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RESEARCH ARTICLE

# Impacts of global environmental change drivers on non-structural carbohydrates in terrestrial plants

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## Abstract

1. Non-structural carbohydrates (NSCs, including soluble sugars and starch) are essential to support the growth and survival of terrestrial plants. Starch and sugars play different roles in multiple plant ecological functions such as drought tolerance, growth and plant defence, and several other processes which are being rapidly shaped by global environmental change. However, it is uncertain whether soluble sugars and starch show different responses across plant functional types, tissue types and treatment conditions (i.e. the intensity and duration of environmental variability) to global-change drivers.
2. Here based on a database of 275 plants (including 17 plant functional types), we conducted a meta-analysis to examine the effects of elevated atmospheric $CO_2$ concentration ($eCO_2$), nitrogen (N) addition, drought and warming on NSCs and its components.
3. We found NSCs responses to global environmental change were mainly driven by (a) soluble sugar changes in response to N addition and drought, as well as (b) starch changes in response to $eCO_2$ and warming. The different responses between soluble sugars and starch were more evident under $eCO_2$ and drought, especially in herbs or leaves. Interactive effects of multiple environmental change drivers on soluble sugars and starch were mainly additive. The divergent main and interactive effects on soluble sugars and starch depend on experimental conditions. For example, the starch responses to $eCO_2$ and its interaction with N addition were the strongest in short-term experiments.
4. Overall, our study shows the divergent responses of soluble sugars and starch in terrestrial plants to different global environmental change drivers, suggesting a changed carbon sink–source balance in plants under future global changes. The findings also highlight that predicting plant functional changes into the future requires a mechanistic understanding of how NSCs and its components are linked to specific environmental change drivers.

KEYWORDS

$CO_2$, drought, nitrogen addition, non-structural carbohydrates, soluble sugars, starch, warming

  

## 1 | INTRODUCTION

Non-structural carbohydrates (NSCs) are crucial to fulfilling multiple functions in plants, including metabolism, transport, osmoregulation and export as substrates for soil organisms (Hartmann & Trumbore, 2016; Smith & Smith, 2011). NSCs are largely comprised of soluble sugars and starch, which have distinct ecological functions. Soluble sugars are mainly synthesized from newly assimilated carbon by daytime photosynthesis and translocated to different organs by mass flow (Kozlowski, 1992). They are crucial in metabolism, osmotic regulation, translocation of energy, signal transduction as well as synthesis of defence chemicals, such as monoterpene olefins (turpentine) and diterpene resin acids (rosin) (Chaves, Maroco, & Pereira, 2003; De Schepper, De Swaef, Bauweraerts, & Steppe, 2013; Hartmann & Trumbore, 2016; Plavcová & Jansen, 2015; Rolland, Baena-Gonzalez, & Sheen, 2006; Steele, Lewinsohn, & Croteau, 1995). Soluble sugars are converted to starch when carbon assimilation exceeds carbon demand for growth and maintenance (Chapin III, Schulze, & Mooney, 1990). The starch can be converted back to soluble sugars when carbon assimilation is insufficient to support metabolic activities (e.g. at night; Chapin III et al., 1990; Gibon et al., 2009; Sulpice et al., 2014). Starch is of great importance because its degradation can produce energy, sugars and metabolites to enhance plant resilience under stressful conditions (Thalmann & Santelia, 2017), and its synthesis can reserve carbon for future use and lower the concentration of soluble sugars, avoiding more respiratory consumption (Chapin III et al., 1990). In short, soluble sugars act as a short-term NSCs reserve for immediate functions and starch is mainly a long-term storage reserve (Dietze et al., 2014; Hartmann & Trumbore, 2016; Thalmann & Santelia, 2017).

Global rises in atmospheric $CO_2$ concentration, nitrogen (N) deposition rate, air temperature and drought occurrence have become the major external drivers for many recent changes in global patterns of plant growth and survival (Hughes, 2000; Parmesan & Yohe, 2003; Reich, Hobbie, & Lee, 2014; Xu et al., 2013). For example, the increasing atmospheric $CO_2$ concentration and N deposition have driven the enhancing vegetation growth and greenness over global land areas during the past three decades (Huang et al., 2018; Zhu et al., 2016), whereas climate warming and the associated drought have increased the rate of tree mortality at the global scale (McDowell & Allen, 2015). In order to cope with these environmental changes, plants need to develop different strategies to keep the carbon sink–source balance by adjusting the use of NSCs (Dietze et al., 2014; Körner, 2003). Thus, how NSCs and its components respond to these global-change factors is critical in determining the terrestrial carbon feedback to climate changes (Dietze et al., 2014; Hartmann & Trumbore, 2016; Martínez-Vilalta et al., 2016).

In the past decades, many new insights about NSCs' responses to environmental changes have been reported by experimental studies. Those experimental data have been synthesized by a few meta-analyses to explore general response patterns of NSCs to different global environmental change drivers. For example, Li et al. (2018) has synthesized data of 71 trees species and found more enhancement of starch than soluble sugars in leaves under $eCO_2$. However, the stimulation induced by $eCO_2$ is higher in soluble sugars than starch in a meta-analysis of 31 plant species, which include 7 gymnosperms and 24 angiosperms (8 woody and 16 herbaceous species; Zvereva & Kozlov, 2006). Starch is decreased more than soluble sugars in roots of trees under N addition (Li et al., 2018), but the contrary response pattern of a larger reduction in soluble sugars than starch has been reported under warming (Zvereva & Kozlov, 2006). It has been reported that soluble sugars are increased yet starch is decreased under drought in both leaves and roots of trees (Adams et al., 2017; Li et al., 2018).

However, it is uncertain whether the observed pattern is consistent between tissue types, plant functional types and experimental conditions such as treatment intensities and durations. The leaf is the productive organ in plants and has higher metabolic activities than roots and stems (Brüggemann et al., 2011). Sugars are loaded through lignified and suberized walls, which can be developed as a barrier to limit spread of sugars progressively (Jacobsen, Fisher, Maretzki, & Moore, 1992; Rae, Perroux, & Grof, 2005; Slewinski, 2012). Compared with woody plants, herbaceous plants have less lignified tissues. Hence, one can expect that soluble sugars and starch in leaves or herbaceous plants are more sensitive to environmental changes. Plants can quickly acclimate or adapt to global changes such as climate warming (Atkin & Tjoelker, 2003). Plants grown under $CO_2$ enhancement are limited by other resources in the long-term, such as N (Reich et al., 2014), but the consumption of NSCs is accelerated under long-term severe drought (e.g. McDowell, 2011). Thus, we further hypothesize that the responses of soluble sugars and starch could be stronger under short- than long-term treatment.

Different global change factors can interact with each other to affect NSCs and its two major components. For example, Huttunen, Saravesi, Markkola, and Niemelä (2013) has found that N addition can alleviate the positive effect of elevated $CO_2$ and the negative impact of warming on NSCs in *Betula pendula* respectively. Similarly, the combination of elevated $CO_2$ and temperature can mitigate the main positive effects of $CO_2$ enhancement and the negative effects of warming on starch in *Panicum maximum* (Habermann et al., 2019). Some other studies have reported that the negative impact of drought on NSCs can be alleviated by $CO_2$ enrichment or N addition but exacerbated by warming (Agami, Alamri, El-Mageed, Abousekken, & Hashem, 2018;Duan et al., 2013). However, it is uncertain whether these combined effects of global change drivers are additive or not. The additive interaction means the interactive impact of multiple drivers has no significant difference from the sum of individual impacts (Yue, Fornara, Yang, Peng, Peng, et al., 2017). To date, multiple meta-analyses have found that additive effects are dominant in plant C pool, N concentration, phosphorus (P) pool and C:N:P stoichiometry (Yuan & Chen, 2015; Yue, Fornara, Yang, Peng, Li, et al., 2017; Yue, Fornara, Yang, Peng, Peng, et al., 2017; Yue et al., 2018). Also, Li et al. (2018) have found that the interactions of $eCO_2$ with nitrogen or drought on NSCs and its components in trees are predominantly additive. Hence, we hypothesize

the additive interactions are dominant across various combinations of global-change factors. Also, few studies have explored whether these interactions are consistent across different durations of environmental changes. It limits our understanding of how global environmental changes affect carbon cycle in terrestrial ecosystems.

Here a comprehensive meta-analysis focusing on NSCs' responses to the primary global environmental change drivers, including $eCO_2$, N addition, drought and warming, was conducted based on 341 published studies (see Appendix S1). Our study aims to answer three specific questions, including (a) how soluble sugars and starch differently respond to global-change drivers?; (b) how their responses vary with plant functional type, tissue type and experimental conditions; and (c) whether and how different environmental change drivers interact to impact NSCs and its components?

## 2 | MATERIALS AND METHODS

### 2.1 | Data compilation

Peer-reviewed journal articles reporting NSCs and its components in response to multiple environmental change drivers (i.e. elevated $CO_2$, nitrogen addition, drought and warming) were searched in Web of Science and Google Scholar. The search term combinations were as follows: (non-structural carbohydrates or nonstructural carbohydrates or soluble sugar or starch) and (nitrogen or $CO_2$ or temperature or warming or drought or water) and (plant or production or productivity or biomass or mass). Moreover, we set the following criteria to minimize the potential uncertainties and select proper observations: (a) experimental duration and magnitude were clearly indicated; (b) full-factorial design was used to examine interactive effects of multiple global change factors; (c) the means, standard deviations/errors and samples sizes of the selected variables in both of the control and experimental groups could be extracted directly from text, tables or figures using GetData Graph Digitizer 2.24 (http://getdata-graph-digitizer.com/). For studies with multiple levels of experimental treatments, multiple measurements in time, multiple plant species and plant parts, they were considered as multiple independent observations. Overall, 341 articles published before March 2019 were compiled into the literature database (see Appendix S1). It should be noted that there are six studies to use plants grown at alpine or boreal system, but they did not impact the response patterns of NSCs and its components to experimental warming.

To further assess the main and interactive effects of multiple environmental change drivers on NSCs and its components, relevant experimental information was complied. In our database, plants were divided into several groups based on growth forms (woody and herbaceous plants, or tree, shrub, grass and forb), life history (annual, biennial and perennial herb; the results of biennial plants were not shown in results because of limited data), photosynthetic pathways ($C_3$, $C_4$ and CAM herbs) and other functional types (broadleaved and coniferous trees, evergreen and deciduous trees or legume and non-legume). In order to detect responses of NSCs and its components to different treatment intensities, we grouped them into three categories: 'low intensity', 'moderate intensity' and 'high intensity'. For example, according to enhanced magnitude, elevated $CO_2$ concentration experiments could be divided into low (≤300 p.p.m.), moderate (>300 and ≤600 p.p.m.) and high (>600 p.p.m.) intensity. For N addition experiments, they were classified into low (≤200%), moderate (>200% and ≤400%) and high (>400%) intensities based on comparison of N addition amount between experimental and control groups within a given study (Li et al., 2018). However, for remaining experiments where control groups were not fertilized with nitrogen, they were grouped into low (<50 kg N/ha), moderate (≥50 and <150 kg N/ha) and high (≥150 kg N/ha) intensities. Among studies, experimental drought decreased water by 14%–100%, which could be classified into low (<50%), moderate (≥50% and <70%) and high (≥70%) intensity. Warming experiments were grouped as low (≤3°C), moderate (>3°C and ≤6°C) and high (>6°C) intensity based on warming magnitude. The studies were conducted in greenhouse, growth chamber, pot, Free-Air $CO_2$ Enrichment (FACE) and natural habitats. Hence, we grouped them into laboratory conditions (greenhouse, growth chamber, pot) and field conditions (FACE and natural habitats; Xu, Yan, & Xia, 2019).

### 2.2 | Data analysis

Owing to differences in quantification methods, NSCs cannot be compared directly among laboratories (Landhäusser et al., 2018; Quentin et al., 2015). However, relative changes of NSCs between experimental and control groups are comparable among studies (Adams et al., 2017; Li et al., 2018; Liu et al., 2016). Hence, we calculated the natural logarithm of the response ratio (ln RR) and Hedges' *d* to measure the responses of NSCs and its components to individual and interactive environmental change drivers respectively (Hedges, Gurevitch, & Curtis, 1999). The ln RR and Hedges' *d* can both reflect the relative changes of variables. For these test statistics, a value larger than zero represents a positive treatment effect, while a value less than zero represents a negative treatment effect on NSCs and its components. The RR is defined as the ratio of the mean of NSCs and its components in the experimental group ($X_e$) to that in control group ($X_c$). The log transformation was to improve statistical behaviour (Equation 1):

$$\ln \mathrm{RR} = \ln\left(\frac{X_e}{X_c}\right). \quad (1)$$

The variance ($v_1$) was estimated by Equation 2:

$$v_1 = \frac{S_e^2}{N_e X_e^2} + \frac{S_c^2}{N_c X_c^2}, \quad (2)$$

where $S_e$ and $S_c$ are standard deviations of NSCs and its components in the experimental and control group respectively. $N_e$ and $N_c$ represent sample size in the corresponding groups. The reciprocal of the variance ($v_1$) was considered as the weight ($w_1$) of each ln RR (Equation 3).

A nonparametric weighting function was used to calculate mean effect size because some studies include two or more observations (Hedges et al., 1999; Li et al., 2018; Liu et al., 2016). The $w_1'$ is the average of the $w_1$ over the total number of observations ($n$) in a study (Equation 4). Then, a fixed-effect model (Equation 5) was conducted to calculate the mean effect size and generate 95% confidence interval in MetaWin 2.1 (Rosenberg, Adams, & Gurevitch, 2000):

$$w_1 = \frac{1}{v_1}, \tag{3}$$

$$w_1' = \frac{w_1}{n}, \tag{4}$$

$$\overline{\ln RR} = \frac{\sum_i w_i' \times \ln RR_i}{\sum_i w_i'}, \tag{5}$$

where $w_i'$ represents the weight of the $i$th study. The main influence on NSCs and its components was evaluated as significant if the 95% confidence intervals (95% CI) did not overlap with zero. A resampling bootstrapping method based on 9,999 iterations was used if the sample size was lower than 20.

Furthermore, a random-effect model was used to compare heterogeneity of NSCs and its components within ($Q_w$) and between ($Q_b$) categories (i.e. different plant functional types, tissue types, experimental intensities and approaches; Borenstein, Hedges, Higgins, & Rothstein, 2009; Li et al., 2018). The random-effect model assumes the effect size is different among studies and considers the variance of each effect size as a sum of within-study variance and between-study variance (Borenstein, Hedges, Higgins, & Rothstein, 2010). A significant between-group heterogeneity ($Q_b$) suggested that the effect size differed among categories (Hedges et al., 1999). The meta-regression considered different weights of NSCs and is components (Thompson & Higgins, 2002). It was used to explore the relationship between NSCs and its components as well as the relationship between soluble sugars or starch and experimental duration. The meta-regression was conducted with the METAFOR package in R 3.4 (R Development Core Team, 2016). The difference in regression slope was examined in SPSS 23.0 (SPSS). The relative contribution of changes in soluble sugars or starch to NSCs responses was analysed using the RELAIMPO package in R.

Hedges' $d$ is an estimate of the standardized mean difference not biased by small sample sizes (Gurevitch & Hedges, 2001). Thus, we employed Hedges' $d$ to calculate interactive effects for each study according to the method of Crain, Kroeker, and Halpern (2008). For a study with two factors (A and B), main effect of factor A ($d_A$), main effect of factor B ($d_B$) and interactive effect ($d_I$) were calculated as following Equations 6–8:

$$d_A = \frac{(X_{AB} + X_A) - (X_C + X_B)}{2s} J(m), \tag{6}$$

$$d_B = \frac{(X_{AB} + X_B) - (X_C + X_A)}{2s} J(m), \tag{7}$$

$$d_I = \frac{(X_{AB} + X_C) - (X_A + X_B)}{2s} J(m), \tag{8}$$

where $X_C$ is the mean value in the control group, and $X_A$, $X_B$ and $X_{AB}$ are mean values in the experimental groups of A, B and their combination (A and B). $J(m)$ and $s$ represent correction term for small sample bias and pooled standard deviation respectively (Hedges & Olkin, 1985), which were estimated by the following Equations 9 and 10, respectively:

$$J(m) = 1 - \frac{3}{4m - 1}, \tag{9}$$

$$s = \sqrt{\frac{(n_C - 1)s_C^2 + (n_A - 1)s_A^2 + (n_B - 1)s_B^2 + (n_{AB} - 1)s_{AB}^2}{n_C + n_A + n_B + n_{AB} - 4}}, \tag{10}$$

where $m$ is the degree of freedom ($m = n_C + n_A + n_B + n_{AB} - 4$), $n_C$, $n_A$, $n_B$ and $n_{AB}$ are the sample sizes, and $s_C$, $s_A$, $s_B$ and $s_{AB}$ are the standard deviations in the corresponding groups. The variance of $d_I(v_2)$ was calculated by Equation 11:

$$v_2 = \frac{1}{4}\left[\frac{1}{n_C} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_I^2}{2(n_C + n_A + n_B + n_{AB})}\right]. \tag{11}$$

The weight ($w_2$) can be calculated as reciprocal of variance ($v_2$). Likewise, it can be adjusted by the total number of observations per study ($n$) to calculate $w_2'$ (Li et al., 2018):

$$w_2 = \frac{1}{v_2}, \tag{12}$$

$$w_2' = \frac{w_2}{n}. \tag{13}$$

The mean $d_I(d_{++})$ and standard error $[s(d_{++})]$ were estimated by Equations 14 and 15, respectively.

$$d_{++} = \frac{\sum_{i=1}^{I}\sum_{j=1}^{k} w_{ij}' d_{ij}}{\sum_{i=1}^{I}\sum_{j=1}^{k} w_{ij}'}, \tag{14}$$

$$s(d_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{I}\sum_{j=1}^{k} w_{ij}'}}, \tag{15}$$

where $I$ is the number of groups, $k$ is the number of comparisons in the $i$th group. The 95% CI of $d_{++}$ was estimated as $d_{++} \pm C_{\partial/2} \times s(d_{++})$, where $C_{\partial/2}$ is the two-tailed critical value of the standard normal distribution. If the sample size was lower than 20, a bootstrapping method based on 9,999 iterations was used.

The interactive effect between two environmental change drivers was classified as additive, synergistic or antagonistic (Crain et al., 2008). If the 95% confidence interval (CI) overlapped with zero, then their interactive impact was additive. For the non-additive interactions (synergistic or antagonistic), there were three cases: (a) For two-driver pairs whose individual impacts were both

negative, then their interactive impacts lower than zero was synergistic and greater than zero was antagonistic. (b) In cases where the individual effects were both positive, their interactive impact greater than zero was synergistic and lower than zero was antagonistic. (c) If the individual main impact was negative for one driver but positive for the other driver, the type of interactive effect was jointly determined by the arithmetic sum of the two individual main impacts and the calculated interactive effect by Equation 8 (Zhou et al., 2016). If the arithmetic sum of the two drivers' main effects (e.g. 0.56 for the $eCO_2$ × warming on sugars) and their interactive effect (e.g. 0.36 for the $eCO_2$ × warming on sugars) were both positive or negative, then their interactive effect was defined as synergistic. Otherwise, the interactive effect was defined as antagonistic.

## 3 | RESULTS

### 3.1 | Main effects of global change drivers on NSCs and its components

Elevated $CO_2$ concentration significantly increased NSCs (+27.8%), soluble sugars (+22.2%) and starch (+43.8%), and the enhancement of starch was nearly two times as large as that of soluble sugars. Nitrogen addition induced significant increases in NSCs (+4.1%), soluble sugars (+6.0%) and starch (+1.2%). NSCs (−4.1%) and starch (−8.5%) were significantly reduced under drought, yet soluble sugars were increased by 4.5%. Warming significantly reduced NSCs (−8.7%), soluble sugars (−7.0%) and starch (−10.2%; Figure 1a).

We further examined the relative impacts of soluble sugars and starch on the total NSCs in response to global-change drivers. The response ratio of NSCs exhibited positive correlations with response ratio of soluble sugars or starch under four different environmental changes (Figure 2). As shown by the difference in correlation slopes in Figure 2, the changes in response of NSCs to N addition and drought were more sensitive to that of soluble sugars than starch (both $p < 0.01$). Moreover, the relative contribution analysis showed that NSCs were mainly driven by soluble sugars under N addition (52%) and drought (76%), but by starch under $eCO_2$ (57%) and warming (92%; Figure 2).

Stronger enhancement of starch than soluble sugars under $eCO_2$ was found in woody and herbaceous plants as well as most plant functional types (Figure 3a; Table S1). Under N addition, starch was increased more than soluble sugars in woody plants, whereas it was contrary to herbaceous plants. The different responses between soluble sugars and starch were found in broadleaved trees, forbs and annual herbs under N addition (Figure 3b; Table S1). The drought-induced different response between soluble sugars and starch was common except for conifers, deciduous trees and CAM herbs (Figure 3c; Table S1). Severe reduction of starch than soluble sugars under warming was found mainly in herbaceous species, such as forbs, perennial herbs, $C_3$ herbs (Figure 3d; Table S1).

Moreover, the responses of soluble sugars and starch under environmental changes varied with tissue types (Figure 4). Soluble sugars and starch were stimulated most in leaves under $eCO_2$. The significant difference between soluble sugars and starch was found in leaves and roots of woody plants as well as leaves and stems of herbaceous plants (Figure 4; Table S2). In woody plants, soluble sugars and starch were decreased in leaves (−9.2%) and roots (−19.9%) under N addition. In herbaceous plants, soluble sugars (+4.3%) were increased but starch (−28.4%) was decreased in leaves under N addition. Then the different response between starch and soluble sugars was only found in herbaceous leaves (Figure 4; Table S2). In leaves of woody plants and roots of herbaceous plants, soluble sugars were increased and starch was decreased under drought. Drought resulted in different responses between soluble sugars and starch in leaves and roots (Figure 4; Table S2). Decrease of soluble sugars was found in leaves and stems of woody plants and leaves and roots of herbaceous plants under warming. However, decrease of starch was only found in leaves of woody and herbaceous species. The different response between soluble sugars and starch was significant in the leaves of herbs (Figure 4; Table S2).

Soluble sugars (+27.2%) and starch (+53.8%) were enhanced most under moderate and low $eCO_2$ treatment respectively. The different response between soluble sugars and starch disappeared under high $eCO_2$ treatment (Figure 5a; Table S2). Soluble sugars (+19.7%) and starch (+2.1%) were increased under low N addition treatment. No significant difference between soluble sugars and starch was observed under N addition (Figure 5b; Table S2). Soluble sugars (+14.8%) were stimulated most under high drought treatment, yet starch (−24.3%) was decreased most under high drought treatment. The different response between them was found across the three intensities (Figure 5c; Table S2). Soluble sugars and starch were significantly decreased across the three intensities of warming,

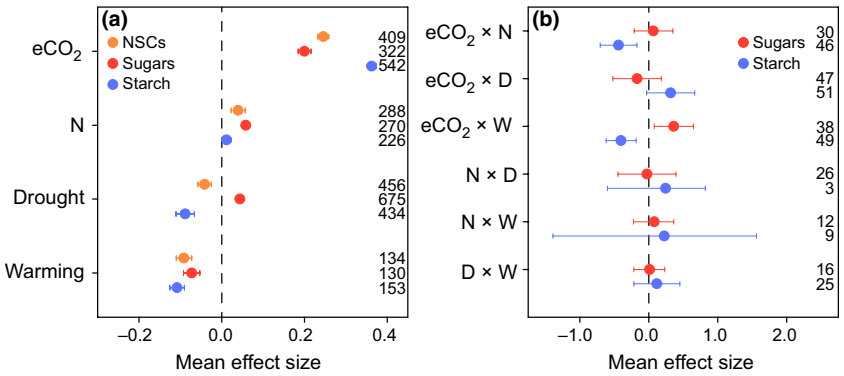


**FIGURE 1** Mean effect size of non-structural carbohydrates (NSCs), soluble sugar (sugars) and starch under individual (a) and interactive (b) effects of multiple global change drivers. The error bars indicated the 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The sample size for each variable is shown in the right column of the figure

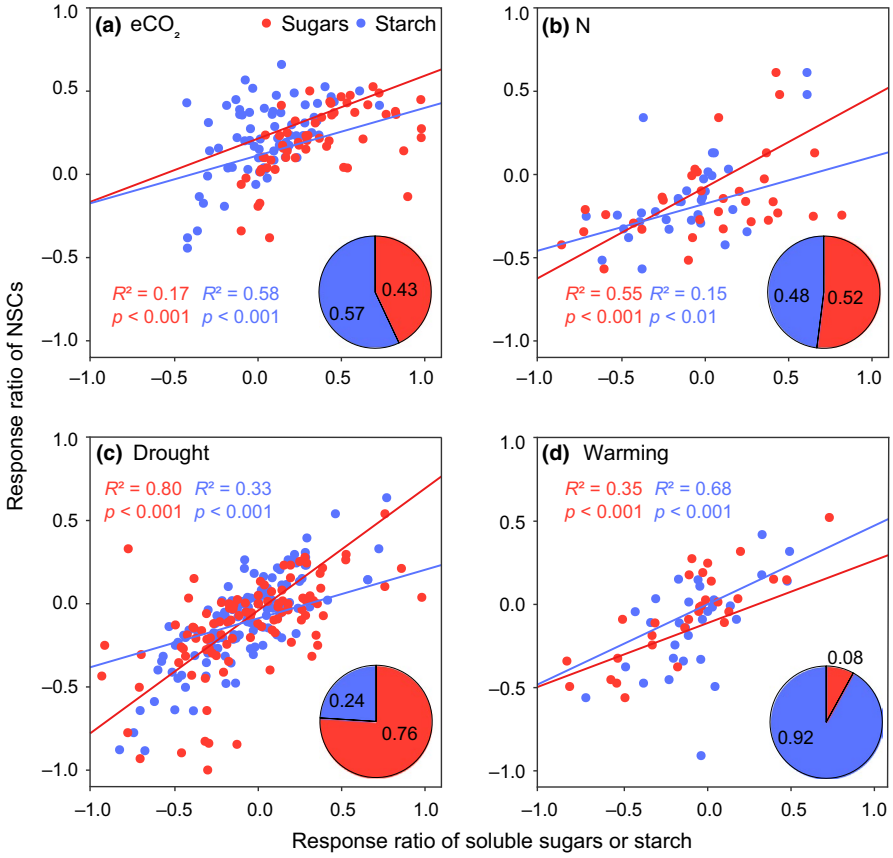


**FIGURE 2** Correlations of response ratio of NSCs with response ratios of its components (soluble sugars and starch) under (a) $eCO_2$, (b) N addition, (c) drought and (d) warming. The pies represent the relative contributions of response ratios of soluble sugar and starch to responses ratio of NSCs. Points represent single pairs of data

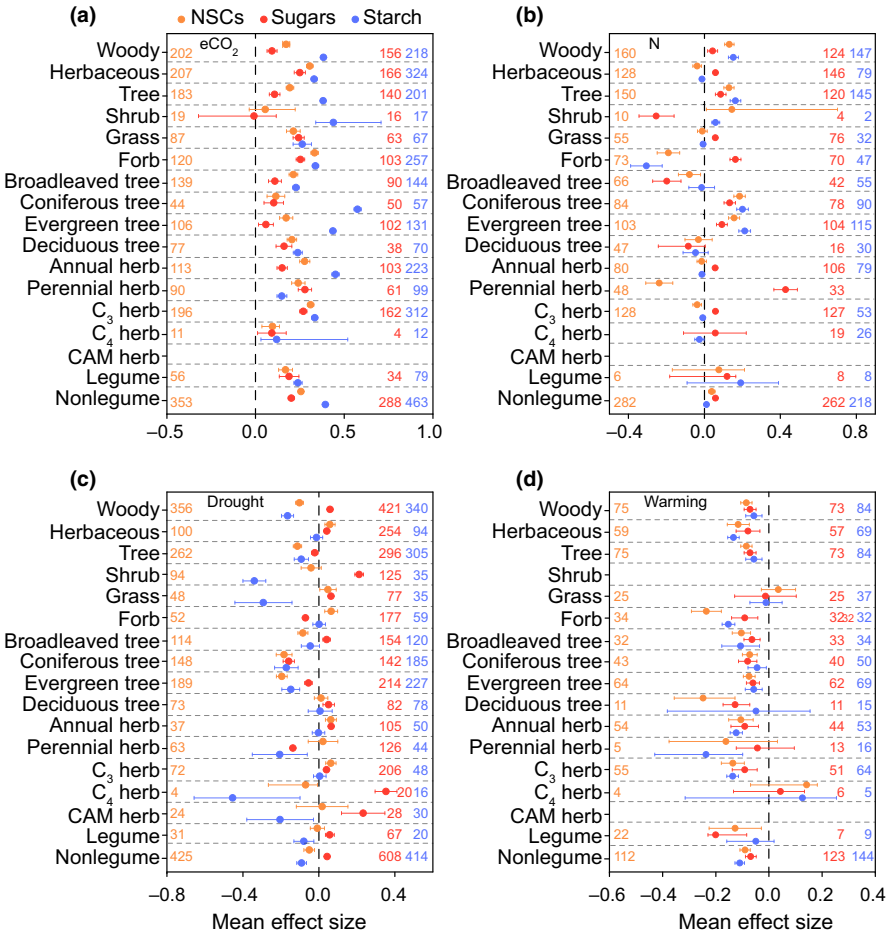


**FIGURE 3** Mean effect size of NSCs, soluble sugars and starch in different plant functional types under elevated $CO_2$ (a), N addition (b), drought (c) and warming (d). The error bars indicated 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The sample size for each variable is shown in the same colour in the left and right column of the figure

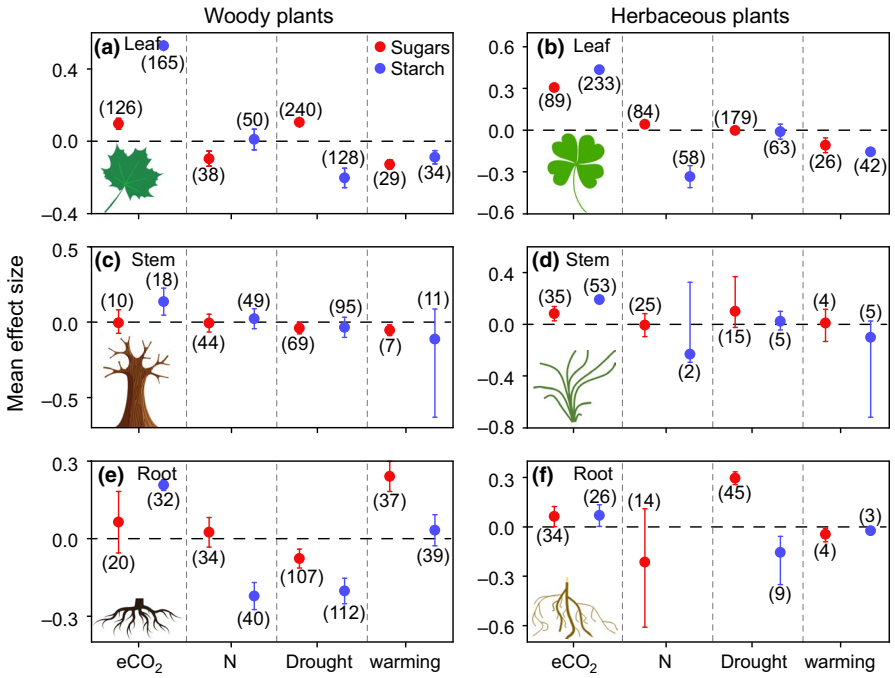


**FIGURE 4** Mean effect size of soluble sugars and starch in woody (a, c, e) and herbaceous (b, d, f) tissues (i.e. leaves, stems and roots). If the confidence interval did not overlap with zero, a response was considered to be significant. The sample size for each variable is shown near the dots

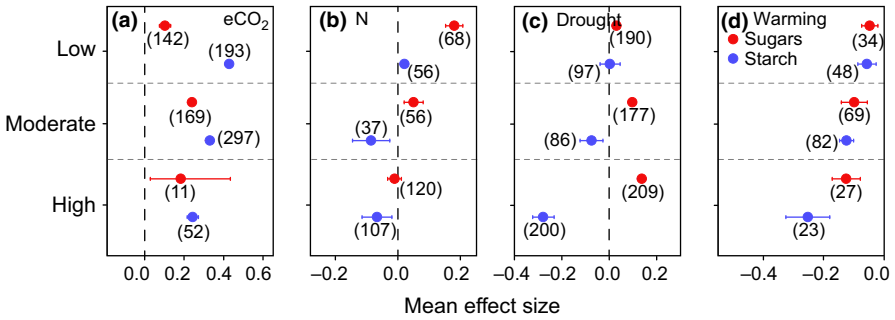


**FIGURE 5** Mean effect size of soluble sugars and starch categorized by experimental intensities (i.e. low, moderate and high) under elevated $CO_2$ (a), N addition (b), drought (c) and warming (d). If the confidence interval did not overlap with zero, a response was considered to be significant. The sample size for each variable is shown near the dots

especially under high warming treatment. Low or high warming treatment induced a significant difference between soluble sugars and starch (Figure 5d; Table S2).

The increases of starch under $eCO_2$ and soluble sugars under drought decreased with the experimental duration (Figure S3). However, under N addition and warming, the effect size was independent of the experimental duration. The difference between soluble sugars and starch was found in both the field and laboratory conditions under $eCO_2$ and drought. However, it was significant only under field warming and insignificant under either natural or laboratory N addition experiment (Figure S5). Moreover, the response ratio of soluble sugars or starch was irrelative to mean annual temperature (Figure S6).

### 3.2 | Interactive effects of environmental change drivers on soluble sugars and starch

The interactive effects of $eCO_2$ with drought, N with drought, N with warming as well as drought with warming were all additive (Figure 1b). The mean effect size of soluble sugars (0.36) was greater than zero under $eCO_2$ with warming. The sum of main effects of $eCO_2$ and warming (0.56) on soluble sugars was larger than zero. Hence, their interactive effect was synergistic (Figure 1b; Figure S2). The mean effect size of starch was lower than zero under $eCO_2$ with N addition (−0.44) or $eCO_2$ with warming (−0.40). However, the sum of main effects of $eCO_2$ and N addition (0.52) or $eCO_2$ and warming (0.78) on starch was larger than zero. Hence, their interactive effects were both antagonistic (Figure 1b; Figure S2).

The interactive effects of $eCO_2$ with drought, $eCO_2$ with warming, nitrogen with drought and nitrogen with warming were unrelated to experimental duration. However, the interactive effect of $eCO_2$ with N addition and drought with warming on starch showed a positive and negative relationship with experimental duration respectively (both $p < 0.01$; Figure S4).

## 4 | DISCUSSION

### 4.1 | Main effects of environmental change factors on NSCs and its components

Our study found that soluble sugars and starch reacted differently under four environmental changes. For example, starch was stimulated more than soluble sugars under $eCO_2$, especially in leaves

(Figure 4). It is in accordance with results of Li et al. (2018), which has found $eCO_2$ increased starch and soluble sugars in leaves of trees by 125.3% and 20.5% respectively. Although leaf stomatal conductance is lowered under $eCO_2$ (Medlyn et al., 2011), the rate of carbon assimilation is still increased (Delucia, Sasek, & Strain, 1985; Long & Drake, 1992; Moore, Palmquist, & Seemann, 1997). Soluble sugars have higher metabolic activities and excessive sugars in the cytoplasm cause higher respiration rates and declined growth (Chapin III et al., 1990; Schulze, Stitt, Schulze, Neuhaus, & Fichtner, 1991). Moreover, cells with high sugar concentration are susceptible to osmotic dehydration (Ahmed, Qazi, & Jamal, 2016). In contrast, respiration is less affected by starch than sugars under $eCO_2$ because starch is insoluble and a long-term storage compound which is not readily available to participate in plant metabolic processes (Chapin III et al., 1990; Hoch, Richter, & Körner, 2003). We also found more enhancement of starch than soluble sugars across the three treatment intensities under $CO_2$ enhancement. However, starch was enhanced most under low or short-term $CO_2$ enhancement treatment (Figure 5a; Figure S3a). It suggests this stimulation is not persistent and limited by other factors, such as, N (Reich et al., 2014).

It has been suggested that the NSCs were significantly decreased in trees and herbs under N addition (Liu et al., 2016; Figure 4). Also, our meta-analysis found that starch decreased by 15.2% in the roots of trees under N addition. N addition commonly increases leaf photosynthesis and plant growth (Hyvonen et al., 2007; Lambers, Chapin III, & Pons, 2008; Nakaji, Fukami, Dokiya, & Izuta, 2001; Xia & Wan, 2008). For example, Xia and Wan (2008) have found that biomass and N concentration in plants are commonly increased by N addition. This increase in N concentration could be expected to be correlated with greater leaf respiration, based on the large-scale leaf-trait coordination. Hence, the consumption of stored starch could be enhanced to meet the increased carbohydrates demand for maintaining respiratory activities. Also, starch was significantly decreased under moderate or high N addition, which may arise from the elevated stimulation on root respiration and biomass along N addition gradients (Figure 4e; Li et al., 2015).

Our study detected that starch was significantly reduced, but soluble sugars were increased under drought (Figure 1a), consistent with the results of a recent data synthesis (Adams et al., 2017). It can occur by interconversion between soluble sugars and starch to meet osmoregulatory and metabolic demands of plants (McDowell, 2011). However, starch was not decreased and the NSCs were increased in herbs (Figure 3). Compared with woody species, herbaceous plants, especially herbaceous angiosperms, have similar abilities to avoid drought-induced embolism (Lens et al., 2016). Furthermore, herbaceous plants have more strategies to cope with water deficit (Volaire, 2018). For example, annual herbs with short growing seasons can end growth to escape water deficit (Kooyers, 2015). Herbs can coordinate plasticity of xylem to maintain hydraulic safety, such as, sunflowers (Cardoso, Brodribb, Lucani, DaMatta, & McAdam, 2018). Hence, herbaceous species are more tolerant to drought (Volaire, 2018). The discrepant utilization strategies of soluble sugars and starch were found in leaves and roots (Figure 4). These two organs are especially sensitive to water availability and more starch will be converted into sugars in order to repair embolism and avoid catastrophic xylem failure (Sala, Woodruff, & Meinzer, 2012). Owing to stronger inhibition of photosynthesis under severe drought, the enhancement of soluble sugars disappeared, and starch was severely depleted in the long-term (Martínez-Vilalta et al., 2016; McDowell, 2011).

Warming-induced reductions of soluble sugars and starch in plants were common (Zvereva & Kozlov, 2006; Figures 1 and 3). It has been reported that rising temperature stimulates sucrose phosphate synthase (Dai et al., 2015; Hussain, Allen, & Bowes, 1999; Stitt & Grosse, 1988) and the starch-consuming α-amylase (Yamakawa, Hirose, Kuroda, & Yamaguchi, 2007). However, the activity of several enzymes involved in starch biosynthesis is reduced by warming (Hurkman et al., 2003; Jiang, Dian, & Wu, 2003; Wilhelm, Mullen, Keeling, & Singletary, 1999; Yamakawa et al., 2007). Furthermore, climate warming at night leads to a greater depletion of starch which can even in turn accelerate the accumulation of soluble sugars in the following day with enhanced leaf photosynthesis (Turnbull, Murthy, & Griffin, 2002; Turnbull et al., 2004; Wan, Xia, Liu, & Niu, 2009). Warming accelerates starch remobilization to provide energy for other activities and tissues (Thalmann & Santelia, 2017). Moreover, the positive response of respiration is enlarged with enhancing warming intensity (Liang, Xia, Liu, & Wan, 2013). Hence, starch was reduced most under high warming treatment (Figure 5). Effects of warming on plants are different among climate types, and different response between soluble sugars and starch was only found under field warming (Figure S5). It may because laboratory experiments have benign conditions for plant growth, such as temperature, water and nutrients (Poorter et al., 2016). However, response ratio of soluble sugars ($p = 0.63$) or starch ($p = 0.92$) was irrelative to mean annual temperature (Figure S6). The different functions performed by soluble sugars under drought (osmoregulation and metabolism mainly) and warming (metabolism mainly) explain discrepant relative contribution of response ratio of soluble sugars to response ratio of NSCs (Figure 2).

## 4.2 | Interactive effects of environmental change drivers on soluble sugars and starch

In our study, we found that additive effects on soluble sugars and starch were common between different global-change factors (Figure 1b). It is in accordance with the findings of Li et al. (2018). $CO_2$ enhancement and N addition significantly increased and decreased starch respectively (Figure S2). However, the interaction of $eCO_2$ with N addition reduced starch, suggesting that N is critical in limiting the positive impact of $eCO_2$ on starch accumulation (Wong, 1990). Considering starch is a long-term storage to support plant growth, such N limitation might be an important driver of the widely reported progressive N limitation on canopy growth and ecosystem productivity under $eCO_2$ (e.g. Luo et al., 2004; Norby, Warren, Iversen, Medlyn, & McMurtrie, 2010; Reich et al., 2014). The significant increase of soluble sugars and decrease of starch under $eCO_2$ with warming could result from more C allocation to

immediate metabolism (mainly respiration and growth; Hussain et al., 1999; Liang et al., 2013) or decreased photosynthetic carbon accumulation under higher temperature (Aranjuelo, Irigoyen, Sánchez-Díaz, & Nogués, 2008). The antagonistic effects of $eCO_2$ with N addition and the additive effects of drought with warming showed significant relationships with experimental duration (Figure S4a,f). It implies these interactions may be changed in the long term.

## 5 | CONCLUSIONS

Our study quantifies the main and interactive effects of multiple environmental change factors on NSCs and its components. It reveals that (a) dynamics of NSCs are driven by starch under $eCO_2$ and warming, but by soluble sugars under N addition and drought; (b) Antagonistic interactions of $eCO_2$ with N addition and $eCO_2$ with warming on starch were found. Synergistic interaction of $eCO_2$ with warming was found on soluble sugars; (c) Responses of soluble sugars and starch are closely related to plant functional types, tissue types and experimental conditions (i.e. treatment intensities, durations and approaches). Although additive interactions are dominant across two-pair drivers, it should be noted that experiments including interactions among three or more factors are still scarce. The discrepant responses of soluble sugars and starch under varying environmental conditions indicate that their different ecological functions need to be considered in canopy photosynthesis models (Dietze et al., 2014; Richardson et al., 2015). Thus, the consideration of NSCs' dynamics in vegetation models could be important under future global environmental changes, especially with the increasing frequency and intensity of extreme climate events such as heat waves and drought which will drastically alter the dynamics of NSCs in plants (Hansen, Sato, & Ruedy, 2012; Meehl & Tebaldi, 2004; Shi, Kloog, Zanobetti, Liu, & Schwartz, 2015).

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### AUTHORS' CONTRIBUTIONS

J.X. designed the study and Y.D. conducted the analysis; R.L. contributed to the data collection and discussion of results; J.X. and Y.D. wrote the manuscript. The authors declare no competing financial interests.

### DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.j6q573n9n (Du, Lu, & Xia, 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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