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Faculty of Science

**Carbohydrates drive growth and longevity tradeoff strategies of
plants in the Western United States**

Master's thesis

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Annotation:

This study explores the relationship between non-structural carbohydrates (NSCs), growth, and longevity in over 200 vascular plant species across diverse Western U.S. habitats. The research identifies specific roles for NSC compounds—fructans enhance longevity, while simple sugars support rapid growth at the expense of longevity. By elucidating the roles of individual NSC compounds and their relationship with growth and longevity, we are contributing to a deeper understanding of plant adaptation and survival strategies.

DECLARATION:

I declare that I am the author of this qualification thesis and, that in writing it, I have used the sources and literature displayed in the list of used sources only.

České Budějovice, 08/12/2023

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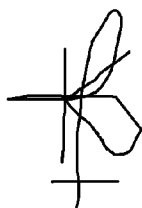


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Abstract

- Species from resource-limited environments are thought to have more total non-structural carbohydrates (NSCs) to promote survival and longevity at the cost of rapid growth, leading to trade-offs between total NSC content, growth, and longevity. However, the importance of individual NSC compounds, including starch, fructans, and simple sugars, for plant growth and longevity remains largely unexplored, especially in herbs.
- Here we anatomically determined annual radial growth, its temporal variation, and the age of over 200 vascular plant species native to the Western United States to elucidate the trade-offs between plant longevity, growth, and total NSC content and composition under a wide range of habitats, from arid and hot deserts to cool and humid mountains. In particular, we test the relationship between individual NSC compounds and growth, growth temporal variation, and longevity. Finally, we examine whether NSCs passively accumulate as reserves or actively promote growth or longevity depending on the life history strategy.
- Our results show the trade-off between total NSC and growth after accounting for the confounding effects of environmental conditions, growth forms, and phylogeny. Furthermore, individual NSC compounds have a different relationship with growth and longevity. In particular, a negative correlation is observed between growth and starch and fructans, whereas a positive correlation is noted with simple sugars. Additionally, fructans are associated with increased longevity, while simple sugars are correlated with decreased longevity. Surprisingly, none of our predictors showed any relationship with the growth temporal variation.
- These results suggest that NSCs do not accumulate passively in slow-growing, long-lived plants due to more constrained meristematic processes relative to carbon assimilation. Instead, plants utilize specific NSCs, such as osmoprotective fructans defending against drought or cold stress to enhance their longevity at the expense of rapid growth or metabolize readily available energy sources in the form of simple sugars to support rapid growth at the cost of shorter longevity.
- This study is the first comprehensive interspecific research investigating the trade-offs between carbohydrates, growth, its temporal variation, and longevity in vascular dicot plant species across diverse thermal and precipitation regimes. By elucidating the roles of individual NSC compounds and their relationship with growth and longevity, we are contributing to a deeper understanding of plant adaptation and survival strategies.

Keywords: Carbon allocation strategies; Environmental adaptation; Non-structural carbohydrates (NSCs); Plant growth dynamics; United States of America.

Introduction

Understanding how plants gain and allocate their carbon resources to optimize growth and longevity is crucial for comprehending their distribution patterns, community stability, and responses to environmental changes (Tilman, 1988; Simberloff & Dayan, 1991; Dietze et al., 2014). In the context of natural selection, biological diversity and species boundaries are defined by the concept of trade-offs (Futuyma & Moreno, 1988; Tilman, 1988), which is the fundamental notion that any beneficial change in one trait is associated with a simultaneous detrimental change in another trait (Mooney, 1972; Agrawal et al., 2020). The importance of trade-offs is critical when exploring how plants distribute their scarce carbon resources for reproduction, defense, and reserve - a process known as carbon allocation (Chapin et al., 1990; Herms & Mattson, 1992). Plant survival strategies, largely determined by carbon allocation trade-offs, are shaped by growth form type and habitat preferences and significantly influence growth rates and longevity (Lundgren & Des Marais, 2020; Chondol et al., 2023). By possessing stores of non-structural carbohydrates (NSCs), in the form of starch, fructans, and simple sugars, plants can effectively allocate the available carbon supply to balance growth and other metabolic processes while ensuring survival under resource-limited unfavorable conditions (Mooney, 1972; Chapin et al., 1990; Herms & Mattson; Dietze 2014; Hartmann et al., 2020). This carbon allocation strategy may have a major impact on the mean annual growth rate, its temporal variability, and the longevity of plants (Smith & Stitt, 2007; Sulpice et al., 2009; Hartmann & Trumbore, 2016).

The current knowledge regarding the role of NSCs for plant growth and longevity primarily draws upon their total quantity, rather than specifically investigating the impact of compositional differences of stored NSCs between plants (Chlumská et al., 2022). To properly reveal carbon allocation strategies and generalize their links to growth patterns and longevity, all NSC compounds must be considered, investigating beyond the total amount of NSCs. For instance, under challenging environmental conditions, plants generally remobilize complex carbohydrate compounds (such as starch) into simpler sugars to provide energy (Martínez-Vilalta et al., 2016). Starch, as the primary reserve storage carbohydrate, likely plays a key role in sustaining growth and survival during resource-limited periods (Chapin et al., 1990, Hartmann & Trumbore, 2016). On the other hand, simple sugars such as glucose and fructose may serve as readily available energy sources to support rapid growth responses under favorable conditions (Martínez-Vilalta et al., 2016). Moreover, certain NSC compounds, like fructans, are involved in osmoprotection and can help plants withstand environmental stresses by acting as cryoprotectants and enabling plants to

maintain cellular integrity during freezing events, especially in cold environments (Livingston et al., 2009; Ende, 2013; Hartmann & Trumbore, 2016). Therefore, under environmental constraints, measurements of total NSCs could be misleading, as they could have equal amounts and yet exhibit different compositions (and therefore strategies) of their carbohydrates supplies (Martínez-Vilalta et al., 2016; Pinkard, 2018). A comprehensive investigation that goes beyond total NSC quantities is required to gain deeper insights into the adaptive importance of these carbohydrates across diverse plant taxa and ecological settings (Blumstein et al., 2022). Such knowledge will provide a more nuanced understanding of how different NSC compounds contribute to growth, its temporal variation, and longevity in the face of changing environmental conditions.

Plant growth limitations can either stem from carbon supply constraints (carbon source limit) or carbon utilization constraints (carbon sink limit) (Korner, 2003; Holland et al., 2019). This carbon source versus carbon sink limitation concept is central to the carbon allocation strategies of plants (Wiley & Helliker, 2012; Hartmann et al., 2020). The Carbon Surplus Hypothesis, an integral component of the carbon sink versus source limitation concept, posits that harsh environmental conditions reduce the carbon utilization of plants more than the carbon availability (Korner, 2003; Prescott et al., 2020; Dietze et al., 2014), due to meristematic processes responsible for growth being typically more affected than photosynthetic efficiency (Chapin et al., 1990), leading to a passive accumulation in total NSC content (Prescott et al., 2020; Zepeda et al., 2022). Alternatively, the Growth-Longevity Trade-off hypothesis states that, under stressful conditions, plants actively prioritize carbon storage over immediate growth as part of a life strategy trade-off (Sala et al., 2012; Blumstein et al., 2022). This strategy of storing carbohydrates for long-term reserves or as osmolytes for defense contributes to the plant's ability to endure prolonged periods of nutrient scarcity and potentially promotes enhanced longevity (Korner, 2003; Suprasanna et al., 2016). We hypothesize that large investments in total NSC storage will be part of a life history strategy that provides persistence and longevity at the cost of growth in line with the Growth-Longevity Trade-off.

So far, there is a noticeable gap in research focused on comprehending how carbohydrate allocation varies across environmental conditions, plant families, or growth form types (Dietze et al., 2014; González-Paleo & Ravetta, 2015; Chlumská et al., 2022). In terrestrial ecosystems, high annual precipitation and optimal temperature primarily determine the primary productivity of plants (Tilman, 1988; Schuur, 2003), exerting a greater influence on plant growth than total NSC content. Other factors can also obscure total NSC effects on growth, growth variability, and longevity.

Different plant species or growth forms have evolved diverse strategies for NSC allocation (Hiltbrunner et al. 2021), depending on their ecological niches and the associated environmental challenges they face (Chapin et al., 1990; Hartmann & Trumbore, 2016). Large environmental gradients would reflect the different responses to evolutionary pressure and constraints that shaped distinct phylogenetic groups' NSC allocation strategies. Phylogenetic comparative models are commonly employed to account for similarities among species that share part of their evolutionary history (Adams & Collyer, 2017), as phylogenetic relatedness may cause similar 'blueprints' (Desdevises et al., 2003). By accounting for the variations explained by environmental conditions, growth forms, and the phylogenetic relatedness of the species sampled in our study, we can better discern the direct impact of NSCs on growth and longevity. While numerous studies show the relationship between growth and total NSCs, large interspecific studies taking into account environmental conditions, variation in yearly growth, phylogeny relatedness, and growth forms (e.g. short-lived herbs vs. woody perennials) are completely missing. As carbon allocation trade-offs embody the strategic use of limited carbon supply to ensure growth and longevity (Mooney, 1972; Hartmann et al., 2020), we must account for these multiple sources of variation that could obscure carbon allocation strategies.

The vast and diverse landscapes found within the western United States offer an ideal natural setting for examining the interplay between carbohydrate storage, radial growth, and longevity in vascular herbaceous plants. While dryland ecosystems cover much of the Western United States, the area exhibits considerable variation in temperature due to its diverse geographical features and elevational range (Abatzoglou & Williams, 2016). The region encompasses diverse temperature and precipitation regimes, ranging from arid and semi-arid conditions in the Mojave and Sonoran desert areas to more humid and Mediterranean-like climates in California and higher precipitation in the Rocky Mountains. These different climatic zones influence plant growth, phenology, and the accumulation and utilization of carbohydrate storage (Tilman, 1988; Chapin et al., 1990; Dietze et al., 2014). Significant strides in anatomical determination techniques have helped unravel the tradeoff between longevity and plant growth in herbaceous dicot species (Thomas, 2012; Doležal et al., 2018; Chondol et al., 2023). However, studies comprehensively exploring the specific roles of various NSC compound's influence on growth and longevity remain lacking (Smith & Stitt, 2007; Sala et al., 2012). Studies targeting NSCs in herbaceous plants have primarily focused on small regional scales and intraspecific responses (Yang et al., 2015), limiting our understanding of the implications of NSCs for plant resilience, species distribution patterns, and ecosystem

functioning. By conducting an interspecific study expanding the taxonomic diversity of species in our research pool, we can gain a more holistic understanding of the role of individual NSC compounds and their effect on radial growth, its temporal variability, and the longevity of plants. In this study, we investigate the growth, longevity, and NSCs across a diverse selection of 201 vascular dicotyledonous species found in various taxonomic groups and habitats in the western United States. Initially, we analyze how different factors (such as environmental conditions, growth forms, and phylogeny) impact the variations in growth, longevity, and NSCs among these species. Subsequently, after factoring out the influences of environmental conditions, growth forms, and phylogeny, we examine the following: (1) whether there exists a negative correlation between total NSCs and interspecific growth rates. (2) How different non-structural carbohydrate (NSC) compounds—such as starch, fructans, and simple sugars—affect annual growth rates and plant longevity. (3) Whether carbohydrates tend to accumulate passively as reserves due to growth limitations or actively contribute to promoting growth and longevity, considering the variation driven by the environment. A positive correlation would back the Carbon Surplus Hypothesis, suggesting that high NSC content indicates sufficient photosynthesis to support meristematic processes without compromising carbohydrates allocated for growth (Körner, 2003). This would indicate that accumulated carbohydrate stores incur no cost to growth-related carbohydrates (Wyka, 1999). On the other hand, a negative correlation aligns more with the active accumulation of NSCs for reserves or defense, potentially at the expense of growth, reflecting a trade-off between growth and survival strategies (Körner, 2015; Blumstein et al., 2022).

Material and Methods

Topography, geology of the study area and sampling locations

This study focuses on 201 species (562 individual plants) belonging to 49 families collected from 43 sites in seven states (Arizona, California, Colorado, Idaho, New Mexico, Utah, and Wyoming) of the Western United States during 2018-2019 (Figure 1). The Western United States encompasses diverse bioclimatic zones, shaped by distinct temperature and precipitation regimes related to varied geomorphological features and orographic barriers (McLaughlin, 1989; Seager et al., 2018). The study spanned a wide climatic range, from the northern cold Rockies to the desertic Sonoran and Mojave in the south. Total annual precipitation exhibited significant variability across the region, with measurements ranging from < 520 mm in the western areas to > 2300 mm in the eastern reaches. Furthermore, mean annual temperatures displayed an equally wide gradient, ranging from -5°C to 25°C, reflecting the contrasting thermal regimes experienced within the area. Lastly, elevation ranged from 533m a.s.l. in Organ Pipe National Park to 4313m a.s.l. in the Colorado Rockies.

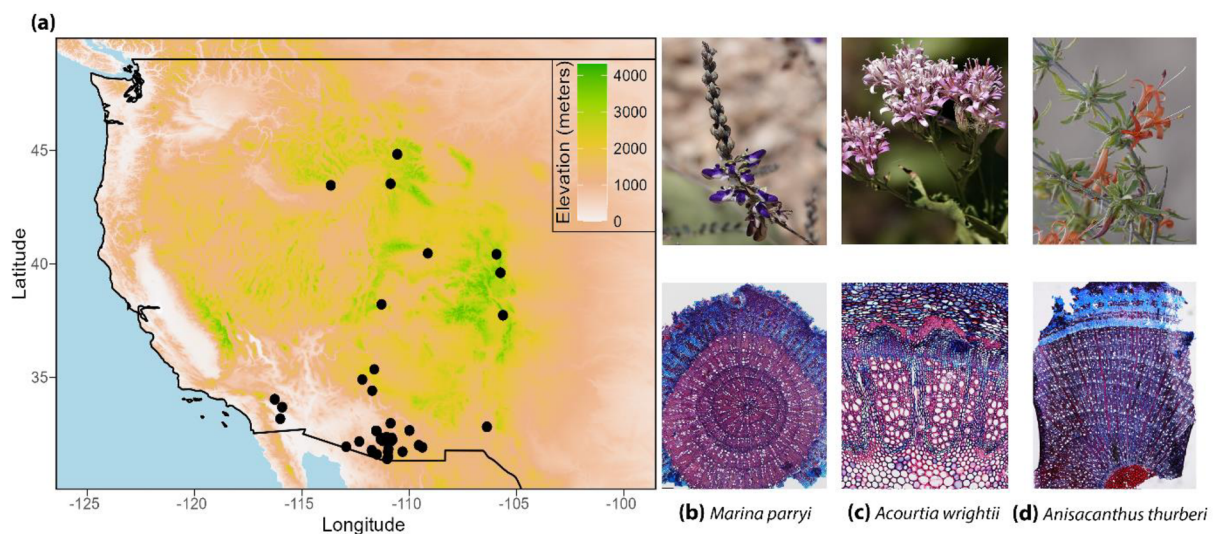


Figure 1: a) Elevation map depicting the study area in the Western United States, with sampled locations denoted by black dots. b-d) Examples of studied species and their double-stained cross-sections of root collars with growth rings.

Anatomical growth and age analysis

To obtain age and growth data for each individual, a segment of the oldest root or rhizome portion (approximately 5 cm long) was excised from each plant and placed in 40% ethanol tubes to keep the root tissue soft and prevent mold growth. Standardized procedures (Gärtner & Schweingruber,

2013) were used in the laboratory. These included cutting multiple cross-sections for each individual from the oldest plant tissue between the hypocotyl and the primary root (root collar) using a sledge microtome, staining with Astra Blue and Safranin, and permanently fixing the sections to a slide with Canada balsam (Doležal et al., 2018). All annual rings of perennial dicotyledonous plants were expected to be present in the root collar zone (Büntgen et al., 2015). High-resolution images of these microsections were then captured using an Olympus BX53 microscope, Olympus DP73 camera, and cellSense Entry 1.9 software to measure annual radial growth increments. The age of each individual was estimated from the maximum number of annual rings counted along the four radii for each cross-section.

Environmental variables

This study investigated how environmental factors, specifically temperature and precipitation, influence our targeted variables, deepening our understanding of their relationships. Our analysis exclusively used temperature and precipitation data from the CHELSA Bioclim dataset (Karger et al., 2017; Karger et al., 2021), which includes a comprehensive range of bioclimatic variables derived from monthly mean, maximum, and minimum temperature, as well as mean precipitation values. We employed Bio1 and Bio12 for our analysis, representing mean annual air temperature (mean annual daily air temperatures averaged over one year) and annual precipitation amount (accumulated over one year), respectively. The dataset had a 1/24 degree spatial resolution and covered the period from 1901 to 2021, forming a robust foundation to explore the relationships between environmental factors and the variables under investigation.

NSCs analyses

The samples from the plant individuals used for NSC analysis were oven-dried to constant weight immediately after collection. Carbohydrate analysis was conducted on belowground stem or root organs of the collected plant samples (e.g. Janeček et al. 2015). Total NSC values were obtained by summing all carbohydrate types found in one sample and were expressed as a percentage of storage organ dry mass.

Starch analysis

Approximately 100 mg of the sample is extracted in 80% ethanol at 83°C for 12 minutes in a water bath, centrifuged at 3000 rpm for 10 minutes, the supernatant is strained, and the entire procedure

is repeated a total of three times, and then is set aside for future analysis. Starch in the pellet remaining after ethanol extraction and centrifugation is partially hydrolyzed enzymatically by thermostable α -amylase at 100°C and completely dissolved. Starch dextrins were hydrolyzed to glucose by amyloglucosidase at 50°C. The amount of glucose is measured spectrophotometrically after addition of glucose oxidase/peroxidase (GOPOD) reagent, which causes the formation of the quinoneimine dye.

Fructans analysis

The fructans content was analyzed with an additional initial step that removed galactosyl sucrose oligosaccharides (raffinose family oligosaccharides, RFOs), similar to previous studies that focused on the analysis of carbohydrate concentrations (Chlumská et al., 2022). This method also included specific hydrolysis of fructans by fructanase.

To extract the fructans, approximately 100 mg of the original sample was boiled in 25 ml of distilled water for 15 minutes on a hot plate with a magnetic stirrer. The resulting suspension was cooled and filtered through a paper that retained particles $< 11\mu\text{m}$ (Whatman, grade 1). In the first step, 0.2 mL of the filtered solution was treated with 50 μL of α -galactosidase (200 U/mL in 50 mM sodium acetate buffer at pH 4.5) for 30 minutes at 40°C to remove all RFOs. Subsequently, sucrase, β -amylase, pullulanase, and maltase were added, and the solution was incubated at 30°C to eliminate other poly-, di-, and monosaccharides. The third step involved the addition of alkaline borohydride at 40°C to ensure the reduction of the products (glucose, fructose) from the preceding reactions into sugar alcohols. These compounds were then eliminated by the addition of acetic acid. Finally, the fructans and FOS reduced by borohydride were hydrolyzed by exo-inulinases, endo-inulinases, and endo-levanase at 40°C. The glucose and fructose formed during enzymatic hydrolysis were reduced by PAHBAH solution (p-hydroxybenzoic acid hydrazide), and the resulting color complex was measured spectrophotometrically.

Carbohydrates soluble in ethanol (simple sugars) analysis

The supernatant from the earlier analysis (as described in the starch analysis) was dried at 50°C and then redissolved in 10 ml of distilled water. It was shaken for half a day and subsequently filtered through nitrocellulose nitrate membrane filters with a particle retention threshold greater than 0.4 μm (Pragopor 6). The resulting filtrate was transferred to vials and subjected to analysis for ethanol-soluble carbohydrates (including sugar alcohols, glucose, galactose, fructose, sucrose,

raffinose, and verbascose) using ion exchange chromatography (HPAEC-PAD). An ion exchange chromatography system with a non-linear elution gradient of distilled water and 5-225mM NaOH was employed. The analysis of the species samples was carried out using the Dionex ICS-3000, utilizing the CarboPac PA10 column with an isocratic elution profile involving 18 mM NaOH at a flow rate of 1 mL/min and a temperature of 40°C. The chromatography program duration lasted approximately 65 minutes.

Data analyses

First, we examined relationships among variables within three groups: environmental conditions, NSCs, growth (mean and coefficient of variation) and longevity using a standardized major axis for all variable pairs and tested their correlations. Second, we investigated the effect of NSCs on growth and longevity, the effect of environmental conditions on NSCs, and the effect of environmental conditions on growth and longevity using phylogenetic linear models (Freckleton et al., 2002). To do so, we assessed the effects of all variables within the predictor group on the response group variables. To discern direct effects of environmental conditions' and NSCs' influence on growth and longevity, two models were employed: one with solely environmental conditions or NSCs as predictors, and another with both environmental conditions and NSCs as predictors. This assessment encompassed running the models using total NSCs and NSCs' individual compounds - starch, fructans, and simple sugars. F tests with type II sum of squares were used to evaluate predictor effects in all models. All models included growth form as a covariate. Before analysis, we transformed growth, longevity, and total NSCs, starch, fructans, and simple sugars dry content using natural logarithm. In all models, we estimated phylogenetic signal strength (Pagel's λ ; Pagel, 1999) through maximum likelihood.

We conducted the analyses using mean values of all variables for each species (across localities; when multiple individuals existed per locality, mean values were computed for that locality). This approach might have weakened the examined relationships for species with individuals sampled from multiple localities, particularly if significant intraspecific variability was present. Therefore, all analyses were also performed using data from randomly chosen localities for each species with representation in multiple localities, aiming to verify the robustness of the outcomes. In total, 201 species were included in all analyses, except for analyses concerning the coefficient of variation of growth, where 154 species were considered due to some species having only one annual growth ring (Fig. 2). Additionally, the analyses were separately carried out for the two herbaceous growth

forms, which yielded a substantial number of observations (short-lived herbs: 70 species; perennial herbaceous: 112 species). This separation allowed us to assess whether the influence of growth forms on these relationships was additive as assumed. We prepared the phylogenetic tree using the V.PhyloMaker package (version 0.1.0; Jin and Qian, 2019) with scenario 2 which takes a mega-tree (GBOTB.extended, based on Smith & Brown, 2018) and randomly binds missing species below their genus crown node. We did all analyses in R (version 4.2.2; R Core Team, 2022) using package caper (version 1.0.1; Orme et al., 2013) for phylogenetic linear models, package diversitree (version 0.9-16; FitzJohn, 2012) for phylogeny visualization, and package smart for standardized major axis (version 3.4-8; Warton et al., 2012).

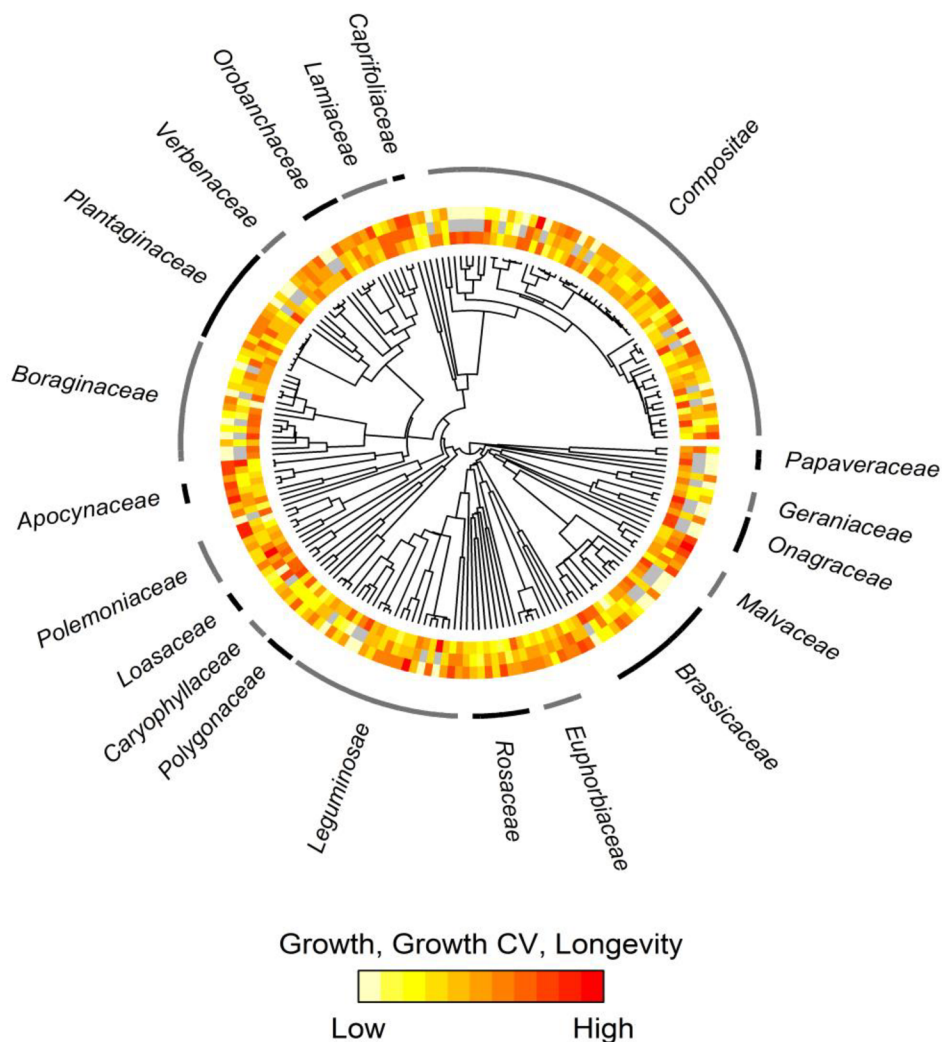


Figure 2: Phylogenetic tree depicting growth, growth CV, and longevity of plant species. Coloured rings visualize growth as the inner circle, growth CV as the middle circle and longevity as the outer circle. Missing values for growth CV (coefficient of variation) are visualized in grey color.

Results

Relationships of variables within groups

We found negative relationships between temperature and precipitation and between growth and longevity. There was a positive, yet weak, relationship between growth and its coefficient of variation, and no relationship between growth CV and longevity (Fig. 3). Among NSCs, we found only a weak positive relationship between the concentration of starch and simple sugars (Fig. 4).

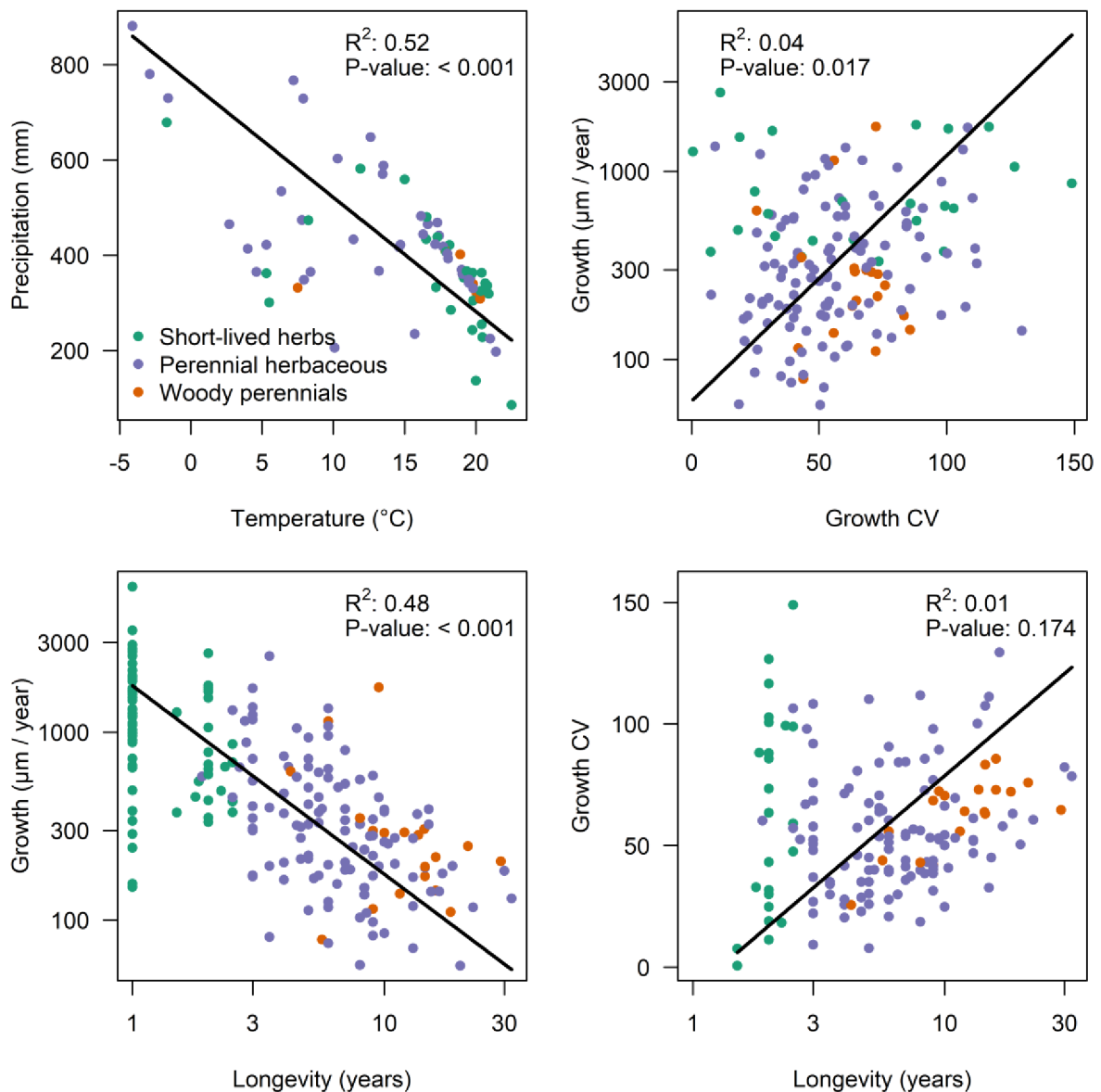


Figure 3: Standardized major axis of the selected environmental predictors (mean annual temperature and annual precipitation amount), and measurements of radial growth, including mean values, coefficient of variation (Growth CV), and longevity. Plant growth forms are indicated by color.

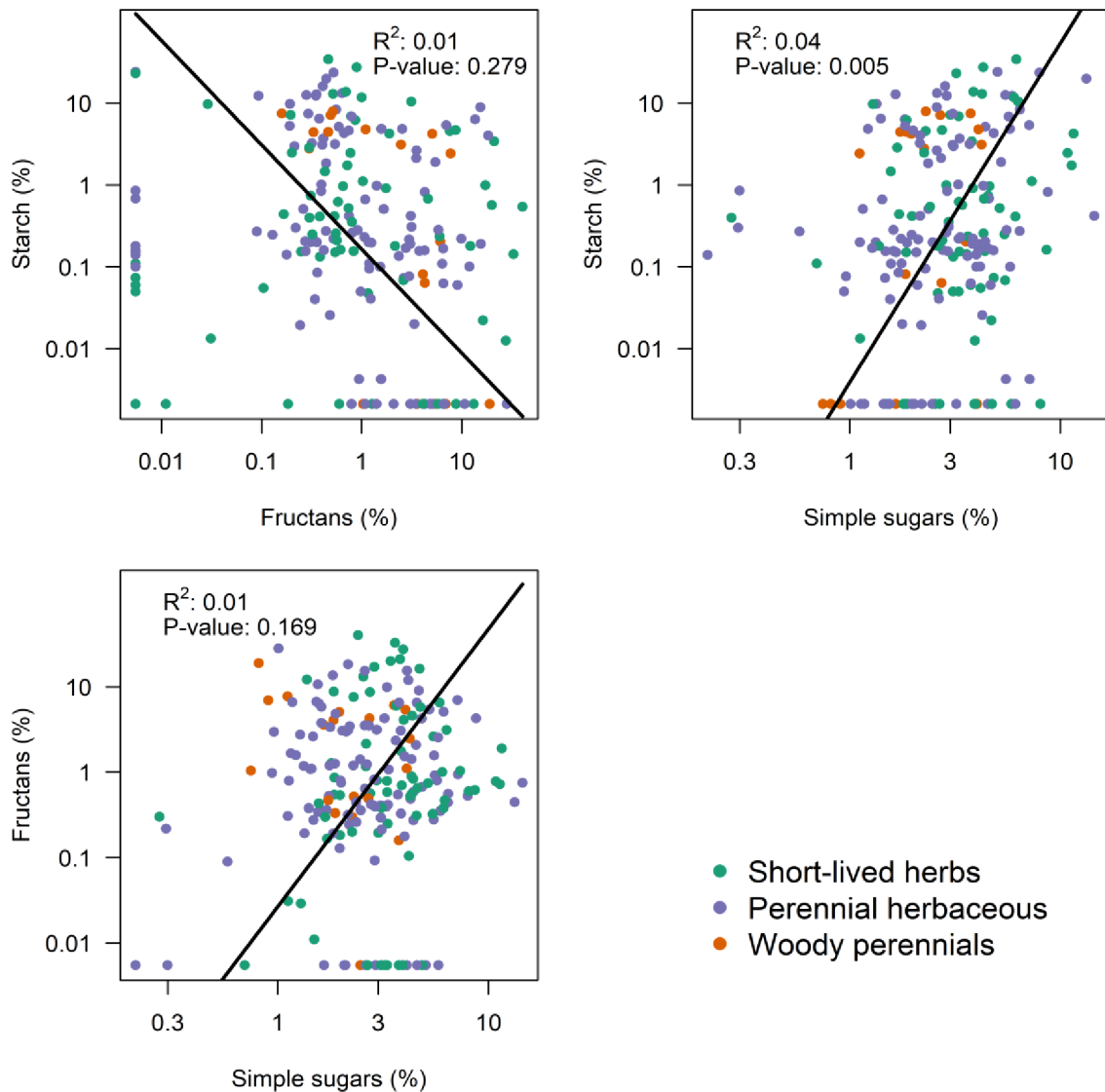


Figure 4: Standardized major axis of starch, fructans, and simple sugars (NSCs) of 201 species sampled at 43 locations across the Western United States. NSC values are expressed as a percentage of content in storage organ dry mass.

Effect of growth forms on growth, longevity, and carbohydrate reserves

We found a significant variation in mean annual growth, longevity, and simple sugars among different plant growth forms (Table S2, Figure 5). On average, short-lived herbs exhibited the highest growth rates, compared to the longer-lived perennials and woody plants. Among the investigated NSCs, only simple sugars exhibited significant variation between growth forms (Table S2), with the highest concentration in short-lived plants and the lowest in woody perennials. While simple sugars were variable in the analyzed samples, they never composed more than 15 % of dry mass content.

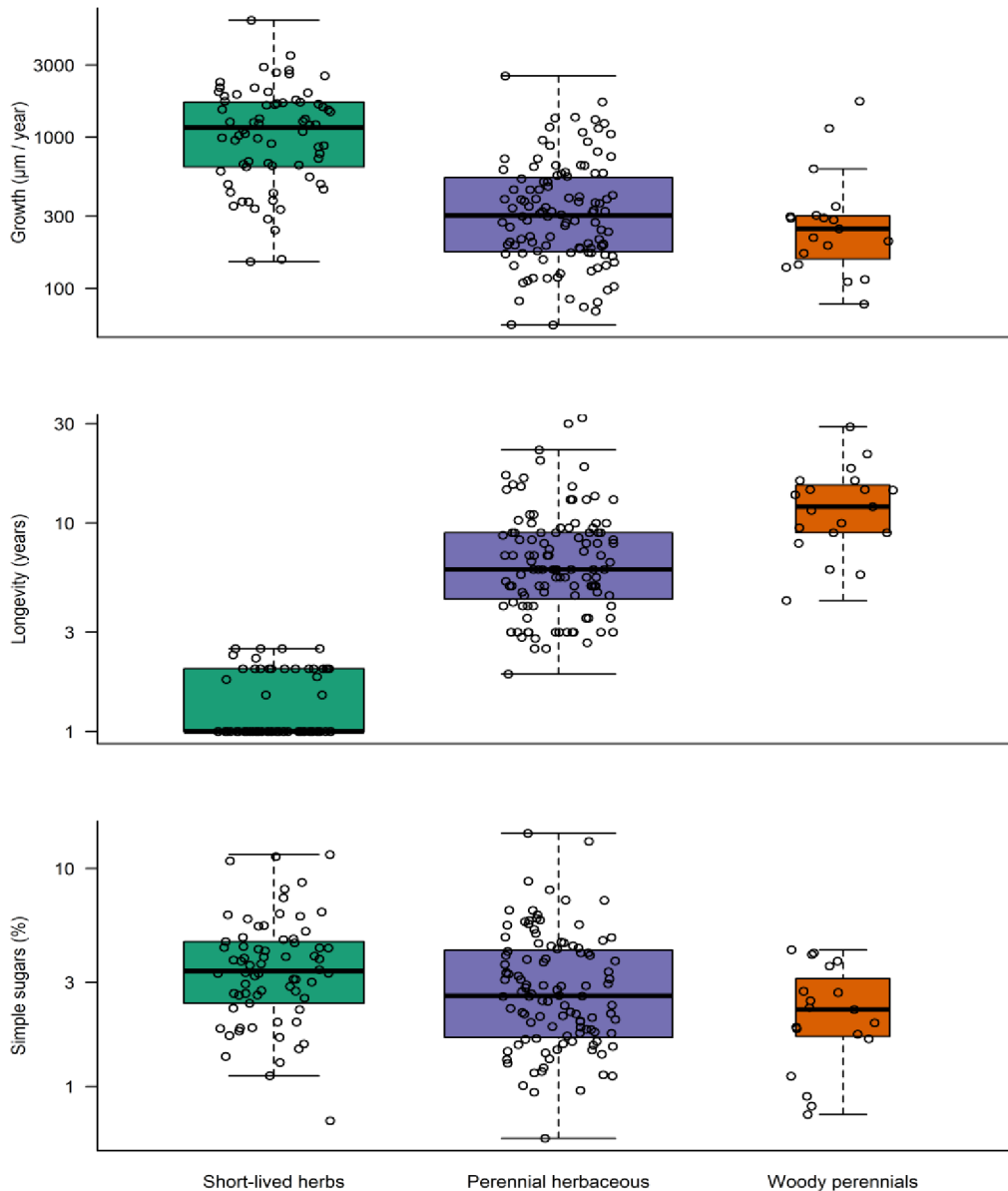


Figure 5: Growth, longevity, and simple sugars for the three growth forms. Width of the boxes correspond to square-root of number of observations. Thick middle line denotes median, boxes range from the first to the third quartile, whiskers range up to $3/2$ of interquartile range from the box.

Effect of environmental conditions on carbohydrates, radial growth, and longevity

Environmental conditions affected starch and fructan content but explained only a small amount of variation, whereas no effect was found on simple sugars (Table S2). Effects of both precipitation and temperature on starch were positive, while fructans were negatively linked to precipitation (Fig. 6). We found a direct effect of environmental conditions on growth and growth variability (Growth CV) but not on longevity (Table S2). Higher radial growth was identified in plants from drier conditions, while more variable growth was associated with higher temperatures (Fig. 6).

When we accounted for carbohydrates, growth was not only negatively affected by precipitation but also positively affected by temperature (Table S2). There was no change in the effects of environmental conditions on growth variability (positive effect of temperature) and longevity (no effects; Fig. 6).

Carbohydrates, radial growth rates, and longevity

We did not find any significant effect of the environment on total NSCs. Precipitation was generally negatively related to growth and temperature was positively related to growth CV, both directly and after accounting for interspecific differences in total NSCs. A negative relationship between total NSCs and growth was observed only after accounting for precipitation and temperature (Fig. 6).

All three types of analyzed NSCs groups had significant relationship with growth (Table S2). We observed high mean radial growth in species with low starch and fructans but high levels of simple sugars. Additionally, higher fructan and simple sugar contents were significantly coupled with plants exhibiting higher longevity, while no NSCs showed any relationship on the variability of annual growth (coefficient of variation of growth; Table S2). Fructans had positive relationship with longevity, whereas simple sugars had a negative relationship (Fig. 7). All these effects were found in both analyses with and without accounting for environmental variables.

Robustness check and phylogenetic inertia

Results showed no significant change when utilizing individuals from random localities instead of species averages: the direct effect of precipitation on growth was no longer significant ($p = 0.074$), the direct effect of temperature on NSCs became significant ($p = 0.042$), and the indirect effect of precipitation on growth was no longer significant ($p = 0.061$). When we analyzed herbaceous growth forms separately, there was no change in the direction of identified relationships (Fig. S1; many relationships identified for the dataset were no longer significant for separate growth forms – which was expected since the number of species was lower).

The estimated phylogenetic signal (λ) in individual analyses varied from very low ($\lambda = 0$) to moderate ($\lambda = 0.44$) (where $\lambda = 0$ corresponds to no phylogenetic signal and $\lambda = 1$ to the Brownian motion model of evolution), indicating a minor influence of phylogeny on these relationships (Table S2).

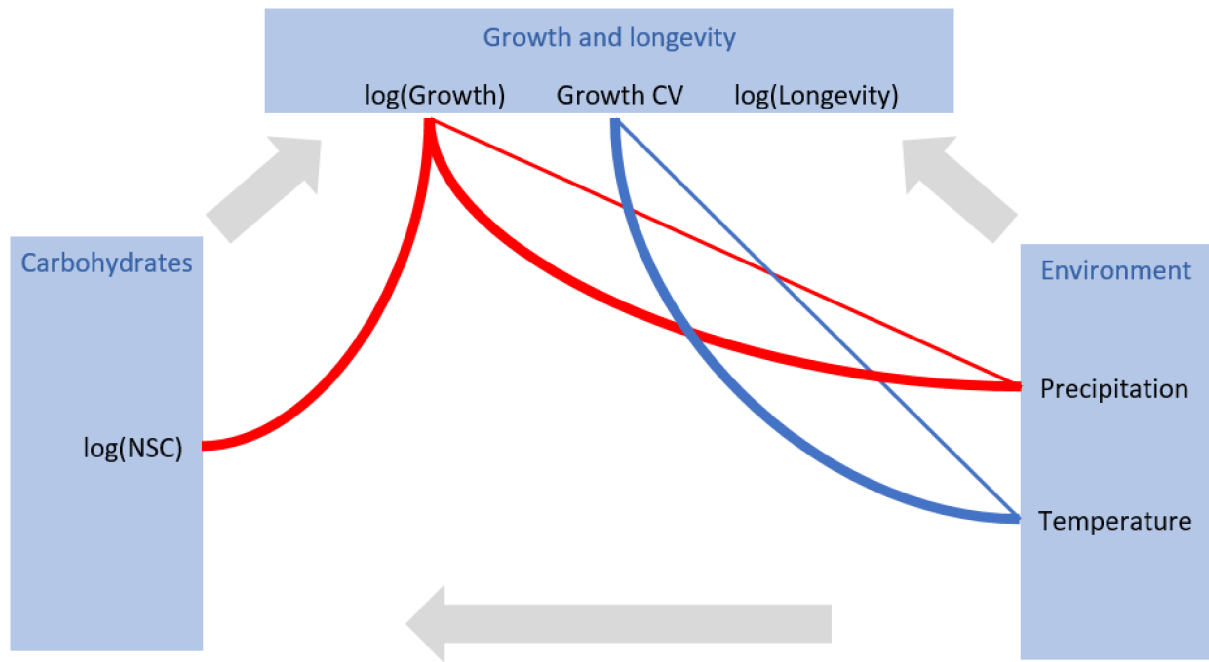


Figure 6: Diagram illustrating the complex interplay among environmental factors, total non-structural carbohydrates (NSCs), and their influence on growth and longevity. Red lines denote negative effects, while blue lines positive effects (Table S2). Curved lines represent analyses accounting for both carbohydrate compounds and environmental variables. The "log" notation signifies natural logarithm, and "CV" represents the coefficient of variation.

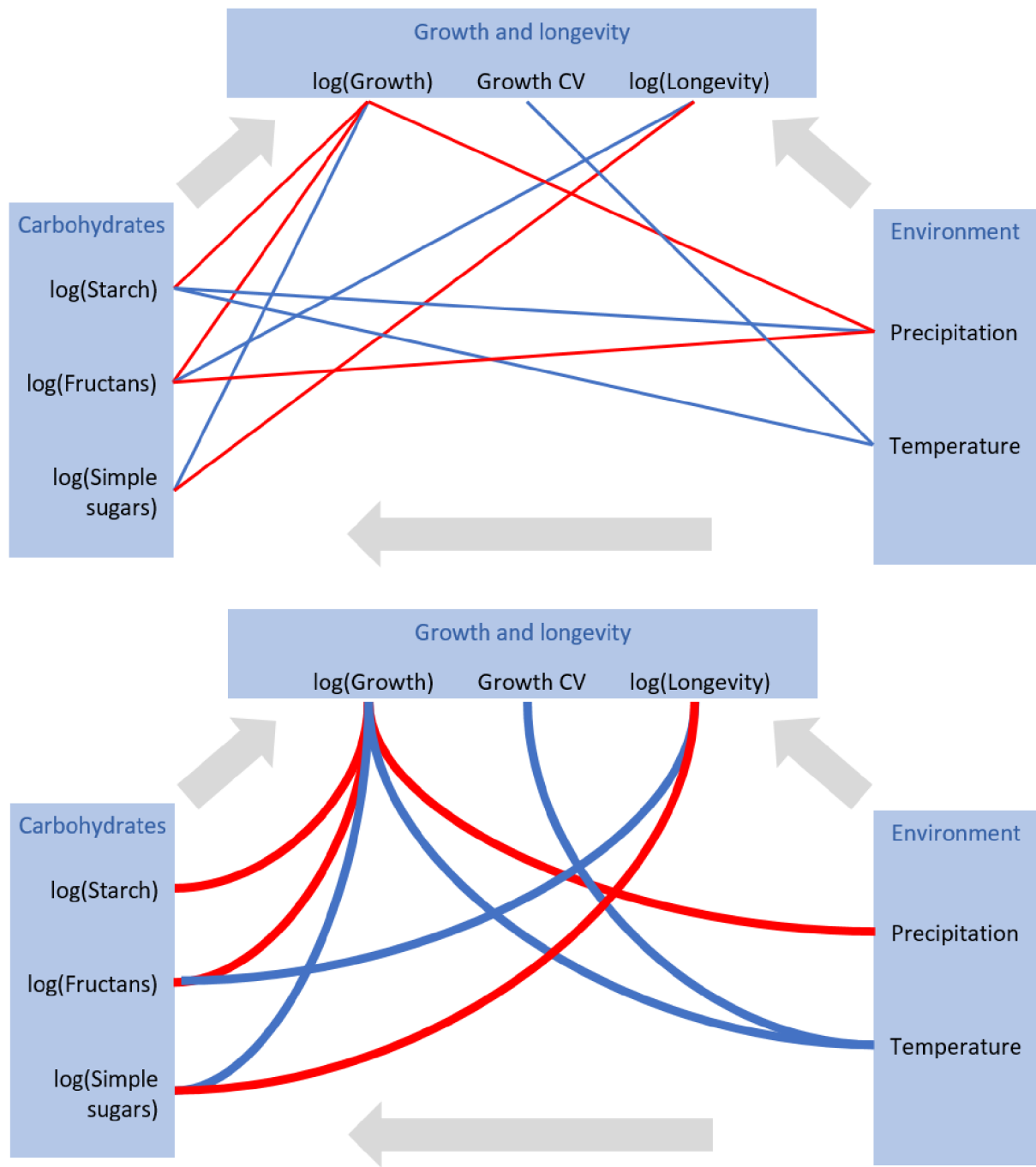


Figure 7: Diagrams illustrating the complex interplay among environmental factors, carbohydrate compounds, and their influence on growth and longevity. Red lines denote negative effects, while blue lines positive effects (Table S2). Curved lines represent analyses accounting for both carbohydrate compounds and environmental variables. The "log" notation signifies natural logarithm, and "CV" represents the coefficient of variation.

Discussion

Exploring the relationship between total NSC and growth

Our study revealed a significant negative relationship between total non-structural carbohydrates (NSCs) and radial growth in the sampled plant species only after accounting for the inherent environmental conditions, life strategies, and phylogenetic differences. The considerable variability in total non-structural carbohydrate (NSC) content makes it challenging to establish direct links between growth patterns and total NSC content in an interspecific context (Fung, 2000; Huang et al., 2019). This result highlights the fact that the different carbon allocation strategies of plant species lead to a high variation in carbon sink content, and therefore one must consider variation in the carbon supply when conducting interspecific studies exploring relationships that include total NSC content (Fung, 2000; Sala et al., 2012; Blumstein et al., 2022). Previous studies have shown that for highly productive plant species, variation in carbon supply can blur the trade-off between growth and carbon sinks (van Noordwijk & de Jong, 1986; Osnas et al., 2018; Agrawal, 2020). Indeed, a previous study found that when controlling for the variation in carbon supply, the relationship between growth and storage filled flipped from a positive association to a negative one (Blumstein et al., 2022). These findings underscore the importance of taking into account the inherent environmental conditions, life strategies, and phylogenetic differences of plant species when investigating the effect of total NSCs on growth, growth variation, and longevity in plant species.

Impacts of individual NSC Compounds on Growth and Longevity

To determine if carbohydrates predominantly accumulate as passive reserves due to growth limitations or actively promote growth and longevity, we explored the relationship between individual NSC compounds and growth, growth temporal variation, and longevity. We hypothesized that if there were an inverse correlation between total NSCs and growth, and if none of the NSC compounds exhibited a significant relationship with growth or longevity, then NSCs likely functioned as an energy reservoir for plants to draw on during constrained meristematic processes, preventing carbon starvation and supporting the Carbon Surplus hypothesis (Prescott et al., 2020; Zepeda et al., 2022). Alternatively, a negative relationship between growth and NSC and a significant relationship between distinct NSC compounds and growth, growth temporal variation, and longevity could challenge the Carbon Surplus hypothesis by implying active utilization of different types of NSCs by plants to be used as osmolytes for defense or as a quick energy source

to enhance growth rates and longevity, rather than simply accumulating excess carbon as reserves, as suggested by the Growth/Longevity Trade-off hypothesis (Sala et al., 2012; Blumstein et al., 2022).

Our results show that all three primary storage carbohydrate types (starch, fructans, and simple sugars) significantly affected the annual growth of the studied plant species. However, only fructans and simple sugars had an impact on longevity. Specifically, starch and fructans negatively correlated with growth, whereas a positive correlation was noted with simple sugars. Additionally, fructans are associated with increased longevity, while simple sugars are correlated with decreased longevity. Surprisingly, none of our distinct NSC compounds showed any significant effect on the growth temporal variation.

Our finding suggests that the simple sugars are used from the NSC pool to promote optimal growth at the expense of longevity. Similar patterns were observed in other studies, where C fluxes in and out of the simple sugars NSC pool to achieve regular growth rates under non-optimal conditions and avoid carbon starvation (Gibon et al., 2009; Hartmann et al., 2013; Huang et al., 2019). Indeed, the observed positive correlation between high annual radial growth and levels of simple sugars in the short-lived desert species under investigation stems from the higher availability of simple sugars for energy production and other metabolic processes (Couée et al., 2006; Guo et al., 2020; Blumstein et al., 2023). This is exemplified by the high growth experienced by the sugar-rich *Chylismia claviformis* and *Palafoxia arida* individuals collected in the Sonoran Desert. While starch undergoes degradation into glucose, especially under stress like drought or nutrient deficiency (Stitt & Zeeman, 2012; Janeček et al., 2015), plants efficiently mobilize and utilize these sugars with fewer constraints during heightened metabolic demand to avoid carbon starvation (Smith & Stitt, 2007; Sulpice et al., 2009; Bihmidine et al., 2015). In contrast to the availability of simple sugars, the negative correlation of starch with growth is likely attributed to its tightly regulated nature, rendering it a strategic reserve formation that occurs at the expense of growth and is subject to controlled breakdown under specific stress conditions (Chapin et al., 1990; Wiley et al., 2013; Martínez-Vilalta et al., 2016).

Fructans positively affecting longevity can be attributed to the versatility of its functionalities transcending their conventional role as simple reserve carbohydrates (Livingston et al., 2009), to the point that plants that store fructan polymers often forgo starch production as a reserve (Pollock, 1986; Hendry, 2008). These functionalities encompasses multiple roles such as reserve

carbohydrates, membrane stabilizers, osmoprotectants, and stress tolerance mediators, which contributes to the heightened overall fitness and resilience of plant species leading to longer longevity (Livingston et al., 2009; Ende, 2013).

Our results showcase the influence that all three distinct NSC compounds have on either growth or longevity, indicating that specific types of NSCs play a pivotal role in a plant's development and carbon allocation strategies. Additionally, our findings highlight the positive effects of the multifunctionality of fructans by emphasizing the heightened longevity of desert shrubs and alpine herbs with low growth rates and higher fructan content and the effective prioritization of starch breakdown into energy-rich simple sugars that are then allocated towards growth and reproduction, resulting in a maximization of growth in herbaceous species (Couée et al., 2006; Livingston et al., 2009; Hartmann & Trumbore, 2016; Blumstein et al., 2023). These findings insights shed light on the critical role of distinct NSCs in the carbon allocation strategies of plants, and align more closely with the Growth/Longevity Trade-off hypothesis, suggesting that NSCs actively contribute to plant growth and longevity rather than mere passive accumulations due to growth limitations (Prescott et al., 2020; Zepeda et al., 2022).

Implications for Plant Carbon Allocation Strategies

Whether NSCs actively accumulate to promote plant growth and longevity under carbon stress or are passive build-ups due to growth limitations has been debated extensively in recent years (Sala et al., 2012; Wiley et al., 2013; Dietze et al., 2014; Blumstein et al., 2022). Our findings are in line with studies showing the negative relationship, or trade-off, found between storage and growth indicative of carbon storage being actively allocated by plant species (Sala et al., 2012; Blumstein et al., 2022). We demonstrate that the distinct regulatory behavior of starch contrasts with the more flexible response exhibited by simple sugars, which plants efficiently harness during heightened metabolic demands (Martínez-Vilalta et al., 2016; Tixier et al., 2018), allowing them to make the most of favorable conditions, maximizing their growth potential while also avoiding or escaping the negative effects of limited water availability in harsh environments (Aronson et al., 1992; Guo et al., 2020). This contributes to their adaptive strategies for maximizing growth during optimal environmental conditions at the cost of longevity (Hartmann & Trumbore, 2016). As a result, these plant species can complete their life cycles during periods when water is more readily available, providing them with a survival advantage (Aronson et al., 1992; Ekwealor et al., 2020). Additionally, fructans actively engaging in a spectrum of physiological functions, including the

stabilization and maintenance of cell membrane hydration during drying and the facilitation of water-related stress tolerance (Ende, 2013), makes them versatile agents that might heighten the overall fitness and resilience of plant species leading to longer longevity (Livingston et al., 2009; Suprasanna et al., 2016). The differing effect of distinct NSC compounds on growth and longevity is consistent with previous research on carbon allocation strategies emphasizing their importance in plant physiology and ecology (Smith & Stitt, 2007; Sulpice et al., 2010; Huang et al., 2019; Blumstein et al., 2023). Consequently, the contrasting effect of certain NSC compounds plays a pivotal role in shaping the intricate balance of carbon allocation and utilization in plants (González-Paleo & Ravetta, 2015), ultimately influencing their life history strategies (Lundgren & Des Marais, 2020). Overall, this active role of specific NSC compounds in promoting growth and longevity in a contrasting fashion generally supports the Growth-Longevity Trade-off hypothesis and the active accumulation of certain NSCs for reserves or defense (specifically Fructans) at the expense of growth or the active accumulation of readily available energy suppliers (in the form of simple sugars) resulting in a maximization of growth at the cost of lower longevity.

Conclusions

Our study provides new interspecific insights into trade-offs between carbohydrate reserves, growth, and longevity in over 200 vascular dicot plant species across diverse thermal and precipitation regimes in the Western United States. Our findings confirm the relationship between total NSCs and growth after accounting for environmental conditions and phylogenetic relatedness. We show that certain NSCs likely act as osmoprotectants to defend against drought and cold stress, while others act as a quick energy source to boost growth. In particular, short-lived desert herbs with high growth rates show low starch and high simple sugar content. On the other hand, long-lived desert shrubs and alpine herbs with a low growth rate have higher fructan content. Contrary to our prediction, NSC did not accumulate passively in slow-growing, long-lived plants due to more constrained meristematic processes relative to carbon assimilation. Overall, our study gives new insights into trade-offs between growth, longevity, and total NSC storage using growth, age, and NSCs measured from less commonly sampled herbaceous plants from a broad spectrum of habitats, emphasizing the importance of different types of storage carbohydrates for growth and longevity as a fundamental aspect of a plant's carbon allocation strategy. The results confirm the active role of specific NSC compounds in shaping plant strategies to adapt to different environmental conditions. This research not only improves our understanding of carbon allocation trade-offs, which is crucial for comprehending responses to environmental changes under climate change but also emphasizes the need to consider individual NSC compounds in future studies of plant growth and longevity.

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Supporting information:

The following supporting information is available for this thesis:

Table S1. List of selected species collected - between 2018 and 2019 in the Western United States – and used for this study.

Table S2. Summary of all models. “log” stands for natural logarithm, “CV” for coefficient of variation.

Figure S1. Links between environment, carbohydrates, and growth and longevity for herbaceous growth forms.

Table S1.

Species	Family	Species	Family
<i>Abronia angustifolia</i>	Nyctaginaceae	<i>Callirhoe involucrata</i>	Malvaceae
<i>Abronia villosa</i>	Nyctaginaceae	<i>Carphochaete bigelovii</i>	Asteraceae
<i>Abutilon abutiloides</i>	Malvaceae	<i>Castilleja applegatei</i>	Orobanchaceae
<i>Achillea millefolium</i>	Asteraceae	<i>Castilleja exserta</i>	Scrophulariaceae
<i>Acmispon neomexicanus</i>	Fabaceae	<i>Castilleja integra</i>	Orobanchaceae
<i>Acmispon rigidus</i>	Fabaceae	<i>Castilleja pallescens</i>	Orobanchaceae
<i>Acmispon strigosus</i>	Fabaceae	<i>Celtis reticulata</i>	Cannabaceae
<i>Acourtia wrightii</i>	Asteraceae	<i>Cercocarpus ledifolius</i>	Rosaceae
<i>Agastache breviflora</i>	Lamiaceae	<i>Chaenactis douglasii</i>	Asteraceae
<i>Agrimonia striata</i>	Rosaceae	<i>Chaenactis fremontii</i>	Asteraceae
<i>Ambrosia cordifolia</i>	Asteraceae	<i>Chenopodium berlandieri</i>	Amaranthaceae
<i>Ambrosia deltoidea</i>	Asteraceae	<i>Chorizanthe brevicornu</i>	Polygonaceae
<i>Ambrosia psilostachya</i>	Asteraceae	<i>Chylismia claviformis</i>	Onagraceae
<i>Amorpha canescens</i>	Fabaceae	<i>Cleomella serrulata</i>	Cleomaceae
<i>Amsinckia menziesii</i>	Boraginaceae	<i>Conyza canadensis</i>	Asteraceae
<i>Anagallis arvensis</i>	Primulaceae	<i>Crossosoma bigelovii</i>	Crossosomataceae
<i>Anisacanthus thurberi</i>	Acanthaceae	<i>Cryptantha micrantha</i>	Boraginaceae
<i>Antennaria marginata</i>	Asteraceae	<i>Cryptantha pterocarya</i>	Boraginaceae
<i>Argemone pleiacantha</i>	Papaveraceae	<i>Cymopterus lemmonii</i>	Apiaceae
<i>Arnica latifolia</i>	Asteraceae	<i>Dalea pringlei</i>	Fabaceae
<i>Artemisia dracunculus</i>	Asteraceae	<i>Dalea purpurea</i>	Fabaceae
<i>Artemisia frigida</i>	Asteraceae	<i>Delphinium scaposum</i>	Ranunculaceae
<i>Artemisia scopulorum</i>	Asteraceae	<i>Descurainia pinnata</i>	Brassicaceae
<i>Artemisia tridentata</i>	Asteraceae	<i>Dieteria canescens</i>	Asteraceae
<i>Asclepias asperula</i>	Apocynaceae	<i>Dodonaea viscosa</i>	Sapindaceae
<i>Asclepias viridis</i>	Apocynaceae	<i>Draba grayana</i>	Brassicaceae
<i>Astragalus gracilis</i>	Fabaceae	<i>Draba incerta</i>	Brassicaceae
<i>Astragalus mollissimus</i>	Fabaceae	<i>Drymocallis glandulosa</i>	Rosaceae
<i>Atriplex gardneri</i>	Amaranthaceae	<i>Dryopetalon runcinatum</i>	Brassicaceae

<i>Brickellia coulteri</i>	Asteraceae	<i>Emmenanthe penduliflora</i>	Boraginaceae
<i>Calliandra eriophylla</i>	Fabaceae	<i>Encelia farinosa</i>	Asteraceae
<i>Ephedra torreyana</i>	Ephedraceae	<i>Galium wrightii</i>	Rubiaceae
<i>Ephedra trifurca</i>	Ephedraceae	<i>Geranium caespitosum</i>	Geraniaceae
<i>Ephedra viridis</i>	Ephedraceae	<i>Geum rossii</i>	Rosaceae
<i>Eremothera boothii</i>	Onagraceae	<i>Glandularia gooddingii</i>	Verbenaceae
<i>Eriastrum eremicum</i>	Polemoniaceae	<i>Grayia spinosa</i>	Amaranthaceae
<i>Ericameria cooperi</i>	Asteraceae	<i>Grindelia squarrosa</i>	Asteraceae
<i>Ericameria nauseosa</i>	Asteraceae	<i>Gutierrezia sarothrae</i>	Asteraceae
<i>Erigeron divergens</i>	Asteraceae	<i>Hedeoma hyssopifolia</i>	Lamiaceae
<i>Erigeron oreophilus</i>	Asteraceae	<i>Hedysarum occidentale</i>	Fabaceae
<i>Erigeron simplex</i>	Asteraceae	<i>Helianthus annuus</i>	Asteraceae
<i>Eriogonum inflatum</i>	Polygonaceae	<i>Heterotheca villosa</i>	Asteraceae
<i>Eriogonum ovalifolium</i>	Polygonaceae	<i>Hibiscus denudatus</i>	Malvaceae
<i>Eriogonum umbellatum</i>	Polygonaceae	<i>Hymenoxys grandiflora</i>	Asteraceae
<i>Eritrichium argenteum</i>	Boraginaceae	<i>Hymenoxys hoopesii</i>	Asteraceae
<i>Erodium cicutarium</i>	Geraniaceae	<i>Ipomopsis aggregata</i>	Polemoniaceae
<i>Erodium texanum</i>	Geraniaceae	<i>Isocoma tenuisecta</i>	Asteraceae
<i>Erysimum capitatum</i>	Brassicaceae	<i>Janusia gracilis</i>	Malpighiaceae
<i>Erythranthe guttata</i>	Phrymaceae	<i>Johnstonella angustifolia</i>	Boraginaceae
<i>Eschscholzia californica</i>	Papaveraceae	<i>Krameria bicolor</i>	Krameriaceae
<i>Eulobus californicus</i>	Onagraceae	<i>Lactuca serriola</i>	Asteraceae
<i>Euphorbia arizonica</i>	Euphorbiaceae	<i>Larrea tridentata</i>	Zygophyllaceae
<i>Euphorbia esula</i>	Euphorbiaceae	<i>Lepidium densiflorum</i>	Brassicaceae
<i>Euphorbia hyssopifolia</i>	Euphorbiaceae	<i>Lepidium lasiocarpum</i>	Brassicaceae
<i>Euphorbia pediculifera</i>	Euphorbiaceae	<i>Lepidium oblongum</i>	Brassicaceae
<i>Euphorbia polycarpa</i>	Euphorbiaceae	<i>Lepidium virginicum</i>	Brassicaceae
<i>Evolvulus arizonicus</i>	Convolvulaceae	<i>Linum lewisii</i>	Linaceae
<i>Fallugia paradoxa</i>	Rosaceae	<i>Lithospermum occidentale</i>	Boraginaceae
<i>Fouquieria splendens</i>	Fouquieriaceae	<i>Lupinus caudatus</i>	Fabaceae
<i>Fragaria virginiana</i>	Rosaceae	<i>Lupinus concinnus</i>	Fabaceae
<i>Funastrum cynanchoides</i>	Apocynaceae	<i>Lupinus neomexicanus</i>	Fabaceae

<i>Gaillardia spathulata</i>	Asteraceae	<i>Lupinus sericeus</i>	Fabaceae
<i>Galium stellatum</i>	Rubiaceae	<i>Penstemon parryi</i>	Plantaginaceae
<i>Lupinus succulentus</i>	Fabaceae	<i>Penstemon procerus</i>	Plantaginaceae
<i>Lycium andersonii</i>	Solanaceae	<i>Perityle emoryi</i>	Asteraceae
<i>Machaeranthera tanacetifolia</i>	Asteraceae	<i>Perityle lemmonii</i>	Asteraceae
<i>Malacothrix glabrata</i>	Asteraceae	<i>Phacelia campanularia</i>	Boraginaceae
<i>Marina parryi</i>	Fabaceae	<i>Phacelia crenulata</i>	Boraginaceae
<i>Melampodium leucanthum</i>	Asteraceae	<i>Phacelia cryptantha</i>	Boraginaceae
<i>Mentzelia albicaulis</i>	Loasaceae	<i>Phacelia distans</i>	Boraginaceae
<i>Mentzelia integra</i>	Loasaceae	<i>Phacelia sericea</i>	Boraginaceae
<i>Mentzelia procera</i>	Loasaceae	<i>Phlox multiflora</i>	Polemoniaceae
<i>Microseris lindleyi</i>	Asteraceae	<i>Phlox tenuifolia</i>	Polemoniaceae
<i>Monarda citriodora</i>	Lamiaceae	<i>Physaria gordonii</i>	Brassicaceae
<i>Nama demissa</i>	Boraginaceae	<i>Picradeniopsis absinthifolia</i>	Asteraceae
<i>Nicotiana obtusifolia</i>	Solanaceae	<i>Plantago ovata</i>	Plantaginaceae
<i>Noccaea fendleri</i>	Brassicaceae	<i>Polemonium pulcherrimum</i>	Polemoniaceae
<i>Nuttallanthus texanus</i>	Plantaginaceae	<i>Polemonium viscosum</i>	Polemoniaceae
<i>Oenothera hartwegii</i>	Onagraceae	<i>Polygala alba</i>	Polygalaceae
<i>Oenothera primiveris</i>	Onagraceae	<i>Porophyllum gracile</i>	Asteraceae
<i>Oxalis dillenii</i>	Oxalidaceae	<i>Potentilla diversifolia</i>	Rosaceae
<i>Oxytropis sericea</i>	Fabaceae	<i>Potentilla gracilis</i>	Rosaceae
<i>Packera cana</i>	Asteraceae	<i>Rafinesquia neomexicana</i>	Asteraceae
<i>Packera neomexicana</i>	Asteraceae	<i>Rosa arkansana</i>	Rosaceae
<i>Palafoxia arida</i>	Asteraceae	<i>Rudbeckia laciniata</i>	Asteraceae
<i>Pectocarya heterocarpa</i>	Boraginaceae	<i>Rumex hymenosepalus</i>	Polygonaceae
<i>Pectocarya recurvata</i>	Boraginaceae	<i>Sabulina rubella</i>	Caryophyllaceae
<i>Pedicularis procera</i>	Orobanchaceae	<i>Salvia arizonica</i>	Lamiaceae
<i>Pediomelum argophyllum</i>	Fabaceae	<i>Salvia columbariae</i>	Lamiaceae
<i>Pediomelum cuspidatum</i>	Fabaceae	<i>Senecio atratus</i>	Asteraceae
<i>Penstemon albidus</i>	Plantaginaceae	<i>Senecio bigelovii</i>	Asteraceae
<i>Penstemon angustifolius</i>	Plantaginaceae	<i>Senecio flaccidus</i>	Asteraceae
<i>Penstemon barbatus</i>	Plantaginaceae	<i>Senecio integerrimus</i>	Asteraceae

<i>Penstemon cyaneus</i>	Plantaginaceae	<i>Senna covesii</i>	Fabaceae
<i>Penstemon deaveri</i>	Plantaginaceae	<i>Silene laciniata</i>	Caryophyllaceae
<i>Penstemon palmeri</i>	Plantaginaceae	<i>Tragopogon dubius</i>	Asteraceae
<i>Silene scouleri</i>	Caryophyllaceae	<i>Triodanis leptocarpa</i>	Campanulaceae
<i>Simmondsia chinensis</i>	Simmondsiaceae	<i>Vachellia constricta</i>	Fabaceae
<i>Sisymbrium irio</i>	Brassicaceae	<i>Valeriana arizonica</i>	Caprifoliaceae
<i>Solidago rigida</i>	Asteraceae	<i>Verbena bipinnatifida</i>	Verbenaceae
<i>Sonchus oleraceus</i>	Asteraceae	<i>Verbena bracteata</i>	Verbenaceae
<i>Sphaeralcea coccinea</i>	Malvaceae	<i>Verbena stricta</i>	Verbenaceae
<i>Sphaeralcea laxa</i>	Malvaceae	<i>Veronica americana</i>	Plantaginaceae
<i>Stachys coccinea</i>	Lamiaceae	<i>Veronica wyomingensis</i>	Plantaginaceae
<i>Streptanthus carinatus</i>	Brassicaceae	<i>Vicia americana</i>	Fabaceae
<i>Symphoricarpos occidentalis</i>	Caprifoliaceae	<i>Vitis arizonica</i>	Vitaceae
<i>Symphyotrichum ascendens</i>	Asteraceae	<i>Xanthisma gracile</i>	Asteraceae
<i>Symphyotrichum foliaceum</i>	Asteraceae	<i>Zinnia acerosa</i>	Asteraceae
<i>Tetradymia axillaris</i>	Asteraceae	<i>Zygophyllum californicum</i>	Zygophyllaceae
<i>Thamnosma texana</i>	Rutaceae		
<i>Townsendia parryi</i>	Asteraceae		

Table S2.

Response	Predictor/parameter	Estimate	F	P-value	Adj-R²	λ
log(Growth)	Intercept	5.856	-	-	0.36	0.00
	Short-lived herbs	1.209	57.572	0.000	0.36	0.00
	Woody perennials	-0.151				
	log(NSC)	-0.074	1.275	0.260		
<hr/>						
Growth CV	Intercept	52.872	-	-	0.00	0.18
	Short-lived herbs	8.649	1.447	0.239	0.00	0.18
	Woody perennials	8.319				
	log(NSC)	1.149	0.170	0.681		
<hr/>						
log(Longevity)	Intercept	1.787	-	-	0.73	0.02
	Short-lived herbs	-1.619	276.279	0.000	0.73	0.02
	Woody perennials	0.587				
	log(NSC)	0.045	1.169	0.281		
<hr/>						
log(NSC)	Intercept	1.830	-	-	0.05	0.06
	Short-lived herbs	-0.009	0.076	0.927	0.05	0.06
	Woody perennials	0.073				
	Temperature	0.002	3.842	0.051		
	Precipitation	0.000	0.688	0.408		
<hr/>						
log(Growth)	Intercept	6.361	-	-	0.43	0.00
	Short-lived herbs	0.972	40.673	0.000	0.43	0.00
	Woody perennials	-0.329				
	log(NSC)	-0.151	5.579	0.019		
	Temperature	0.002	2.894	0.091		
	Precipitation	-0.001	5.907	0.016		
<hr/>						
Growth CV	Intercept	56.931	-	-	0.10	0.15
	Short-lived herbs	0.429	0.103	0.902	0.10	0.15
	Woody perennials	2.961				
	log(NSC)	-1.459	0.289	0.592		
	Temperature	0.095	6.218	0.014		
	Precipitation	-0.017	1.104	0.295		
<hr/>						
log(Longevity)	Intercept	1.721	-	-	0.74	0.00

	Short-lived herbs	-1.671				
	Woody perennials	0.551	261.086	0.000		
	log(NSC)	0.029	0.461	0.498		
	Temperature	0.001	1.449	0.230		
	Precipitation	0.000	0.000	0.989		
log(Growth)	Intercept	5.358	-	-	0.41	0.00
	Short-lived herbs	1.109	49.527	0.000		
	Woody perennials	-0.083				
	log(Starch)	-0.060	9.586	0.002		
	log(Fructans)	-0.056	5.170	0.024		
	log(Simple sugars)	0.282	11.718	0.001		
Growth CV	Intercept	57.301	-	-	-0.01	0.17
	Short-lived herbs	9.592	1.607	0.204		
	Woody perennials	8.102				
	log(Starch)	-0.095	0.013	0.911		
	log(Fructans)	0.432	0.082	0.775		
	log(Simple sugars)	-2.207	0.371	0.543		
log(Longevity)	Intercept	2.064	-	-	0.74	0.08
	Short-lived herbs	-1.557	246.746	0.000		
	Woody perennials	0.551				
	log(Starch)	0.017	1.668	0.198		
	log(Fructans)	0.043	7.099	0.008		
	log(Simple sugars)	-0.143	6.809	0.010		
log(Starch)	Intercept	-2.989	-	-	0.03	0.44
	Short-lived herbs	-0.444	0.555	0.575		
	Woody perennials	-0.278				
	Temperature	0.009	7.820	0.006		
	Precipitation	0.003	6.170	0.014		
log(Fructans)	Intercept	2.272	-	-	0.08	0.09
	Short-lived herbs	-0.705	2.367	0.096		
	Woody perennials	0.127				
	Temperature	-0.003	1.465	0.228		

	Precipitation	-0.005	15.868	0.000		
log(Simple sugars)	Intercept	1.342	-	-	0.03	0.31
	Short-lived herbs	0.213	3.387	0.036		
	Woody perennials	-0.187				
	Temperature	0.000	0.245	0.621		
	Precipitation	0.000	1.329	0.250		
log(Growth)	Intercept	6.092	-	-	0.41	0.00
	Short-lived herbs	0.972	40.075	0.000		
	Woody perennials	-0.341				
	Temperature	0.001	1.856	0.175		
	Precipitation	-0.001	5.157	0.024		
Growth CV	Intercept	54.537	-	-	0.11	0.16
	Short-lived herbs	-0.085	0.099	0.906		
	Woody perennials	2.813				
	Temperature	0.091	5.951	0.016		
	Precipitation	-0.017	1.092	0.298		
log(Longevity)	Intercept	1.774	-	-	0.74	0.00
	Short-lived herbs	-1.671				
	Woody perennials	0.553	262.102	0.000		
	Temperature	0.001	1.732	0.190		
	Precipitation	0.000	0.001	0.980		
log(Growth)	Intercept	5.651	-	-	0.48	0.00
	Short-lived herbs	0.844	31.736	0.000		
	Woody perennials	-0.275				
	log(Starch)	-0.073	15.371	0.000		
	log(Fructans)	-0.081	11.840	0.001		
	log(Simple sugars)	0.255	10.744	0.001		
	Temperature	0.002	4.491	0.035		
	Precipitation	-0.001	5.135	0.025		
Growth CV	Intercept	54.282	-	-	0.10	0.15
	Short-lived herbs	0.408	0.074	0.929		
	Woody perennials	2.523				

	log(Starch)	-0.679	0.667	0.415		
	log(Fructans)	-0.449	0.096	0.757		
	log(Simple sugars)	-1.556	0.203	0.653		
	Temperature	0.098	6.264	0.013		
	Precipitation	-0.016	0.906	0.343		
log(Longevity)	Intercept	1.96	-	-	0.74	0.05
	Short-lived herbs	-1.599	228.625	0.000		
	Woody perennials	0.530				
	log(Starch)	0.016	1.338	0.249		
	log(Fructans)	0.040	5.715	0.018		
	log(Simple sugars)	-0.138	6.370	0.012		
	Temperature	0.001	0.951	0.331		
	Precipitation	0.000	0.022	0.883		

Figure S1.

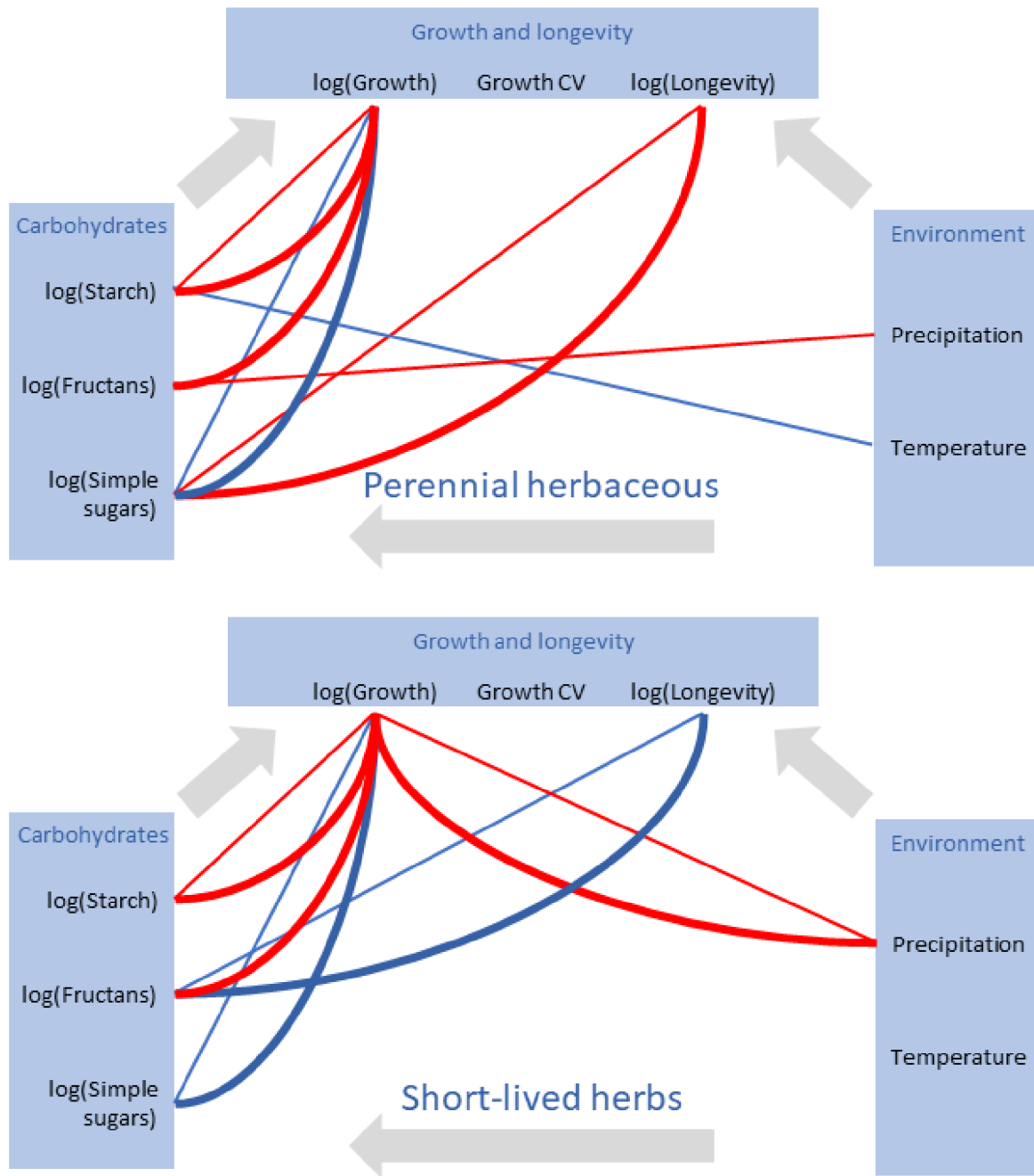


Figure S1: Links between environment, carbohydrates, and growth and longevity for herbaceous growth forms. Grey arrows show studied relationships. Red lines denote negative effect and blue lines positive effect. Curved lines are for analyses which take both carbohydrates and environmental variables into account. “log” stands for natural logarithm and “CV” stands for coefficient of variation.