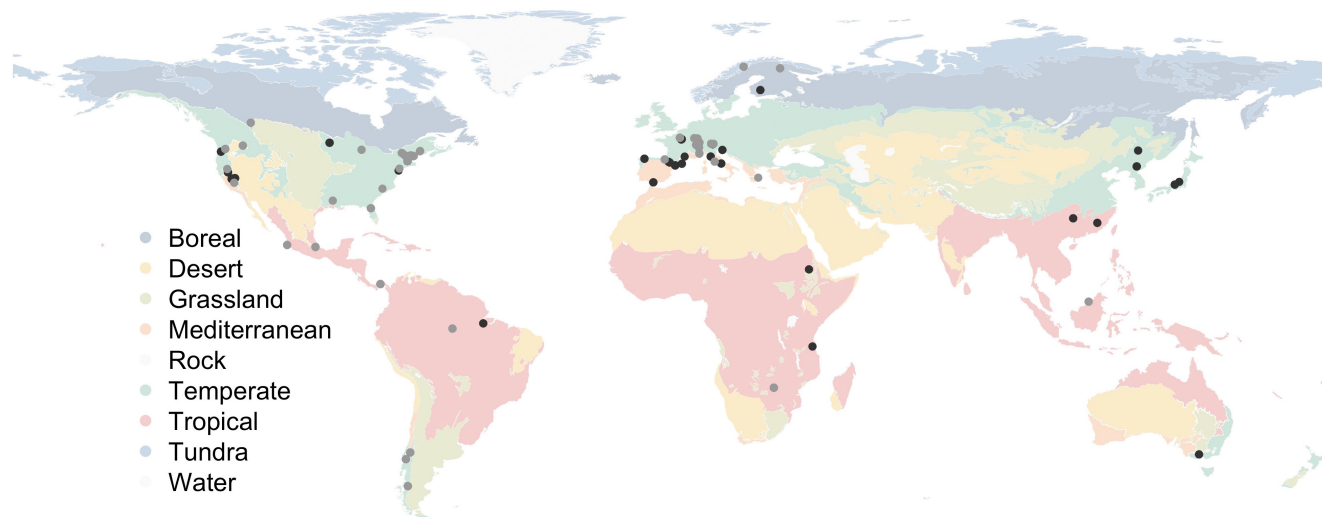


FIGURE 1 Map depicting locations of studies included in the nonstructural carbohydrate (NSC) database. Black dots indicate studies included in the original 2016 database (CITE), gray dots indicate studies added between 2012 and 2020. Regions of the world colored by biome.

in the short term, aboveground organs quickly upregulated SS by degrading starch, while root NSCs were only affected under the most severe and prolonged conditions (He et al., 2020).

4.2 | Hypothesis 2: NSC stores confer freezing resistance as back-up reserves or osmolytes

We hypothesized that NSC stores may confer freezing resistance to plants by serving as osmolytes during particularly cold periods. We first examined if plants from cold climates have higher maximal NSC stores in general than those from warmer climates (Figure 2a–c). If stores were higher, it would suggest plants in colder climates might employ a conservative, bet-hedging strategy against extreme cold by allocating more photosynthates toward storage rather than other functions. Alternatively, higher maximum NSC in cold climates could also be indicative of passive carbon accumulation due to temperature limiting growth before photosynthesis (sink limitation; Körner, 2015). However, we found the opposite to be true, plants growing in warmer climates tended to have higher maximum NSC stores than those in colder environments, although only significantly in aboveground tissues (Table 1, Figure 2a–c). This pattern could be reflective of the higher photosynthetic rates and longer growing seasons of tropical species and is consistent with the higher proportion of storage cells per unit mass of woody tropical species (Plavcová & Jansen, 2015). Species that can produce more NSC are also likely to be able to store more NSC, thus patterns driven by climate in storage may be swamped by higher variation in photosynthesis (Agrawal, 2019; Blumstein et al., 2022). We further examined patterns within biome to account for potential differences in productivity among biomes. We found no slope sign changes and the only significant patterns are consistent with those across biomes,

indicating NSC concentrations were higher under warmer climates, both within and across biomes (Figure S3).

In contrast, when total NSC stores were examined against monthly weather at time of sampling samples collected in colder months tended to have higher NSCs than those collected in warmer months. While this pattern may be reflective of seasonal cycles in NSCs (Martinez-Vilalta et al., 2016), the fact that it generally holds across (Figure 4a–c) and within biomes (Figure S4), which vary in the times of year they peak in storage, suggests another factor, like plastic variation in response to cold temperatures, may be driving the cline. This pattern may be reflective of sink limitation (Körner, 2015), where NSCs build up as seasonal temperatures decrease and growth is inhibited. However, the concomitant increase in %SS is difficult to explain by sink limitations alone.

Interestingly, the fact that our results are the inverse when examined by annual climate versus weather at the time of sampling suggest that different mechanisms may be driving carbon storage at different timescales. Over short timescales (like our monthly measurements), the pattern is consistent with sink limitation of growth: labile carbon accumulates seasonally when growth is more limited than photosynthesis. Such seasonal storage may be an important buffer for future periods when carbon demand is in excess of supply (e.g., winter). Conversely, over longer timescales, the pattern is consistent with source limitation: short growing seasons limit carbon assimilation such that once growth and other carbon demands are met, there is less carbon available for storage than in warmer temperatures. This finding demonstrates that the timescale (long term/evolutionary vs. short term/plastic) of the process matters and may help bridge the gap between the theories of source and sink limitations. Our analysis across a large number of species and biomes and at both short and long timescales allows us to draw a unique perspective on the role that NSC stores may play in plants.

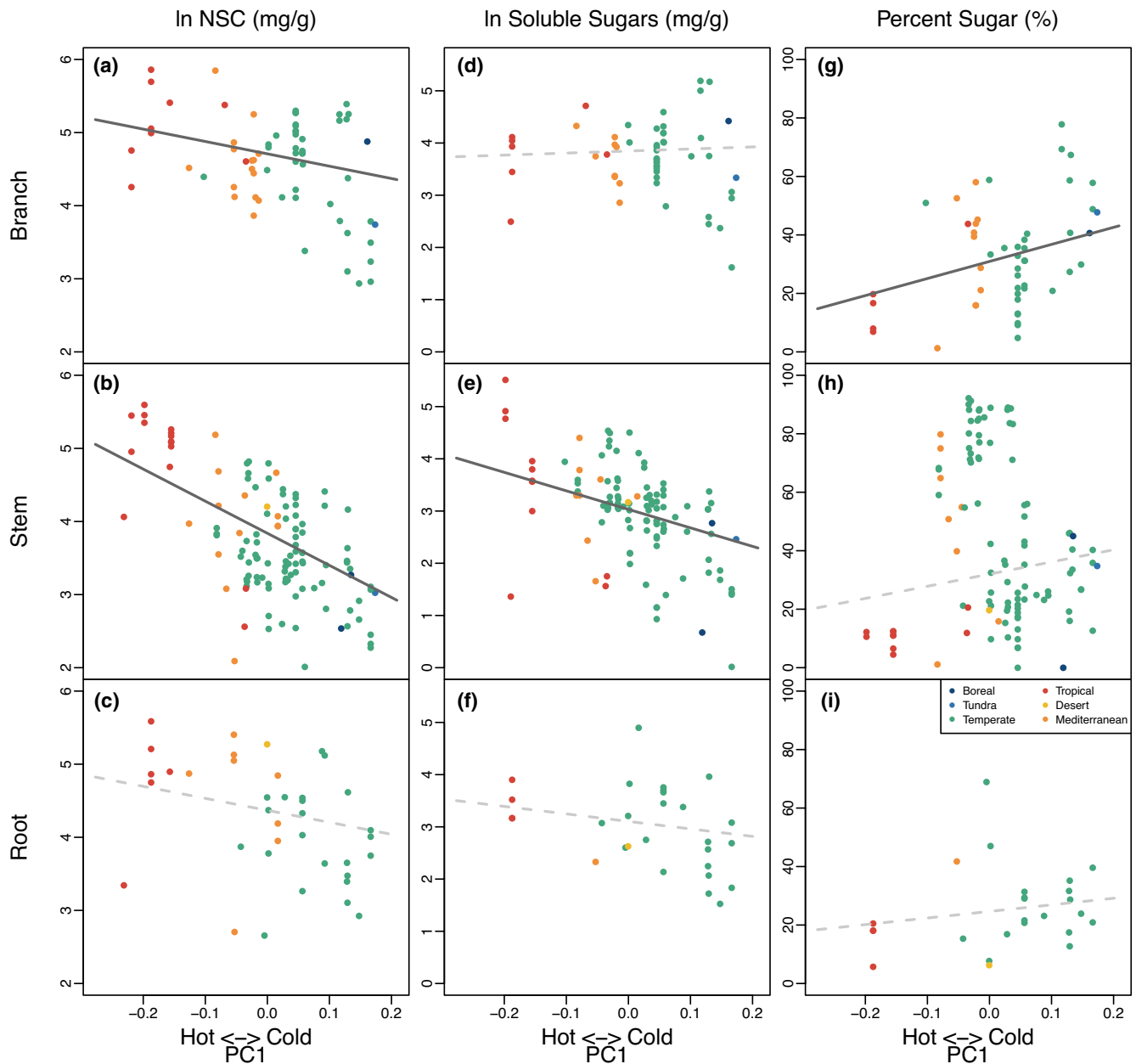


FIGURE 2 The natural log of total nonstructural carbohydrates (NSC) by organ versus average annual (a–c) climate PC1 (PC results in Figure S1). Each point represents (a–c) the natural log of the maxima of total NSC per species, per study, the (d–f) maximal amount of soluble sugars (SS) per species per study, or the (g–i) maximal percent of total NSC in soluble sugars (% SS) per species per study. Line fits are from the Table 1, conditional on the mean value of PC2; solid lines indicate significant slopes.

In both the case of annual climate and the conditions in the month the sample was taken, SSs follow total NSCs; SS and total NSCs increase with average annual temperature (decline along PC1; Figure 2a–f), whereas SS and NSC decrease with temperatures at the time of sampling (Figure 4a–f). However, in contrast to total SS, % SS decreases with annual average temperature (increases along PC1; Figure 2g–i). This indicates that while individuals from warmer climates may have more stores, those from colder climates maintain a higher proportion of their stores as sugar. This could be because they experience colder temperatures and thus convert more starch to SS in response, possibly because of

temperature sensitive starch degradation enzymes (Thalman & Santelia, 2017). *Arabidopsis* mutants in the starch-degrading enzymes GWD and BAM3, had lower sugars under cold stress, leading to higher electrolyte leakage and impaired photosynthesis, respectively (Kaplan & Guy, 2005; Yano et al., 2005). This pattern makes sense in the context of local adaptation to freezing. Studies looking across populations of temperate tree species have found strong patterns of local adaptation in cold hardiness as measured by electrolyte leakage (Hurme et al., 1996; Kreyling et al., 2014), which is tightly linked to the amount of sugars found in the tissues of these trees (Morin et al., 2007). These findings suggest that the

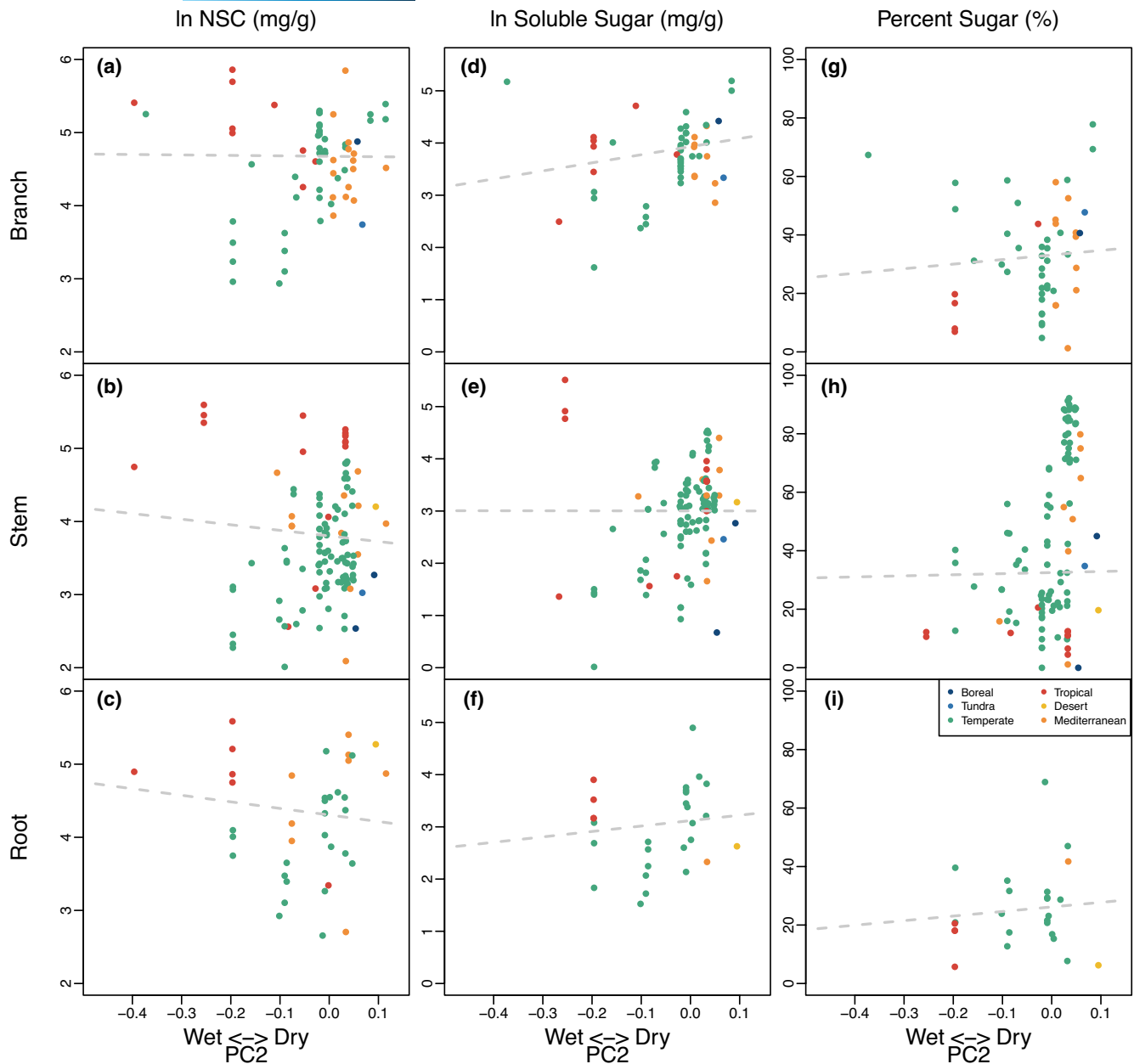


FIGURE 3 The natural log of total nonstructural carbohydrates (NSC) by organ versus average annual (a–c) climate PC2 (PC results in Figure S1). Each point represents (a–c) the natural log of the maxima of total NSC per species, per study, the (d–f) maximal amount of soluble sugars (SS) per species per study, or the (g–i) maximal percent of total NSC in soluble sugars (% SS) per species per study. Line fits are from the Table 1, conditional on the mean value of PC1; solid lines indicate significant slopes.

movement of NSC from starches to Ss is key in protecting plants from freeze damage.

4.3 | Caveats/limitations

While we have amassed the most comprehensive seasonal NSC database to date, the interpretation of our results is still hindered by a few limitations of our approach. The first is that, like most meta-analyses or global analyses, our results are biased toward temperate regions and toward North America/Europe, where most of the studies we included

were conducted (Figure 1). We have very few studies from the tropics and only one from a desert biome. While we do have representation across most major biomes, the oversampling in temperate zones may bias our results to patterns that occur within temperate biomes, rather than across all biomes. However, we did examine within biome patterns in some cases and results were consistent within and across biomes (Figures S3 and S4). We also only examined patterns in reference to climate, ignoring other factors that may shape patterns of variation, such as correlations or tradeoffs with other traits (e.g., Blumstein et al., 2022) or competitive adaptations, like shade and herbivory tolerance (e.g., Myers & Kitajima, 2007).

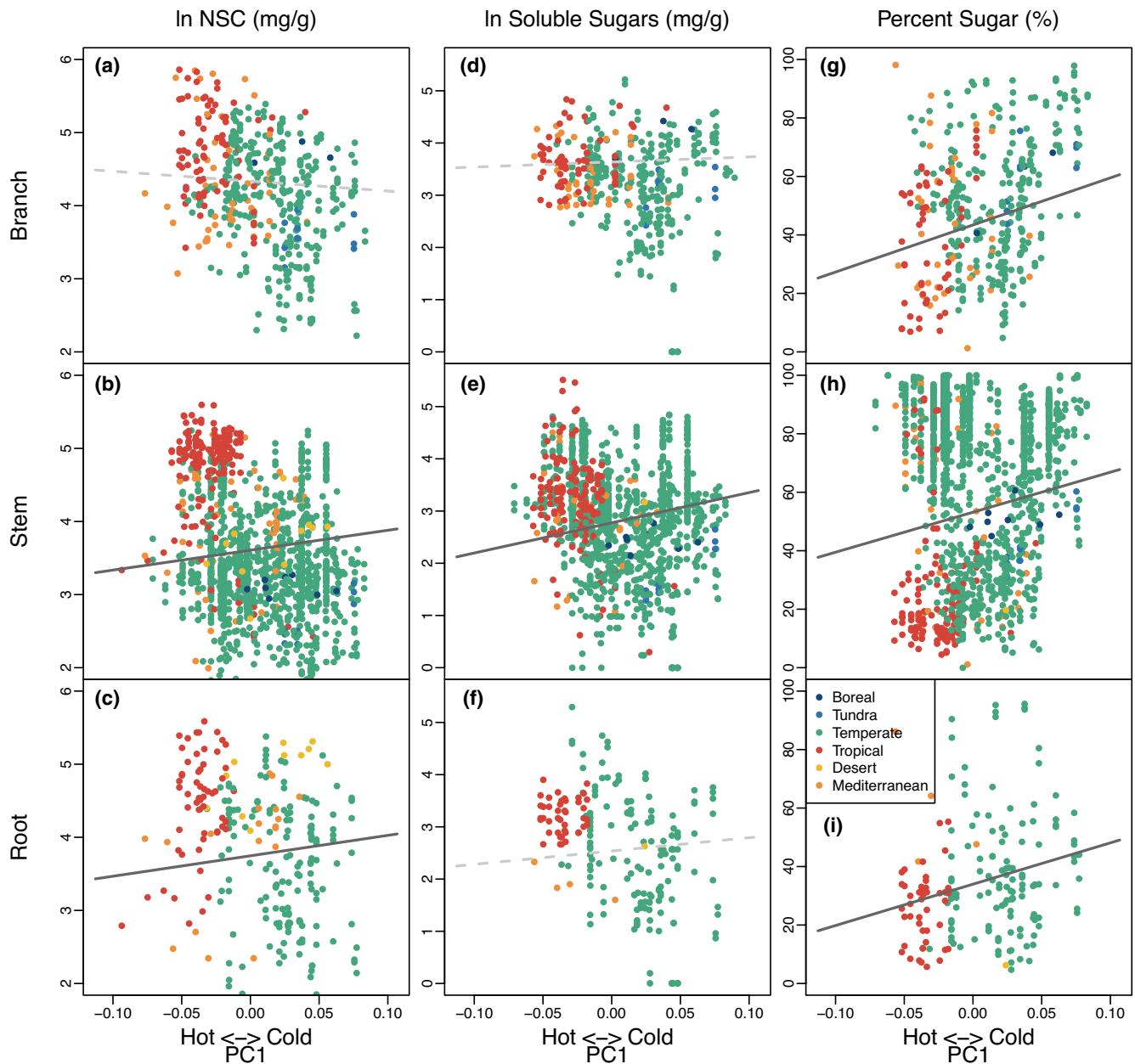


FIGURE 4 The natural log of total nonstructural carbohydrates (NSC) by organ versus (a–c) the conditions in the month the sample was taken as described by PC1 (PC results in Figure S1). Each point represents (a–c) the natural log of the maxima of total NSC per species, per study, the (d–f) maximal amount of soluble sugars (SS) per species per study, or the (g–i) maximal percent of total NSC in soluble sugars (% SS) per species per study. Line fits are from the Table 1, conditional on the mean value of PC2; solid lines indicate significant slopes.

A second caveat of our study is that NSC methods are notoriously difficult to standardize across (Quentin et al., 2015), although when the same methods are used across laboratories, results are relatively consistent (Landhausser et al., 2018). Thus, to deal with potential inconsistencies across methods, we fit our analyses with the methods of sugar and starch quantification as random effects. While methods explain a substantial portion of total variation, it is generally half or less of that explained by species. Notably, however, method explains a larger portion of variation than even species in stems for percent sugar at both the annual and monthly timescales. This could be because percent sugar reflects two possible sources of error—the

quantification of sugars and the quantification of starches separately. In addition, stems are the most commonly measured tissue by a greater diversity of laboratories, which may lead to a higher variability in methods. For example, our whole database has 14 different sugar methods encoded in it and stems alone have 13 of those methods represented, while roots and branches have only 8. This likely means that roots and branches are collected and processed by a smaller number of laboratories, leading to a more uniform result when compared to our stem data. These results underscore previous calls for more standardized and consistent methods in order for us to better compare values measured across laboratories (Landhausser et al., 2018;

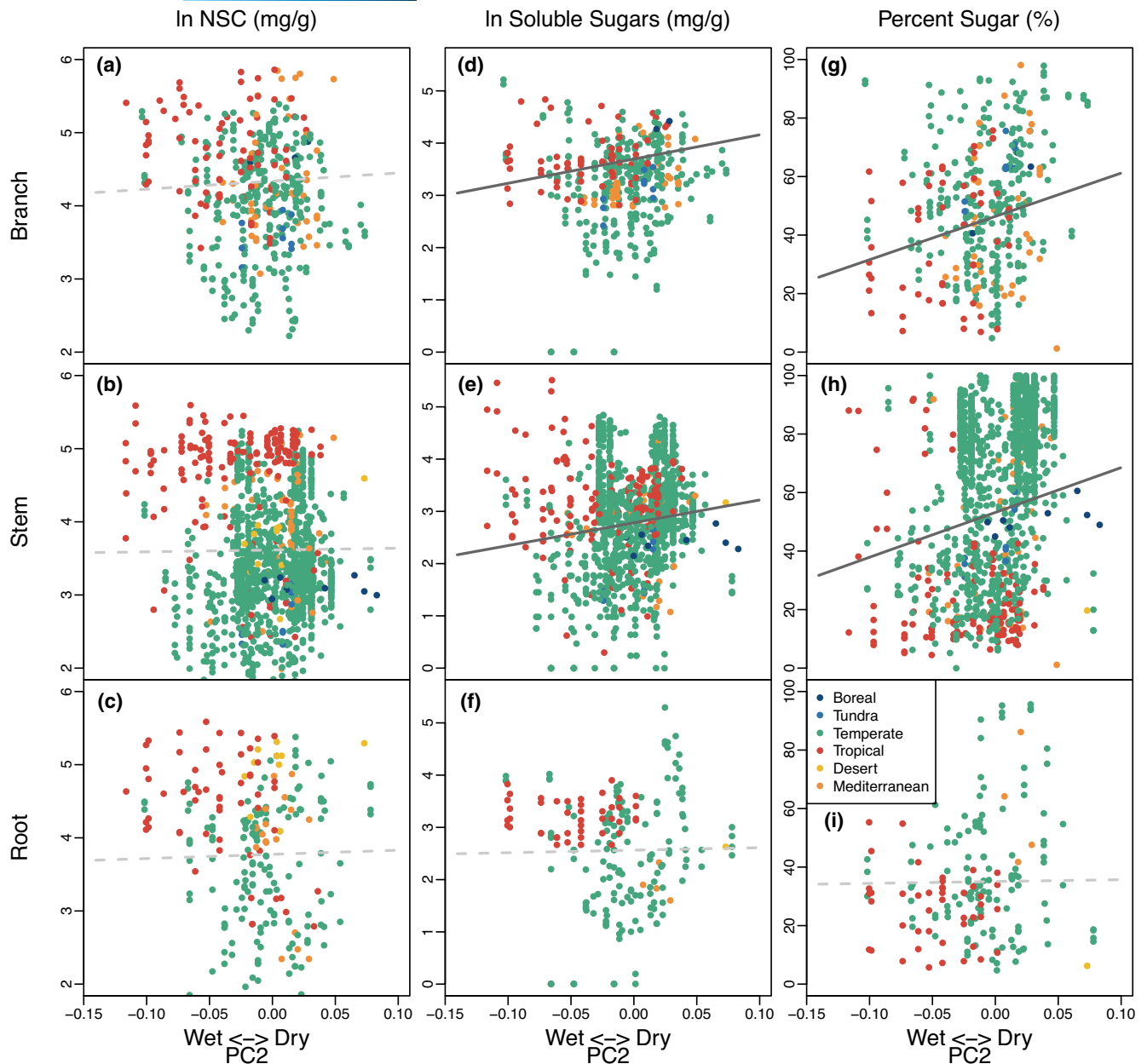


FIGURE 5 The natural log of total nonstructural carbohydrates (NSC) by organ versus (a–c) the conditions in the month the sample was taken as described by PC2 (PC results in Figure S1). Each point represents (a–c) the natural log of the maxima of total NSC per species, per study, the (d–f) maximal amount of soluble sugars (SS) per species per study, or the (g–i) maximal percent of total NSC in soluble sugars (% SS) per species per study. Line fits are from the Table 1, conditional on the mean value of PC1; solid lines indicate significant slopes.

Quentin et al., 2015). Indeed, only in a framework like this where many data are included are we even able to see emergent patterns due to the large amount of noise between laboratories and methods.

Finally, we may not have captured the annual maxima of total NSC or highest percent of NSC in SS for each species and study. This is both because we only considered bulk NSC (glucose, fructose, and sucrose) and because studies sampled intermittently through time. Other compounds, such as sugar alcohols or lipids, may also play key roles in plant storage (Arndt et al., 2008; Hoch et al., 2003), but are often not measured in studies, thus we could not include them here. While we stringently limited studies to those with at least

three measurements over at least a 4-month period, given known seasonal variation in NSC stores (Martínez-Vilalta et al., 2016), we may have missed the absolute maxima in some cases, although almost all studies had at least 1 year of sampling (66/74 studies with 1 year or more of data). In addition, despite the usefulness of using the absolute maxima, it does implicitly assume that absolute NSC levels have similar implications for survival across species. While this may not be true, as suggested by the variability in minimum NSC thresholds reported across species (Barker Plotkin et al., 2021; Piper et al., 2022; Weber et al., 2019), at this scale of study it is a reasonable assumption.

5 | CONCLUSION

In sum, we provide evidence that NSCs likely act as protective osmolytes during both dry and cold conditions, but we found no evidence that plants from stressful environments have higher NSC storage to ensure larger back-up energy reservoirs. Our study represents the most comprehensive examination of NSC storage patterns against climate to date and tests long-standing hypotheses in the field using a unique database. NSC stores cost a great deal of time and money to measure, thus previous studies have not been able to examine NSC variation across global clines. Furthermore, NSCs vary by laboratory methods (Landhausser et al., 2018; Quentin et al., 2015), season (Furze et al., 2019; Martínez-Vilalta et al., 2016), and episodic stress such as drought or herbivory and their interactions (e.g., Adams et al., 2017; Barker Plotkin et al., 2021; Long et al., 2017), requiring large amounts of data to have the power to uncover overarching patterns in variation to climate. Our results highlight overarching patterns in NSCs against climate and suggest some functional roles they may play in woody plants across the globe.

AUTHOR CONTRIBUTIONS

Jessica Gersony, Jordi Martínez-Vilalta, Meghan Blumstein, and Anna Sala were involved in funding acquisition, conceptualization, methodology, and writing—review and editing. Meghan Blumstein was involved in visualization. Meghan Blumstein and Jessica Gersony were involved in writing—original draft.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

All data are available in the main text or the supplementary materials and on Dryad at <https://doi.org/10.5061/dryad.2z34tmpqq>.

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SUPPORTING INFORMATION

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

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