Research paper

The sweet side of global change—dynamic responses of non-structural carbohydrates to drought, elevated CO$_2$ and nitrogen fertilization in tree species

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Non-structural carbohydrates (NSC) play a central role in plant functioning as energy carriers and building blocks for primary and secondary metabolism. Many studies have investigated how environmental and anthropogenic changes, like increasingly frequent and severe drought episodes, elevated CO$_2$ and atmospheric nitrogen (N) deposition, influence NSC concentrations in individual trees. However, this wealth of data has not been analyzed yet to identify general trends using a common statistical framework. A thorough understanding of tree responses to global change is required for making realistic predictions of vegetation dynamics. Here we compiled data from 57 experimental studies on 71 tree species and conducted a meta-analysis to evaluate general responses of stored soluble sugars, starch and total NSC (soluble sugars + starch) concentrations in different tree organs (foliage, above-ground wood and roots) to drought, elevated CO$_2$ and N deposition. We found that drought significantly decreased total NSC in roots (−17.3%), but not in foliage and above-ground woody tissues (bole, branch, stem and/or twig). Elevated CO$_2$ significantly increased total NSC in foliage (+26.2%) and roots (+12.8%), but not in above-ground wood. By contrast, total NSC significantly decreased in roots (−17.9%), increased in above-ground wood (+6.1%), but was unaffected in foliage from N fertilization. In addition, the response of NSC to three global change drivers was strongly affected by tree taxonomic type, leaf habit, tree age and treatment intensity. Our results pave the way for a better understanding of general tree function responses to drought, elevated CO$_2$ and N fertilization. The existing data also reveal that more long-term studies on mature trees that allow testing interactions between these factors are urgently needed to provide a basis for forecasting tree responses to environmental change at the global scale.

Keywords: above-ground woody biomass, foliage, global change, meta-analysis, non-structural carbohydrates, roots.

Introduction

During past decades global environmental change in the form of modified precipitation patterns, elevated temperature, increasing atmospheric CO$_2$ concentrations and nitrogen (N) deposition (IPCC 2012, Fowler et al. 2013) has strongly affected ecosystem functioning and global biogeochemical processes (Reichstein et al. 2013, Bahn et al. 2014, Ciais et al. 2014). Elevated temperature in combination with modified precipitation patterns also caused an increase in intensity, duration and frequency of droughts (Williams et al. 2013), while increased atmospheric CO$_2$ concentration and atmospheric N fertilization together are expected to further affect plant physiology and ecosystem functioning.

These effects include shifts in primary productivity (Melillo et al. 1993, Ciais et al. 2005, Reay et al. 2008, Reichstein et al. 2013), phenology (Parmesan and Yohe 2003), carbon (C) and water budgets (Mystakidis et al. 2016), and plant distribution and mortality (Walther et al. 2002, Allen et al. 2010).

Non-structural carbohydrates (NSC, mainly soluble sugars and starch) are the main substrate for all plant functional processes of primary and secondary metabolism (Hartmann and Trumbore 2016). Simple sugars produced during photosynthesis in foliage and converted to starch during daytime (when supply exceeds demand) are hydrolyzed back into soluble sugars during the night (when demand is larger than supply) to support growth and other metabolic processes (Göttlicher et al. 2006, Gibon et al. 2009). New photosynthetic products are also exported from leaves to other organs (e.g., stems, roots) to support metabolism and bio-mass production (Rennie and Turgeon 2009, De Schepper et al. 2013), and may be allocated to rhizosphere bacteria or mycorrhizal fungi in exchange for mineral nutrients and between neighboring trees (Smith and Smith 2011, Klein et al. 2016). In addition, both soluble sugars and hydrolyzed starch could serve as source of compatible solutes for osmoregulation to maintain whole-plant hydration during drought (Sala et al. 2012).

Apart from direct usage for metabolism and growth, NSC are also stored in tree tissues, potentially for years (Carbone et al. 2013, Richardson et al. 2015, Muhr et al. 2016). It is still a lively debate whether NSC storage is merely an accumulation of excess C during periods when growth is impaired, or results from reserve formation that downregulates C sinks when supply is insufficient to fuel all sinks (Chapin et al. 1990, Sala et al. 2012, Wiley and Helliker 2012, Palacio et al. 2014, Hartmann and Trumbore 2016). Stored NSC can act as a buffer during periods when C supply is smaller than demand, like during nighttime when plants do not photosynthesize but still grow (Augusto et al. 2002) or during springtime growth before leaves have developed in deciduous species. Non-structural carbohydrate storage may also be mobilized and used by trees to support metabolic activity for survival when C assimilation is insufficient to meet demand like during extended droughts (McDowell et al. 2008, McDowell 2011). Hence, the mobilization and use of stored carbohydrates can buffer asynchrony of substrate supply and demand across a range of timescales at the whole-tree level and play a critical role in plant survival, particularly under environmental stress (Galiano et al. 2011, Wiley and Helliker 2012, Hartmann et al. 2013, Dietze et al. 2014, O'Brien et al. 2014).

Drought, elevated CO_2 and N fertilization can strongly impact NSC storage in trees via impacts on photosynthetic rates and C demand for growth (Reich et al. 1998, McDowell et al. 2008, Chaves et al. 2009, Ellsworth et al. 2012, Zhang et al. 2018). Both water and CO_2 are the primary raw material for photosynthesis, and drought as well as higher atmospheric CO_2 concentration can reduce the stomatal aperture (Medlyn et al. 2001, Bréda et al. 2006), which in turn alters leaf CO_2 concentrations

and thus changes C assimilation rates (Farquhar and Sharkey 1982, Ellsworth et al. 2015). Similarly, the photosynthetic capacity of trees is directly related to leaf N content because proteins of the photosystems represent the majority of leaf N (Evans 1989). Drought affects plant water potential and thereby many different processes like assimilation via stomatal closure and cell expansion via reduced cell turgor. Tree growth is affected earlier than C assimilation during drought because cell division and expansion are more sensitive to water stress than photosynthesis (Körner 2003, Muller et al. 2011, Galvez et al. 2013, Palacio et al. 2014), which can lead to an accumulation of NSC via sink limitation (McDowell 2011). In addition, elevated CO_2 can stimulate tree growth (Luo et al. 2006) but this 'CO2 fertilization effect' levels off quickly as other environmental constraints (e.g., from nutrients) become more limiting (Beedlow et al. 2004). In a meta-analysis, Lu et al. (2011) showed that increased growth of foliage, shoots and roots from elevated CO_2 was only sustained with N addition in forest ecosystems.

Generally, positive effects of drought on NSC concentrations in trees are much more common in the literature (Körner 2003, Sala and Hoch 2009, Galvez et al. 2011) than negative effects (Körner 2003, Anderegg 2012). Elevated CO_2 generally increases NSC concentrations (Körner 2003), particularly in leaves (Körner et al. 2005). Earlier meta-analysis found that the overall responses of plant NSC concentrations to N addition were not significant (Liu et al. 2016), but observations of decreased NSC concentrations in leaves and roots from N fertilization are prevalent in the literature (Cheng et al. 2004, Huttunen et al. 2013). Nevertheless, NSC dynamics in response to the mentioned global change drivers may vary across different tree taxonomic groups, leaf habits or development stages (e.g., seedlings, adult, mature tree) due to differences in physiological processes and structures (Sala and Hoch 2009, Ülo 2010, Martínez-Vilalta et al. 2016, Li et al. 2017). For example, deciduous species could increase NSC storage in stem for initial growth in springtime (Dietze et al. 2014), and gymnosperms, which have greater annual variation in NSC than angiosperms (Martínez-Vilalta et al. 2016), may be more likely to show reductions in NSC during drought (Adams et al. 2017). Seedlings are not simply small mature trees because changes in photosynthetic capacity and growth during maturation are not proportional to tree size, which leads to different allocation of NSC between seedlings and mature trees (Hartmann et al. 2018a). In addition, long distances from source to sink organs in tall trees may hamper C transport due to higher pathway resistance and viscosity of the phloem sap during drought (Mencuccini and Hölttä 2010), which could result in uneven distribution of NSC across organs of individual trees, particularly during drought (Landhäusser and Lieffers 2012, Hartmann et al. 2013).

The current challenge to predicting terrestrial biosphere carbon–climate dynamics at large spatial and temporal scales with dynamic global vegetation models (DGVMs) is a lack of

understanding of how vegetation will respond to climate change (Sitch et al. 2008, Friend et al. 2014). In particular, allocation of carbohydrates and their residence time in vegetation is often not well implemented in DGVMs and usually poorly parameterized, preventing realistic simulation of plant functioning under changing environmental conditions (Dietze et al. 2014). Analysis of tree organ-level NSC dynamics across tree taxonomic groups, leaf habits and ages can provide proxies for allocation patterns in response to environmental change (McDowell 2011), but NSC measurements are difficult to compare among labs working with different methodologies and equipment (Quentin et al. 2015). However, Quentin et al. (2015) observed reasonable intra-lab precision and reproducibility that allows relative changes between treatments in NSC values measured in the same laboratory to be compared among studies (Germino 2015, Martínez-Vilalta et al. 2016, Adams et al. 2017). To date, existing meta-analyses have rarely addressed plant NSC responses to elevated CO_2 or N fertilization at the organ level (Zvereva and Kozlov 2006, Liu et al. 2016), and a comprehensive evaluation of tree NSC–climate dynamics is urgently needed.

We compiled 936 observations from 57 individual studies on NSC responses to drought, elevated CO_2 or N deposition. We computed a dimensionless response ratio (Hedges et al. 1999), which indicates the relative change of NSC concentrations between treatment and control groups within a given study. Using this ratio we avoided problematic comparison of absolute NSC concentrations across studies. Our objectives were to (i) identify general responses of total NSC, soluble sugars and starch to drought, elevated CO_2 and N fertilization and their interaction across different tree organs (e.g., foliage, aboveground wood and roots); (ii) identify general responses of tree growth to drought, elevated CO_2 and N fertilization across different tree organs; (iii) investigate how responses vary across taxonomic groups, leaf habit, developmental stage and with treatment intensity; and (iv) highlight current knowledge gaps surrounding the NSC dynamics in trees following drought, elevated CO_2 and N addition. We hypothesized that (i) NSC concentration are increased during drought and from elevated CO_2 treatments, but decreased from N addition; (ii) tree growth is decreased from drought, but increased from elevated CO_2 and N addition treatments; (iii) drought decreases the fertilization effects of CO_2 or N; and (iv) NSC responses to severe treatment are greater in deciduous species and seedlings/saplings than evergreen and mature trees.

Materials and methods

Data collection

To extract tree NSC data from peer-reviewed studies on drought, elevated CO_2 and N addition, we searched in the Web of Science[®] literature published since 1990 using the search terms 'nonstructural carbohydrates' and 'non-structural carbohydrates'

in combination with any of the following terms: (i) 'drought' or 'water stress', (ii) 'elevated CO_2' or (iii) 'N deposition' or 'N fertilization'. We also considered the studies cited by several recent syntheses on NSC (Zvereva and Kozlov 2006, Hartmann and Trumbore 2016, Liu et al. 2016, Martínez-Vilalta et al. 2016, Adams et al. 2017). In total, we selected 57 papers (27 for drought, 31 for elevated CO_2 and 12 for N addition; see Appendix S1 available as Supplementary Data at *Tree Physiology* Online) that reported soluble sugars, starch and total NSC concentrations in trees and that satisfied the following criteria (see databases in Appendix S2 available as Supplementary Data at *Tree Physiology* Online): (i) the study was based on manipulative experimentation and reported also control treatments and (ii) the study was on trees, not on other plant types.

Other treatments, interactions or cycle treatments, like drying–rewetting cycles, were excluded from analysis. For each study, we also collected growth data of different tree organs if reported and noted experimental location, treatment intensities, tree taxonomic and leaf habit groups (71 tree species grouped into evergreen gymnosperms, evergreen angiosperms, deciduous gymnosperms and deciduous angiosperms, Table 1) as well as tree age (grouped into seedlings/saplings (≤10 years) and mature trees (>10 years, Table 1)) as moderator variables. Decreases in soil water content (reductions in irrigation) ranged from −15% to −100% of control, which were grouped into moderate (≤50%) and severe (>50%) treatments, while increases in CO_2 concentration ranged from +37.5% to +400% of control and were grouped into moderate (<100%) and severe (≥100%) treatments (Table 1). Similarly, increases in N-addition ranged from +50% to +9710% of control, which were divided into moderate (≤500%) and severe (>500%) treatments. The sample sizes per treatment class are shown in Table S1 available as Supplementary Data at *Tree Physiology* Online.

Data were either taken directly from tables or extracted from figures of the published articles using the Engauge software (4.1). We calculated the standard deviation from reported standard errors and sampling sizes ($SD = SE \bullet \sqrt{n}$), if it was not reported. A few studies did not report standard deviation or standard error, and we approximated the missing standard deviation by multiplying the reported mean by the average coefficient of variance (CV), which were calculated within each data set (Bai et al. 2013). Studies with multiple tree species were treated as separate entries; when the variables were reported for multiple sampling dates, we considered only monthly means (individual value or means from multiple values during each calendar month).

Meta-analysis

The effect size (*RR*) of individual/combined global change (drought, elevated CO_2 and N fertilization) for individual observations was calculated by the natural log-transformed response

Table 1. Summary of the studies used for data collection showing species, manipulations (treatments) and tree age/size/developmental stage as well as the grouping used for our analysis

Location	Species and tree taxonomic & leaf habit group		Manipulation		Tree age/size/developmental stage		Reference
	Species	Group	Treatment intensity (% change vs control)	Group	Age/year	Group	
Drought							
New Mexico, USA	*Pinus edulis/Juniperus monosperma*	EG	−45.00%	Moderate	Adult	Mature trees	Adams et al. (2015)
Arizona, USA	*Pinus edulis*	EG	−100.00%	Severe	Sapling	Seedling/sapling	Adams et al. (2013)
Colorado, USA	*Pinus edulis/Juniperus monosperma*	EG	−100.00%	Severe	Sapling	Seedling/sapling	Anderegg and Anderegg (2013)
San Juan, USA	*Populus tremuloides*	DA	−50.0%	Moderate	Sapling	Seedling/sapling	Anderegg et al. (2012)
California, USA	*Prunus dulcis*	DA			Mature	Mature trees	Esparza et al. (2001)
Edmonton, Canada	*Populus tremuloides/Populus balsamifera*	DA			Seedling	Seedling/sapling	Galvez et al. (2013)
Nancy, France	*Pinus nigra*	EG			Seedling (15 cm tall)	Seedling/sapling	Guehl et al. (1993)
Jena, Germany	*Picea abies*	EG			Saplings (75 cm tall)	Seedling/sapling	Hartmann et al. (2013)
Jena, Germany	*Picea abies*	EG	−75.00%	Severe	Saplings (75 cm tall)	Seedling/sapling	Hartmann et al. (2015)
Negev desert, Israel	*Pinus halepensis*	EG			45	Mature trees	Klein et al. (2014)
Perth, Australia	*Eucalyptus globulus*	EA	−15.00%	Moderate	<2	Seedling/sapling	Mitchell et al. (2013, 2014)
Perth, Australia	*Pinus radiata*	EG	−15.00%	Moderate	<2	Seedling/sapling	Mitchell et al. (2014)
Sabah, Malaysia	*Dryobalanops lanceolata/Durio oxleyanus/ Hopea nervosa/ Koompassia excelsa/Parashorea malaanonan/Parashorea tomentella/Shorea argentifolia/ Shorea beccariana/Shorea macrophylla/Shorea parvifolia*	DA	−79.20%	Severe	<1	Seedling/sapling	O'Brien et al. (2014)
Canberra, Australia	*Eucalyptus macrorhyncha/ Eucalyptus rossii*	EA			<2	Seedling/sapling	Roden and Ball (1996)
Montpellier, France	*Quercus pubescens*	DA	−62.50%	Severe	<3	Seedling/sapling	Rodriguez-Calcerrada et al. (2011)
	Quercus pubescens	DA	−50.00%	Moderate	<3	Seedling/sapling	
	Quercus ilex	EA	−62.50%	Severe	<3	Seedling/sapling	
	Quercus ilex	EA	−50.00%	Moderate	<3	Seedling/sapling	
Florida, USA	*Pinus palustris*	EG	−50%	Moderate	<3	Seedling/sapling	Runion et al. (1999)
Madrid, Spain	*Quercus ilex*	EA	−47.5%/−42.5%/−30%	Moderate	<3	Seedling/sapling	Villar-Salvador et al. (2004)
Shanxi, China	*Malus domestica*	DA	−25.00%	Moderate	1	Seedling/sapling	Wu et al. (2014)
Florida, USA	*Citrus volkameriana*	EA			<3	Seedling/sapling	Bryla et al. (1997)
New South Wales, Australia	*Eucalyptus saligna*	EA	−100.00%	Severe	5.4 m tall	Seedling/sapling	Crous et al. (2011)
Alberta, Canada	*Populus tremuloides*	DA			<2	Seedling/sapling	Galvez et al. (2011)
Corral, Chile	*Nothofagus dombeyi/Nothofagus nitida*	EA	−95%	Severe	2~3	Seedling/sapling	Piper (2011)
Trieste, Italy	*Quercus pubescens/Prunus mahaleb/Robinia pseudoacacia/ Ailanthus altissima*	DA	−79.5%/−84.8%/ −82.4%/−82.7%	Severe	3	Seedling/sapling	Savi et al. (2016)

(*Continued*)

Table 1. (Continued)

Location	Species and tree taxonomic & leaf habit group		Manipulation		Tree age/size/developmental stage		Reference
	Species	Group	Treatment intensity (% change vs control)	Group	Age/year	Group	
Sydney, Australia	*Eucalyptus radiata*	EA	−76%	Severe	Seedling	Seedling/sapling	Duan et al. (2014)
Sydney, Australia	Pinus radiate/Callitris rhomboidea	EG	−60%	Severe	Seedling	Seedling/sapling	Duan et al. (2015)
Coyhaique, Chile	*Acer pseudoplatanus*	DA	−100.00%	Severe	Seedling	Seedling/sapling	Piper and Fajardo (2016)
Barcelona, Spain	*Pinus sylvestris*	EG	−100%	Severe	Sapling	Seedling/sapling	Garcia Forner et al. (2016)
Elevated CO$_2$							
Basel, Switzerland	*Fagus sylvatica*	DA	50.00%	Moderate	100	Mature trees	Bignucolo et al. 2010
Idaho, USA	*Pinus palustris*	EG	97.30%	Moderate	Seedling	Seedling/sapling	Entry et al. (1998)
North Carolina, USA	*Cercis canadensis/Acer rubrum/ Liquidambar styraciflua*	DA	55.60%	Moderate	13	Mature trees	Finzi et al. (2001)
	Pinus taeda	EG	55.60%	Moderate	13	Mature trees	
New South Wales, Australia	*Eucalyptus tereticornis/Eucalyptus robusta*	EA	60.00%	Moderate	Seedling	Seedling/sapling	Gherlenda et al. (2015)
Ilomantsi, Finland	*Betula pendula*	DA	100.00%	Severe	Seedling (6 cm tall)	Seedling/sapling	Huttunen et al. (2013)
Sichuan, China	*Abies faxoniana*	EG	100.00%	Severe	7	Seedling/sapling	Li et al. (2015)
Tuscania, Italy	*Populus nigra*	DA	100.00%	Severe	2	Seedling/sapling	Luo et al. (2006)
Lisbon, Portugal	*Quercus suber*	EA	100.00%	Severe	<1	Seedling/sapling	Niinemets et al. (1999)
California, USA	*Prunuspersica*	DA	100.00%	Severe	1	Seedling/sapling	Davidson et al. (2016)
Edinburgh, UK	*Betula pendula*	DA	100.00%	Severe	<3	Seedling/sapling	Rey and Jarvis, (1998)
Canberra, Australia	*Eucalyptus macrorhyncha/ Eucalyptus rossii*	EA	100.00%	Severe	<2	Seedling/sapling	Roden and Ball, (1996)
Michigan, USA	*Populus tremuloides*	DA	100.00%	Severe	Seedling	Seedling/sapling	Rothstein et al. (2000)
Florida, USA	*Pinus palustris*	EG	100.00%	Severe	<3	Seedling/sapling	Runion et al. (1999)
Minnesota, USA	*Populus tremuloides/Betula papyrifera*	DA	56.80%	Moderate	<2	Seedling/sapling	Tjoelker et al. (1998)
	Larix laricina	DG	56.80%	Moderate	<2	Seedling/sapling	
	Picea mariana/Pinus banksiana	EG	56.8%	Moderate	5	Seedling/sapling	
Arizona, USA	*Populus deltoides*	DA	90.50%	Moderate	5	Seedling/sapling	Turnbull et al. (2004)
	Populus deltoides	DA	185.70%	Severe	5	Seedling/sapling	
Nancy, France	*Quercus robur*	DA	79.50%	Moderate	Saplings	Seedling/sapling	Vizoso et al. (2008)
Sichuan, China	*Betula albosinensis*	DA	100.00%	Severe	<3	Seedling/sapling	Zhang et al. (2008)
Ilomantsi, Finland	*Betula pendula*	DA	100.00%	Severe	<2	Seedling/sapling	Kellomäki and Wang (2001)
North Carolina, USA	Pinus taeda/Pinus ponderosa	EG	100.00%	Severe	<3	Seedling/sapling	King et al. (1997)
Oregon, USA	*Pseudotsuga menziesii*	EG	50.00%	Moderate	4	Seedling/sapling	Olszyk et al. (2003)
Suonenjoki, Finland	Pinus sylvestris/Picea abies	EG	124.90%	Severe	Seedling	Seedling/sapling	Sallas et al. (2003)
North Carolina, USA	*Pinus taeda*	EG	41.70%/83.30%	Moderate	seedling	Seedling/sapling	Williams et al. (1994)
Tennessee, USA	*Acer rubrum/Acer saccharum/ Lymantria dispar*	DA	83.30%	Moderate	2	Seedling/sapling	Williams et al. (2000, 2003)
Ilomantsi, Finland	*Pinus sylvestris*	EG	100.00%	Severe	20	Mature trees	Zha et al. (2001, 2002)
Basel, Switzerland		DA	52.80%	Moderate	100	Mature trees	Bader et al. (2013)

(*Continued*)

Table 1. (Continued)

Location	Species and tree taxonomic & leaf habit group		Manipulation		Tree age/size/developmental stage		Reference
	Species	Group	Treatment intensity (% change vs control)	Group	Age/year	Group	
	Fagus sylvatica/Quercus petraea/ Carpinus betulus/Acer campestre						
New South Wales, Australia	*Eucalyptus saligna*	EA	66.70%	Moderate	5.4 m tall	Seedling/sapling	Crous et al. (2011)
Florida, USA	*Citrus paradisi*	EA	100.00%	Severe	2	Seedling/sapling	Vu et al. (2002)
Sydney, Australia	*Eucalyptus radiata*	EA	37.5%	Moderate	Seedling	Seedling/sapling	Duan et al. (2014)
Sydney, Australia	Pinus radiate/ Callitris rhomboidea	EG	37.5%	Moderate	Seedling	Seedling/sapling	Duan et al. (2015)
N fertilization							
New York, USA	*Malus domestica*	DA	46.7%/93.5%/140.2%/ 186.9%	Moderate	Sapling	Seedling/sapling	Cheng et al. (2004)
Idaho, USA	*Pinus palustris*	EG	900.00%	Severe	Seedling	Seedling/sapling	Entry et al. (1998)
Ilomantsi, Finland	*Betula pendula*	DA	5400.0%	Severe	Seedling (6 cm tall)	Seedling/sapling	Huttunen et al. (2013)
New York, USA	*Acer rubrum/Acer saccharum/ Quercus alba/Quercus velutina/ Quercus rubra/Prunus serotina/ Fagus grandifolia/Betula papyrifera*	DA	9705.90%	Severe	Seedling	Seedling/sapling	Kobe et al. (2010)
Sichuan, China	*Abies faxoniana*	EG	625.00%	Severe	7	Seedling/sapling	Li et al. (2015)
Tuscania, Italy	*Populus nigra*	DA	3952.80%	Severe	2	Seedling/sapling	Luo et al. (2006)
Lisbon, Portugal	*Quercus suber*	EA	500.00%	Moderate	<1	Seedling/sapling	Niinemets et al. 1999
Michigan, USA	*Populus tremuloides*	DA	430.00%	Moderate	Seedling	Seedling/sapling	Rothstein et al. (2000)
North Carolina, USA	*Pinus taeda*	EG	150%/300%/450%	Moderate	Seedling (stem 9 cm tall)	Seedling/sapling	Rowe et al. (1999)
	Pinus taeda	EG	600.00%	Severe	Seedling (stem 9 cm tall)	Seedling/sapling	
Nancy, France	*Quercus robur*	DA	900.00%	Severe	Saplings	Seedling/sapling	Vizoso et al. (2008)
North Carolina, USA	*Pinus taeda/Pinus ponderosa*	EG	400.00%	Moderate	<3	Seedling/sapling	King et al. (1997)
Kemijärvi, Finland	*Picea abies*	EG	1840%/2130%/ 2420%/2708%3000%	Severe	65	Mature trees	Kaakinen et al. (2007)
Heinola, Finland	*Picea abies*	EG	911%/1183%/1455%/ 1727%/2000%	Severe	49	Mature trees	Kaakinen et al. (2007)

EA, evergreen angiosperms; EG, evergreen gymnosperms; DA, deciduous angiosperms; DG, deciduous gymnosperms.

ratio, which presents the relative change of variables between treatment and control:

$$RR = \ln(\bar{X}_t/\bar{X}_c) = \ln \bar{X}_t - \ln \bar{X}_c \quad (1)$$

where $\bar{X}_t$ is the treatment mean and $\bar{X}_c$ is the control mean (Hedges et al. 1999). The mean, standard deviation (SD = SE$\sqrt{n}$) and sample size of treatment (S_t, n_t) and control (S_c, n_c) groups were used to calculate the variance of effect size (v) (Eq. (2)), and the weighting factor (w) of each observation was calculated by the inverse of the variance (Eq. (3)).

$$v = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2} \quad (2)$$

$$w = \frac{1}{v} \quad (3)$$

Some study cases contain two or more observations, we adjusted the weight by the total number of observations per study to reduce the weight from the same site, and used the total weighting factor (w') to calculate the average effect sizes ($\overline{RR}$) and confidence intervals (CIs, bootstrapping with 9999 iterations) using a fixed effects model in MetaWin software (2.1) (Li et al. 2015, Rosenberg et al. 2000).

$$w' = w/n \quad (4)$$

$$\overline{RR} = \frac{\sum_i w'_i \cdot RR_i}{\sum_i w'_i} \quad (5)$$

Note that our approach avoids the problematic comparison of absolute NSC values among studies where different techniques have been used to measure NSC (Quentin et al. 2015). Instead we only calculate effect size from NSC measurements within each study where the same technique was used to measure NSC in treatment and control groups, following an approach that is analogous to prior cross-study assessments of NSC (Germino 2015, Martínez-Vilalta et al. 2016, Adams et al. 2017).

The effect on a response variable was considered significant if the 95% CI did not overlap with zero, reported as a percentage change from control:

$$\left(e^{\overline{RR}} - 1\right) \times 100\% \quad (6)$$

In addition, the heterogeneity within (Q_w) and between (Q_b) moderator levels was compared using mixed effects models to assess the significance of each categorical moderator (Borenstein et al. 2009). More details on the statistical methods we used can be found in Li et al. (2015). We calculated interaction effect size for each observation using Hedges'd to understand the interaction between individual drivers for a two-driver pair following Yue et al. (2017) with some modifications, which were described in detail in Methods S1 (see Appendix S1

available as Supplementary Data at Tree Physiology Online). If the 95% CI overlapped with zero, the interactive effect was considered to be additive; for two-driver pairs whose individual effects were either both negative or have opposite directions, the interactions <0 were synergistic and >0 antagonistic; in cases where the individual effects were both positive, the interaction effect sizes >0 were synergistic and <0 antagonistic.

Results

Overall responses of NSC to global change factors

For all taxonomic groups, leaf habits and ages combined, drought significantly increased foliar soluble sugar concentration (+13.7%) and reduced foliar starch concentration (−11.7%), but did not significantly change foliar total NSC (Figure 1). There were no significant effects of drought on any carbohydrate in above-ground woody tissues, and only total NSC concentration was significantly affected (−17.3%) in roots.

Elevated CO_2 significantly increased soluble sugars (+20.5%), starch (+125.3%) and total NSC (+26.2%) concentrations in leaves but not in above-ground wood (Figure 1). In roots, both starch (+9.8%) and total NSC (+12.8%) concentrations significantly increased with elevated CO_2.

In leaves, only soluble sugar concentration was significantly affected by N fertilization (−11.7%, Figure 1). In above-ground woody tissues, both soluble sugar (+50.6%) and total NSC (+6.1%) concentrations significantly increased with N fertilization. Nitrogen fertilization significantly decreased root soluble sugar (−14.6%), root starch (−20.5%) and root total NSC (−17.9%) concentrations.

Different NSC responses with tree taxonomic and leaf habit group, tree age and treatment intensity

Drought   Changes in NSC under drought were more prevalent for evergreen tree species than deciduous species (Figure 2). Among evergreen tree species, drought increased foliar soluble sugars in angiosperms (+26.8%), but decreased foliar starch concentration (−22.6%) and root total NSC concentration (−33.5%) in gymnosperms.

Most studies were conducted on seedlings, and fewer data were available on mature trees (≤10, Figure 3). Based on the current limited number of observations, drought significantly increased foliar soluble sugars (+13.8%) in seedlings only, reduced foliar total NSC concentration (−7.5%) in mature trees only, while foliar starch concentration was significantly decreased in both seedlings (−11.5%) and mature trees (−38.7%). In above-ground woody tissues, drought had no significant effect on soluble sugars, starch or total NSC concentrations in either seedlings or mature trees. In roots, soluble sugar (−53.4%), starch (−36.9%) and total NSC (−27.7%) concentrations were reduced by drought only in mature trees (Figure 3).

Foliar soluble sugar concentration was significantly increased in moderate (+24.1%) and severe drought (+22.3%), while foliar starch and total NSC concentrations were not significantly altered in either moderate or severe drought (Figure 4). In above-ground wood and roots, drought had no significant effect on soluble sugars, starch or total NSC concentrations in either moderate or severe drought. Note that it was not always possible to assign severity to drought treatments in studies used in the overall analysis (Figure 1). Therefore, differences in which studies could be assessed for moderate and severe drought treatment (Figure 4) and lower sample size, compared with the overall analysis (Figure 1) may have led to different results for these two analyses.

Elevated CO2   Foliar soluble sugars increased with elevated CO_2 in evergreen species (gymnosperms and angiosperms) only, but foliar starch concentration increased across all species (Figure 2). The total NSC concentration increased with elevated CO_2 in evergreen species (gymnosperms and angiosperms) and deciduous angiosperms, and the small number of observations on deciduous gymnosperms limits the power of our meta-analysis. Elevated CO_2 did not significantly change soluble sugars, starch and total NSC concentrations in above-ground wood in either evergreen gymnosperms or deciduous angiosperms. In roots, elevated CO_2 increased starch in deciduous species (gymnosperms and angiosperms) only, and increased total NSC concentrations in evergreen gymnosperms (+14.7%) and deciduous angiosperms (+15.0%).

Increases in foliar starch (+136.9%) and total NSC concentrations (+43.5%) from elevated CO_2 were more pronounced in seedlings than in mature trees, while the opposite was true for foliar soluble sugars (+24.3% in mature trees) (Figure 3). All data on above-ground wood and roots under elevated CO_2 were from seedling studies, and only root starch (+9.8%) and total NSC (+12.8%) concentrations were significantly increased.

Increases in foliar soluble sugars (+22.0%), foliar starch (+140.7%) and foliar total NSC concentrations (+46.9%) from elevated CO_2 were more pronounced in severe than in moderate elevated CO_2 treatments (Figure 4). In above-ground wood starch concentration was significantly increased in moderate CO_2 treatments only (+12.4%). Increases in root soluble sugars (+17.4%) and total NSC (+14.0%) concentrations were significant in severe elevated CO_2 treatments only, whereas increase in root starch (+6.1%) concentration was significant in moderate elevated CO_2 treatments only.

Nitrogen fertilization   Most studies of N fertilization were conducted on evergreen gymnosperms and deciduous angiosperms, and fewer data were available on evergreen angiosperms and deciduous gymnosperms (Figure 2). Based on the current limited number of observations, N fertilization reduced foliar soluble sugar (−25.2%) and foliar total NSC (−12.7%) concentrations in deciduous angiosperms but not in evergreen gymnosperms. In above-ground wood, soluble sugar concentration was significantly increased in both evergreen gymnosperms (+8.4%) and deciduous angiosperms (+62.0%), while starch (+4.6%) and total NSC (+5.6%) concentrations were increased in evergreen gymnosperms only. Soluble sugars (−16.7%), starch (−28.1%) and total NSC (−27.3%) concentrations were reduced with N fertilization in roots in deciduous angiosperms but not in evergreen gymnosperms.

There were no data on leaves and roots under N fertilization for mature trees. For N fertilization in seedlings, only soluble sugars (−11.7%) were significantly altered in leaves, while for roots, N fertilization significantly reduced soluble sugars (−14.6%), starch (−20.5%) and total NSC (−17.9%) concentrations (Figure 3). In above-ground wood, soluble sugar concentration was significantly increased in both seedlings (+61.2%) and in mature trees (+7.9%), while starch was significantly decreased in seedlings (−26.9%) but increased in mature trees (+4.9%).

Only moderate N fertilization treatments had significant effects on foliar soluble sugar (−32.2%), foliar starch (+5.5%) and foliar total NSC (−11.4%, Figure 4) concentrations. In above-ground wood, both soluble sugars and total NSC were significantly increased in both moderate and severe N fertilization treatments, while starch (−32.7%) declined in moderate N addition only. Root soluble sugars and root total NSC decreased with N fertilization in both moderate and severe N fertilization treatments, while root starch (−35.9%) was significantly reduced by severe N fertilization only.

Responses of tree growth to global change factors

Drought   For all taxonomic groups, leaf habits and ages combined, drought significantly decreased growth in above-ground woody tissues (−15.1%) and roots (−31.5%, Figure 5), but did not change growth in leaves. For different responses with tree taxonomic and leaf habit group, tree age and treatment intensity, drought decreased growth (foliage, above-ground woody tissues and roots) in evergreen angiosperms, but not other species (Figure 5). Decreases in growth of leaves and above-ground woody tissues from drought were more pronounced in mature trees than in seedlings/saplings, and the small number of observations on root growth from mature trees limited our analysis. Note that these growth results come from a subset (where available) of analyzed studies and not a separate literature search on growth effects. However, the number of studies reporting both NSC and growth responses, in particular from severe drought treatment, is small.

Elevated CO2   Elevated CO_2 stimulated tree growth in above-ground tissues (foliage and woody tissues), but not in roots (Figure 5). Increases in foliar growth during elevated CO_2 were more prevalent for evergreen tree species than deciduous species, although there was no available data from deciduous
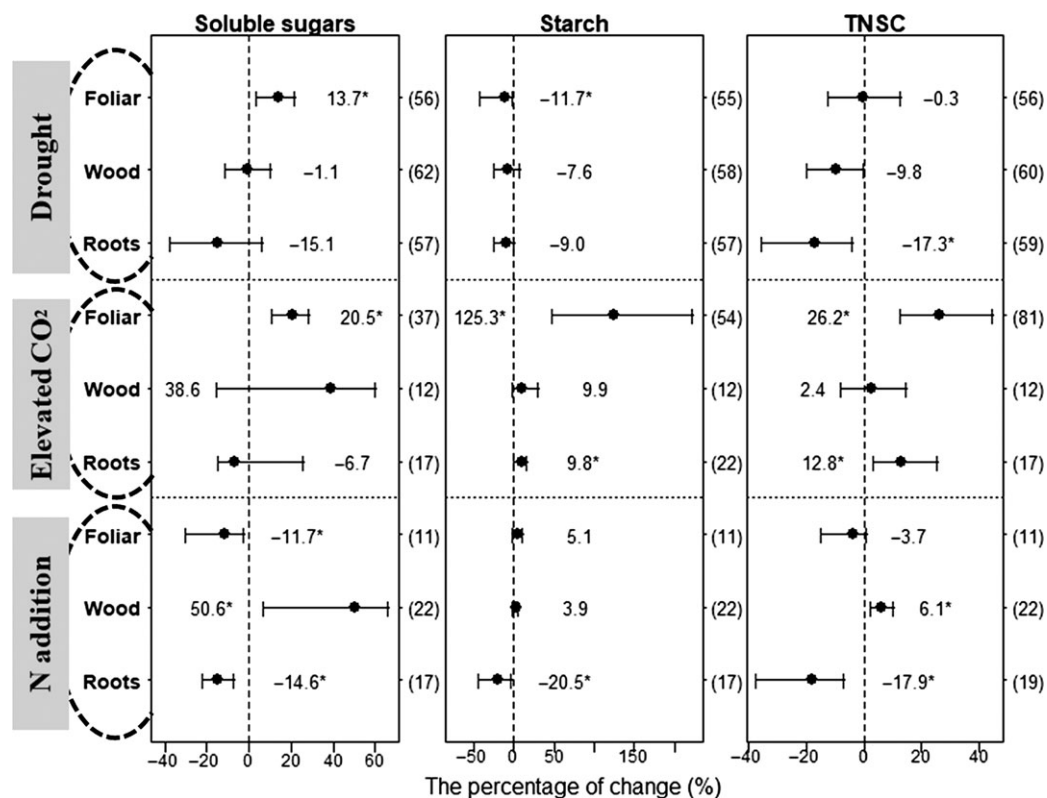
Figure 1. Overall responses (taxonomic and leaf habit groups and age pooled) of soluble sugars, starch and total nonstructural carbohydrate (TNSC) concentrations to drought, elevated CO_2 and N fertilization in different tree organs. Error bars represent 95% confidence intervals (CIs). The percentage of change (%) for each variable is shown next to the point. The number in parentheses represents the sample size for each variable. Wood: above-ground woody tissues.

angiosperms (Figure 5). Elevated CO_2 stimulated foliar growth in both seedlings/saplings (+14.8%) and mature trees (+7.8%), and there was no available observations on above-ground wood and root growth carried out on mature trees. Growth of leaves (+18.4%) and roots (+11.7%) were significantly increased in severe CO_2 treatments only, and above-ground wood growth was increased in both moderate and severe elevated CO_2 treatments.

Nitrogen fertilization   Overall, N fertilization increased tree growth in above-ground woody tissues only (+52.2%, Figure 5). Note that small number of observations on growth from N addition studies limited the analysis of different responses with tree taxonomic and leaf habit group, tree age and treatment intensity.

Discussion

Our meta-analysis provides a comprehensive understanding of the general responses of NSC concentrations in trees to drought, elevated CO_2 and N fertilization, and highlights knowledge gaps concerning the NSC dynamics in mature trees, and under multiple environmental stresses. Inconsistent with our first hypothesis,

our results show that drought reduced root NSC, elevated CO_2 increased NSC in leaves and roots, and N fertilization increased above-ground wood NSC, but decreased root NSC. For elevated CO_2 and N fertilization, these results were consistent with optimal partitioning theory, which would predict C allocation to roots and above-ground woody tissues to pursue more nutrients and light, respectively. According to our second hypothesis, we found that drought significantly decreased growth in above-ground woody tissues and roots, while elevated CO_2 stimulated tree growth in above-ground tissues (foliage and woody tissues) and N addition increased tree growth in above-ground woody tissues. In addition, the response of C allocation patterns to drought, elevated CO_2 and N fertilization varies depending on tree taxonomic and leaf habit group, age, and intensity or severity of environmental change, such that: (i) only deciduous tree species increased C allocation to roots under elevated CO_2; (ii) seedlings/saplings allocated more carbohydrates to roots with drought and older trees allocated more carbohydrates to leaves with elevated CO_2; (iii) only highly elevated CO_2 treatment increased allocation to roots, and severe N enrichment increased allocation to both leaves and above-ground wood while moderate N enrichment increased allocation to above-ground wood only.
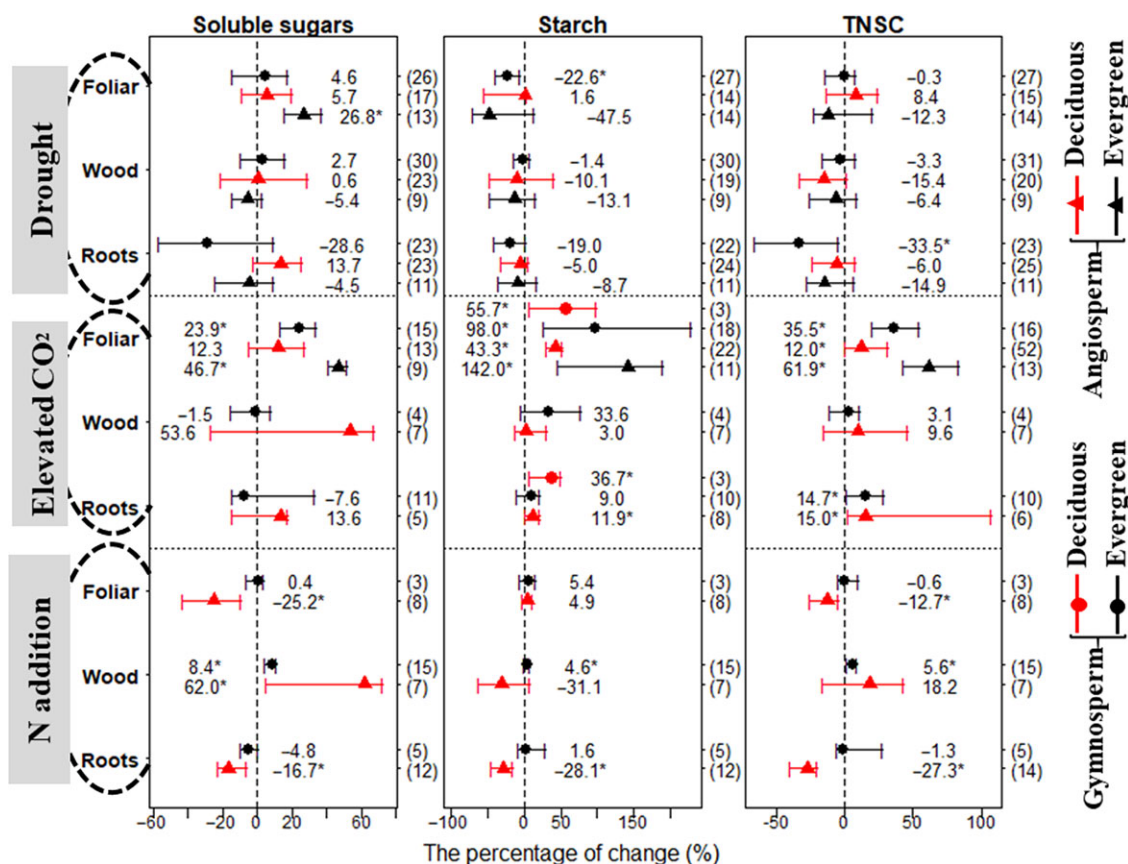
Figure 2. The response of soluble sugars, starch and total nonstructural carbohydrate (TNSC) concentrations to drought, elevated CO_2 and N fertilization in different tree organs, shown separately for evergreen gymnosperms, evergreen angiosperms, deciduous gymnosperms and deciduous angiosperms. Error bars represent 95% confidence intervals (CIs). The percentage of change (%) for each variable is shown next to the point. The number in parentheses represents the sample size for each variable. Wood: above-ground woody tissues.

Overall responses of NSC to drought, elevated CO_2 and N fertilization

When ignoring tree age, tree taxonomic and leaf habit group and treatment intensity, the overall significant effects on NSC (soluble sugars, starch and total NSC) concentrations from both drought and elevated CO_2 were more prevalent in foliage and roots than in above-ground woody tissues, while manipulations of N generally affected NSC concentrations more in above-ground wood and roots (Figure 1). The lack of significant trends in foliar total NSC concentrations in response to drought was due to contrasting and significant effects on NSC components: soluble sugars increased while starch was reduced, an effect noted by others (Adams et al. 2017).

Decreased foliar starch concentrations during drought suggest that C assimilation was lower than C requirements for metabolism and/or export, and foliar starch was apparently remobilized and used for maintenance respiration or converted to osmotically active compounds (i.e., glucose) or exported as sucrose to other organs (e.g., stems, roots) (McDowell et al. 2008, McDowell and Sevanto 2010). Increased foliar soluble sugar concentration in our results could occur by one or a combination of several factors: (i) input from photosynthesis and from starch hydrolysis (Geiger et al. 2000); (ii) downregulation of sink activities (e.g., respiration, growth) and/or upregulation of C storage under stress (Smith and Stitt 2007, Gibon et al. 2009); (iii) osmotic adjustment (Chaves et al. 2003, Bartels and Sunkar 2005, McDowell and Sevanto 2010); and (iv) impediment of phloem transport during drought causing foliar sugar accumulation via reduction of export to other organs like roots (Sevanto 2014).

The decline in root NSC concentrations from drought may indicate isolation of roots from interrupted C translocation and in situ C storage use for metabolic needs (Landhäusser and Leiffers 2012, Hartmann et al. 2013). Non-structural carbohydrate supply to tree roots apparently declined faster than NSC consumption under water deficit, and thus roots may reach first the threshold of C starvation, which has applications for improving mechanistic predictions of tree mortality in DGVMs. Increased NSC concentrations in tree leaves and roots (particularly for starch) under elevated CO_2 suggests upregulation of starch reserve formation as the asynchrony between C supply and demand increases (Körner 2003, Sala et al. 2012,
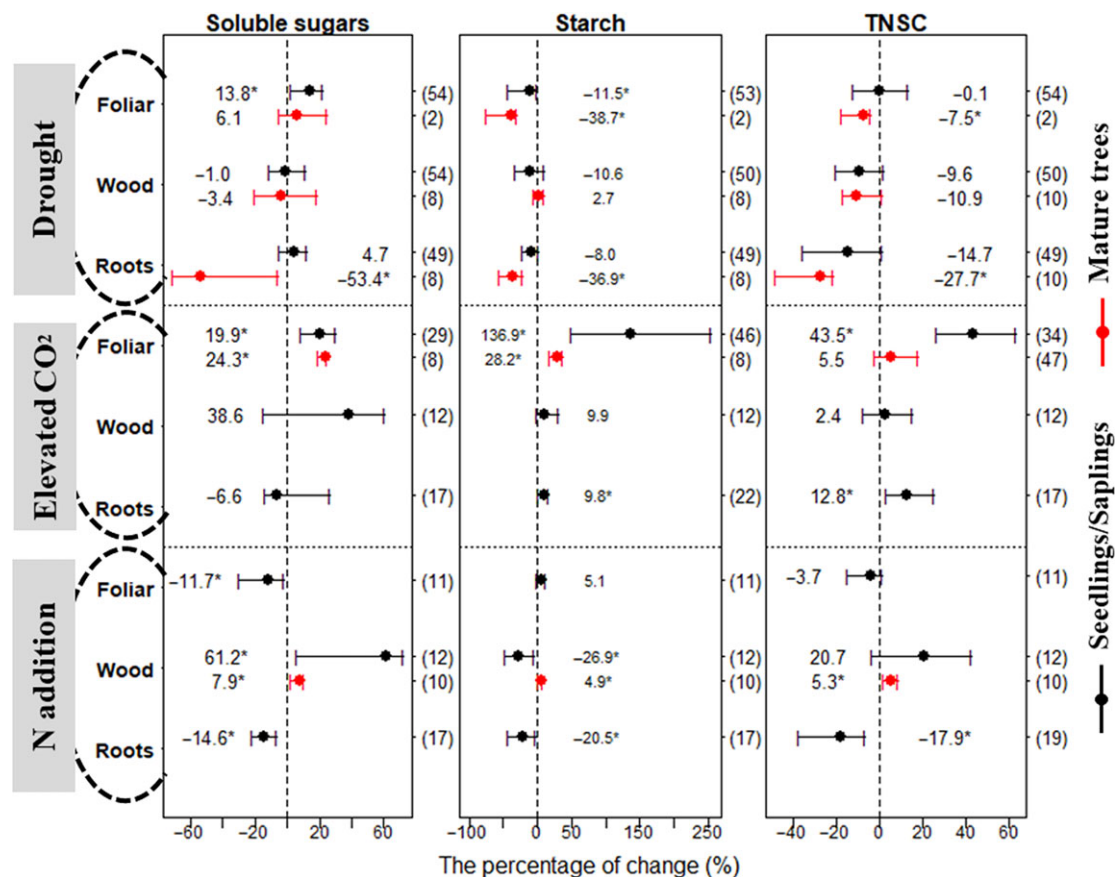
Figure 3. The response of soluble sugars, starch and total nonstructural carbohydrate (TNSC) concentrations to drought, elevated CO_2 and N fertilization in different tree organs, shown separately for seedlings/saplings (<10 years old) and mature trees (≥ 10 years old). Error bars represent 95% confidence intervals (CIs). The percentage of change (%) for each variable is shown next to the point. The number in parentheses represents the sample size for each variable. Wood: above-ground woody tissues.

Martínez-Vilalta et al. 2016) and may promote tree survival and resilience to climatic extremes in the future. Nitrogen fertilization significantly decreased total NSC concentration in roots, with similar effects on soluble sugars and starch. Hence drought or N fertilization may impose source limitations (reduced NSC availability) on tree metabolism while elevated CO_2 could cause sink limitations to increases in tree growth (Körner 2003, Sala et al. 2012, Palacio et al. 2014).

Under elevated CO_2, NSC concentrations were greater in foliage than in roots (particularly for starch, Figure 1). Elevated CO_2 generally increases C assimilation rates (Curtis and Wang 1998, Saxe et al. 1998), while maintenance respiration (in leaves, above-ground wood and roots) may either decrease (Amthor 1995, Hamilton et al. 2001) or remain unchanged (Amthor 1995, Jahnke 2001, Tissue et al. 2002). Therefore, it is logical that NSC accumulate first and to the greatest degree in tree foliage, the source organ. By contrast, roots responded to CO_2 enrichment with greater root production, root respiration and rhizodeposition in forests (Nie et al. 2013) which, in turn, may consume NSC. In addition, since previous synthesis results indicated that sustained tree growth stimulation under elevated CO_2 has

only been documented under high nutrition (e.g., N, P) and long CO_2 fertilization periods (Millard et al. 2007, Norby and Zak 2011), we can deduce that growth limitation by nutrients may be one of the critical reasons for NSC enrichment during elevated CO_2.

By contrast, N fertilization did not stimulate starch storage, but significantly reduced starch concentrations in roots (Figure 1). This suggests that increased C assimilation due to higher foliar N content under N fertilization did not stimulate C storage but instead carbohydrate consumption in trees (Liu and Greaver 2010). This is consistent with results from a previous meta-analysis by Li et al. (2015), who demonstrated that N addition significantly increased root respiration (+18.1%) and total root biomass (+20.4%) in forests. Increased soluble sugars and total NSC concentrations in above-ground wood with N addition suggest that plants may allocate additional C to organs that take up the most limiting resources (optimal partitioning theory; Bloom et al. 1985, Poorter et al. 2012). Nitrogen fertilization thus stimulates allocation of carbohydrates to above-ground wood to support height growth for greater light absorption and C assimilation (N addition increased above-ground wood growth by
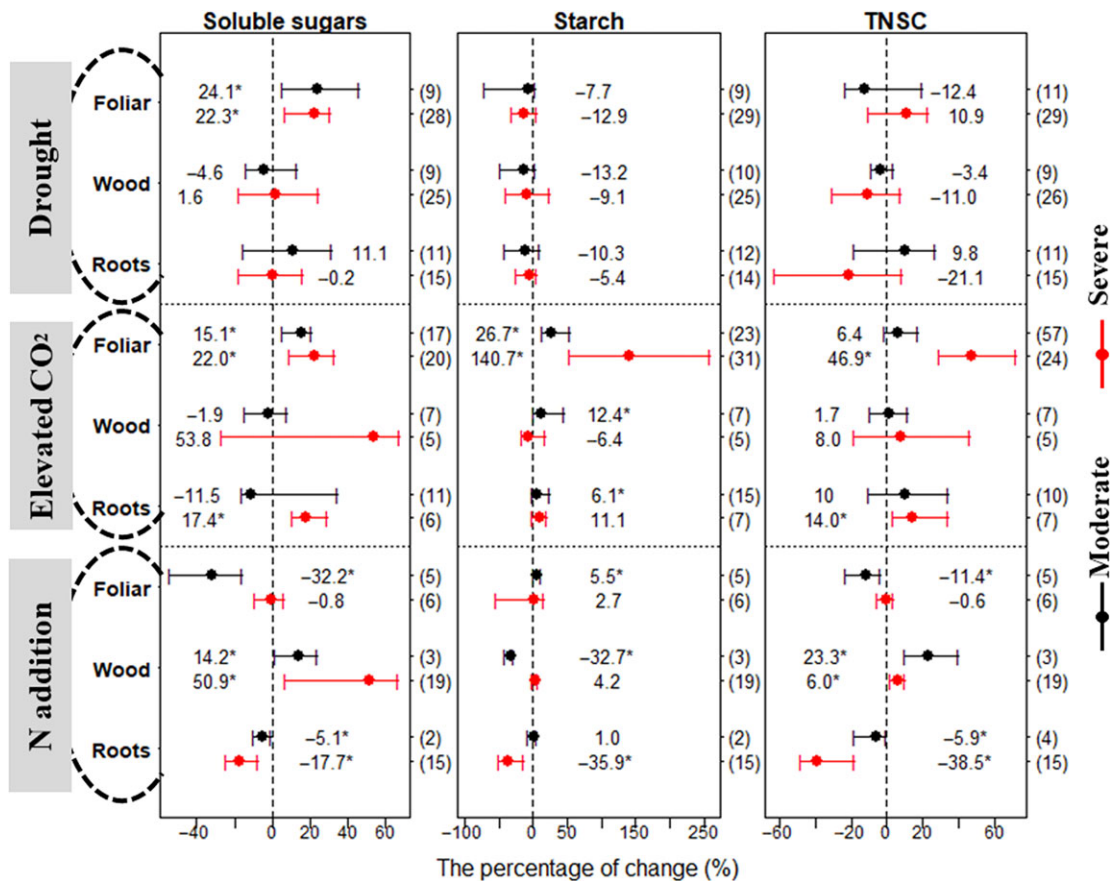
Figure 4. The response of soluble sugars, starch and total nonstructural carbohydrate (TNSC) concentrations to drought, elevated CO_2 and N fertilization in different tree organs, shown separately for moderate and severe treatment intensities. Error bars represent 95% confidence intervals (CIs). The percentage of change (%) for each variable is shown next to the point. The number in parentheses represents the sample size for each variable. Wood: above-ground woody tissues.

52.2%; Figure 5). This is also consistent with our results and other studies showing that N fertilization can substantially increase height growth (Figure 5; Susiluoto et al. 2010).

Different NSC responses with tree taxonomic and leaf habit group, tree age and treatment intensity

Trends in NSC concentrations in response to environmental changes did not differ between gymnosperms and angiosperms, but changes in NSC components depended on tree leaf habits (Figure 2). Our findings suggest that changes in NSC concentrations during drought were more common for evergreen than for deciduous tree species, but data for deciduous gymnosperms were sparse (Figure 2). For evergreen tree species, foliar starch and root total NSC concentrations decreased in evergreen gymnosperms during drought, this was not the case for evergreen angiosperms, which only showed increased foliar sugars (Figure 2). This is similar to results from a multi-species synthesis on physiological responses to lethal drought, where reduced NSC were more common for gymnosperms than for angiosperms (Adams et al. 2017). Starch reserves in both foliage and roots increased during elevated CO_2 in deciduous tree species,

while in evergreen tree species only foliar starch reserves increased (Figure 2). This suggests that CO_2 enrichment stimulated NSC storage in sink organs in deciduous species to support growth and metabolism during springtime, which is consistent with our results that CO_2 enrichment stimulated the growth of above-ground part in evergreen species, but not in deciduous species (Figure 5). For N fertilization, reduced NSC concentrations in leaves and roots were common for deciduous angiosperms, but not for evergreen gymnosperms (Figure 2), suggesting a greater excess of NSC in evergreen gymnosperms. Yet, the small number of observations on deciduous gymnosperms and evergreen angiosperms limits the power of our meta-analysis.

It is surprising that during drought NSC concentrations generally decreased more in foliage and roots of mature trees than seedlings (Figure 3). Seedlings and saplings are thought to be more sensitive to drought than mature, larger trees (McDowell et al. 2013) but mature trees have relatively higher metabolic C requirements than young trees (Hartmann 2011), which may explain our results. Alternatively, large decreases of root NSC concentrations in mature trees may be related to greater impediment of substrate transport in mature and presumably taller trees
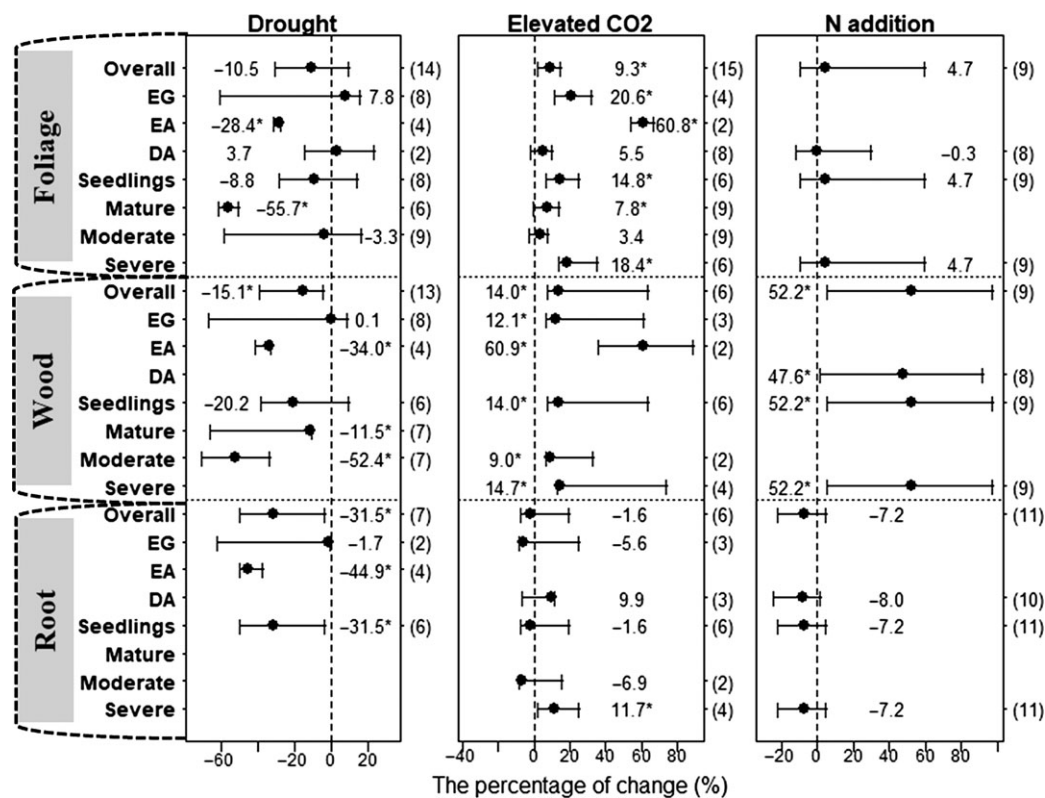
Figure 5. The responses of tree growth to drought, elevated CO_2 and N fertilization in different tree organs, shown separately for evergreen gymnosperms, evergreen angiosperms, deciduous angiosperms, seedlings/saplings, mature trees, moderate treatment intensities and severe treatment intensities. Error bars represent 95% confidence intervals (CIs). The percentage of change (%) for each variable is shown next to the point. The number in parentheses represents the sample size for each variable. EA: evergreen angiosperms; EG: evergreen gymnosperms; DA: deciduous angiosperms; wood: above-ground woody tissues.

due to more negative xylem water potentials (Hölttä et al. 2009, Mencuccini and Hölttä 2010) from greater pathway resistance and gravitational forces with increasing height (Sperry and Tyree 1988, Cochard and Delzon 2013). Extrapolating parameters obtained from manipulations of seedlings and saplings for predictions of mature tree NSC dynamic during drought in DGVMs may therefore be problematic (Hartmann et al. 2018a). Unfortunately, the small number of observations on mature trees grown under elevated CO_2 and N fertilization limits the power of our meta-analysis (Figure 3). A greater positive response of leaf total NSC to elevated CO_2 in seedlings/saplings ($P = 0.007$; see Table S2 available as Supplementary Data at *Tree Physiology* Online) indicates a larger C surplus in seedlings/saplings that are more productive and have lower proportional respiratory requirements than mature trees. In addition, increased above-ground wood NSC from N fertilization in mature trees may be the result of greater allocation of NSC to above-ground wood to support above-ground growth but these carbohydrates accumulated in likely sink-limited mature trees, but not in seedlings/saplings.

Because growth is more sensitive than photosynthesis to drought and trees are more likely to maintain stomatal conductance under moderate drought than severe drought (Körner

2003, McDowell 2011), we expected that reduced NSC would be more likely under severe than moderate drought. However, we found no effect of drought severity on NSC (Figure 4). Highly elevated CO_2 treatments increased total NSC concentrations in leaves and roots, suggesting that greater production of photoassimilates under higher CO_2 concentration was stored in trees rather than consumed through growth and respiration. This is consistent with our results that highly elevated CO_2 treatments increased growth of foliage and roots, but not moderate elevated CO_2 treatments (Figure 5), likely due to sink limitation. Reduction in starch concentration in above-ground wood with moderate N addition and in roots with severe N addition suggest that above-ground wood consumed more NSC for growth in moderate N addition while at severe N addition more NSC were consumed for growth of roots and likely root exudation. This result is consistent with the previous meta-analyses by Li et al. (2015), who reported that N fertilization increased plant fine root biomass for high N addition, but not for low and medium levels of N addition.

Combined and interactive effects

Data on interactive effects of multiple environmental stresses were very sparse (see Appendix S1, Table S3 available as

Supplementary Data at *Tree Physiology* Online). Based on the current limited number of observations, this study showed that the combined effects of drought and elevated CO_2 as well as N fertilization and elevated CO_2 increased total NSC concentrations in foliage by +29.6% and +16.6%, respectively, but did not significantly change total NSC in either above-ground woody tissues or roots (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Combined with individual effects, these results suggest that additional CO_2 enrichment may stimulate C storage under either drought or N addition, thereby potentially alleviating source limitation for tree growth; however, more long-term manipulation experiments with multiple stressors and their interactions are needed to confirm such assumption. The results of interaction effect showed that additive interactions appeared to be much more common compared with synergistic and antagonistic interactions (see Figure S2 available as Supplementary Data at *Tree Physiology* Online). The exception is that the interactive effects of N fertilization × elevated CO_2 on foliar starch and total NSC concentrations were antagonistic and synergistic, respectively.

Conclusion and outlook

Uncertainties still remain as to the generalizability of our findings. First, most studies included in this meta-analysis were in North American, Europe, Australia and China (Table 1), while other regions are underrepresented. Second, the small number of observations on mature trees, particularly under elevated CO_2 and N fertilization, limits the power of our meta-analysis. Third, the classification of drought intensity in our meta-analysis may have concealed the effects of drought severity on NSC concentrations in trees due to lack of a common protocol for treatment applications across studies. Further studies on mature trees, covering several tree taxonomic and leaf habit types, and ideally based on common protocols are needed to elucidate tree responses to environmental stress like drought (Hartmann et al. 2018*b*).

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

Conflict of interest

None declared.

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References

Adams HD, Germino MJ, Breshears DD, Barrongafford GA, Guardiolaclaramonte M, Zou CB, Huxman TE (2013) Nonstructural leaf carbohydrate dynamics of Pinus edulis during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. New Phytol 197:1142–1151.

Adams HD, Collins AD, Briggs SP et al. (2015) Experimental drought and heat can delay phenological development and reduce foliar and shoot growth in semiarid trees. Glob Chang Biol 21:4210–4220.

Adams HD, Zeppel MJ, Anderegg WR et al. (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nat Ecol Evol 1:1285–1291.

Anderegg WR, Anderegg LD (2013) Hydraulic and carbohydrate changes in experimental drought-induced mortality of saplings in two conifer species. Tree Physiol. 33:252–260.

Anderegg WR, Berry JA, Smith DD, Sperry JS, Anderegg LD, Field CB (2012) The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proc Natl Acad Sci USA. 109:233.

Allen CD, Macalady AK, Chenchouni H et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–684.

Amthor JS (1995) Terrestrial higher-plant response to increasing atmospheric CO_2 in relation to the global carbon cycle. Glob Chang Biol 1: 243–274.

Anderegg WRL (2012) Complex aspen forest carbon and root dynamics during drought. Clim Change 111:983–991.

Augusto L, Ranger J, Dan B, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. Ann For Sci 59:233–253.

Bader MKF, Leuzinger S, Keel SG, Siegwolf RT, Hagedorn F, Schleppi P, Körner C (2013) Central European hardwood trees in a high-CO_2 future: synthesis of an 8-year forest canopy CO_2 enrichment project. J Ecol. 101:1509–1519.

Bahn M, Reichstein M, Dukes JS, Smith MD, McDowell NG (2014) Climate-biosphere interactions in a more extreme world. New Phytol 202:356–359.

Bai E, Li S, Xu W, Li W, Dai W, Jiang P (2013) A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. New Phytol 199:441–451.

Bartels D, Sunkar R (2005) Drought and salt tolerance in plants. Crit Rev Plant Sci 24:23–58.

Beedlow PA, Tingey DT, Phillips DL, Hogsett WE, Olszyk DM (2004) Rising atmospheric CO_2 and carbon sequestration in forests. Front Ecol Environ 2:315–322.

Bignucolo O, Koerner C (2010) Leaf miner activity and its effects on leaf chemistry in adult beech under elevated CO_2. Basic Appl Ecol. 11: 251–256.

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants— an economic analogy. Annu Rev Ecol Syst 16:363–392.

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) Introduction to meta-analysis. John Wiley & Sons Ltd, West Sussex, UK.

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63: 625–644.

Bryla D, Bouma T, Eissenstat D (1997) Root respiration in citrus acclimates to temperature and slows during drought. Plant Cell Environ. 20:1411–1420.

Carbone MS, Czimczik CI, Keenan TF, Murakami PF, Pederson N, Schaberg PG, Xu X, Richardson AD (2013) Age, allocation and availability of nonstructural carbon in mature red maple trees. New Phytol 200:1145–1155.

Chapin FS, Schulze E-D, Mooney HA (1990) The ecology and economics of storage in plants. Annu Rev Ecol Syst 21:423–447.

Chaves M, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103:551–560.

Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought—from genes to the whole plant. Funct Plant Biol 30:239–264.

Cheng L, Ma F, Ranwala D (2004) Nitrogen storage and its interaction with carbohydrates of young apple trees in response to nitrogen supply. Tree Physiol 24:91–98.

Ciais P, Reichstein M, Viovy N et al. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533.

Ciais P, Sabine C, Bala G et al. (2014) Carbon and other biogeochemical cycles. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change: Cambridge University Press, Cambridge and New York, NY, pp 465–570.

Cochard H, Delzon S (2013) Hydraulic failure and repair are not routine in trees. Ann For Sci 70:659–661.

Crous KY, Zaragoza-Castells J, Loew M et al. (2011) Seasonal acclimation of leaf respiration in Eucalyptus saligna trees: impacts of elevated atmospheric CO_2 and summer drought. Glob Chang. Biol. 17: 1560–1576.

Curtis PS, Wang X (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113:299–313.

Davidson AM, Da Silva D, Saa S, Mann P, DeJong TM (2016) The influence of elevated CO_2 on the photosynthesis, carbohydrate status, and plastochron of young peach (Prunus persica) trees. Hortic Environ Biote 57:364–370.

De Schepper V, De Swaef T, Bauweraerts I, Steppe K (2013) Phloem transport: a review of mechanisms and controls. J Exp Bot 64:4839–4850.

Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R (2014) Nonstructural carbon in woody plants. Annu Rev Plant Biol 65:667–687.

Duan H, Duursma RA, Huang G, Smith RA, Choat B, O'Grady AP, Tissue DT (2014) Elevated [CO_2] does not ameliorate the negative effects of elevated temperature on drought-induced mortality in Eucalyptus radiata seedlings. Plant Cell Environ 37:1598–1613.

Duan H, O'Grady AP, Duursma RA, Choat B, Huang G, Smith RA, Jiang Y, Tissue DT (2015) Drought responses of two gymnosperm species with contrasting stomatal regulation strategies under elevated [CO_2] and temperature. Tree Physiol 35:756–770.

Ellsworth DS, Thomas R, Crous KY, Palmroth S, Ward E, Maier C, DeLucia E, Oren R (2012) Elevated CO_2 affects photosynthetic responses in canopy pine and subcanopy deciduous trees over 10 years: a synthesis from Duke FACE. Glob Chang Biol 18:223–242.

Ellsworth DS, Crous KY, Lambers H, Cooke J (2015) Phosphorus recycling in photorespiration maintains high photosynthetic capacity in woody species. Plant Cell Environ 38:1142–1156.

Entry JA, Runion GB, Prior SA, Mitchell RJ, Rogers HH (1998) Influence of CO_2 enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. Plant Soil 200:3–11.

Esparza G, DeJong TM, Weinbaum SA (2001) Effects of irrigation deprivation during the harvest period on nonstructural carbohydrate and nitrogen contents of dormant, mature almond trees. Tree Physiol 21: 1081–1086.

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9–19.

Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. Annu Rev Plant Physiol 33:317–345.

Finzi AC, Allen AS, DeLucia EH, Ellsworth DS, Schlesinger WH (2001) Forest litter production, chemistry, and decomposition following two years of free-air CO_2 enrichment. Ecology 82:470–484.

Fowler D, Coyle M, Skiba U et al. (2013) The global nitrogen cycle in the twenty-first century. Philos Trans R Soc Lond 368:20130164.

Friend AD, Lucht W, Rademacher TT et al. (2014) Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc Natl Acad Sci USA 111: 3280–3285.

Galiano L, Martínez-Vilalta J, Lloret F (2011) Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. New Phytol 190:750–759.

Galvez DA, Landhäusser SM, Tyree MT (2011) Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? Tree Physiol 31:250–257.

Galvez DA, Landhäusser SM, Tyree MT (2013) Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings. New Phytol 198:139–148.

Garcia-Forner N, Sala A, Biel C, Savé R, Martínez-Vilalta J (2016) Individual traits as determinants of time to death under extreme drought in Pinus sylvestris L. Tree Physiol. 36:1196–1290.

Geiger DR, Servaites JC, Fuchs MA (2000) Role of starch in carbon translocation and partitioning at the plant level. Funct Plant Biol 27: 571–582.

Germino MJ (2015) A carbohydrate quandary. Tree Physiol 35: 1141–1145.

Gherlenda AN, Haigh AM, Moore BD, Johnson SN, Riegler M (2015) Responses of leaf beetle larvae to elevated CO_2 and temperature depend on Eucalyptus species. Oecologia. 177:607–617.

Gibon Y, Pyl ET, Sulpice R, Lunn JE, Höhne M, Günther M, Stitt M (2009) Adjustment of growth, starch turnover, protein content and central metabolism to a decrease of the carbon supply when Arabidopsis is grown in very short photoperiods. Plant Cell Environ 32:859–874.

Göttlicher S, Knohl A, Wanek W, Buchmann N, Richter A (2006) Short-term changes in carbon isotope composition of soluble carbohydrates and starch: from canopy leaves to the root system. Rapid Commun Mass Spectrom 20:653–660.

Guehl JM, Clement A, Kaushal P, Aussenac G (1993) Planting stress, water status and nonstructural carbohydrate concentrations in Corsican Pine seedlings. Tree Physiol. 12:173–183.

Hamilton J, Thomas R, DeLucia E (2001) Direct and indirect effects of elevated CO_2 on leaf respiration in a forest ecosystem. Plant Cell Environ 24:975–982.

Hartmann H (2011) Will a 385 million year-struggle for light become a struggle for water and for carbon? – How trees may cope with more frequent climate change-type drought events. Glob Chang Biol 17: 642–655.

Hartmann H, McDowell NG, Trumbore S (2015) Allocation to carbon storage pools in Norway spruce saplings under drought and low CO_2. Tree Physiol 35:243–252.

Hartmann H, Trumbore S (2016) Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. New Phytol 211:386–403.

Hartmann H, Ziegler W, Trumbore S (2013) Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. Funct Ecol 27:413–427.

Hartmann H, Adams HD, Hammond WM, Hoch G, Landhäusser SM, Wiley E, Zaehle S (2018a) Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests. Environ Exp Bot. doi:10.1016/j.envexpbot.2018.03.011.

Hartmann H, Moura CF, Anderegg WRL et al. (2018b) Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytol 218:15–28.

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Hölttä T, Mencuccini M, Nikinmaa E (2009) Linking phloem function to structure: analysis with a coupled xylem–phloem transport model. J Theor Biol 259:325–337.

Huttunen L, Saravesi K, Markkola A, Niemela P (2013) Do elevations in temperature, CO_2, and nutrient availability modify belowground carbon gain and root morphology in artificially defoliated silver birch seedlings? Ecol Evol 3:2783–2794.

IPCC (2012) In: Field CB, Barros V, Stocker TF et al (eds) Managing the risks of extreme events and disasters to advance climate change adaptation. Cambridge University Press, Cambridge.

Jahnke S (2001) Atmospheric CO_2 concentration does not directly affect leaf respiration in bean or poplar. Plant Cell Environ 24:1139–1151.

Kaakinen S, Saranpää P, Vapaavuori E (2007) Effects of growth differences due to geographic location and N-fertilisation on wood chemistry of Norway spruce. Trees. 21:131–139.

Kellomäki S, Wang K-Y (2001) Growth and resource use of birch seedlings under elevated carbon dioxide and temperature. Annals of Botany. 87:669–682.

King JS, Thomas RB, Strain BR (1997) Morphology and tissue quality of seedling root systems of Pinus taeda and Pinus ponderosa as affected by varying CO_2, temperature, and nitrogen. Plant Soil 195:107–119.

Klein T, Hoch G, Yakir D, Koerner C (2014) Drought stress, growth and nonstructural carbohydrate dynamics of pine trees in a semi-arid forest. Tree Physiol 34:981–992.

Klein T, Siegwolf RTW, Körner C (2016) Belowground carbon trade among tall trees in a temperate forest. Science 352:342–344.

Kobe RK, Iyer M, Walters MB (2010) Optimal partitioning theory revisited: nonstructural carbohydrates dominate root mass responses to nitrogen. Ecology 91:166–179.

Körner C (2003) Carbon limitation in trees. J Ecol 91:4–17.

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Peláez-Riedl S, Pepin S, Siegwolf RT, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309:1360–1362.

Landhäusser SM, Lieffers VJ (2012) Defoliation increases risk of carbon starvation in root systems of mature aspen. Trees 26:653–661.

Li W, Jin C, Guan D, Wang Q, Wang A, Yuan F, Wu J (2015) The effects of simulated nitrogen deposition on plant root traits: a meta-analysis. Soil Biol Biochem 82:112–118.

Li W, Bai Z, Jin C, Zhang X, Guan D, Wang A, Yuan F, Wu J (2017) The influence of tree species on small scale spatial heterogeneity of soil respiration in a temperate mixed forest. Sci Total Environ 590-591:242–248.

Liu J, Wu N, Wang H, Sun J, Peng B, Jiang P, Bai E (2016) Nitrogen addition affects chemical compositions of plant tissues, litter and soil organic matter. Ecology 97:1796–1806.

Liu L, Greaver TL (2010) A global perspective on belowground carbon dynamics under nitrogen enrichment. Ecol Lett 13:819–828.

Lu M, Zhou X, Luo Y, Yang Y, Fang C, Chen J, Li B (2011) Minor stimulation of soil carbon storage by nitrogen addition: a meta-analysis. Agric Ecosyst Environ 140:234–244.

Luo Y, Hui D, Zhang D (2006) Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. Ecology 87:53–63.

Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F (2016) Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. Ecol Monogr 86:495–516.

McDowell N, Pockman WT, Allen CD et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178:719–739.

McDowell NG (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiol 155:1051–1059.

McDowell NG, Sevanto S (2010) The mechanisms of carbon starvation: how, when, or does it even occur at all? New Phytol 186:264–266.

McDowell NG, Ryan MG, Zeppel MJB, Tissue DT (2013) Improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. New Phytol 200:289–293.

Medlyn BE, Barton CVM, Broadmeadow MSJ et al. (2001) Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. New Phytol 149:247–264.

Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363:234–240.

Mencuccini M, Hölttä T (2010) The significance of phloem transport for the speed with which canopy photosynthesis and belowground respiration are linked. New Phytol 185:189–203.

Millard P, Sommerkorn M, Grelet GA (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytol 175:11–28.

Mitchell PJ, O'Grady AP, Tissue DT, White DA, Ottenschlaeger ML, Pinkard EA (2013) Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. New Phytol 197:862–872.

Mitchell PJ, O'Grady AP, Tissue DT, Worledge D, Pinkard EA (2014) Coordination of growth, gas exchange and hydraulics define the carbon safety margin in tree species with contrasting drought strategies. Tree Physiol. 34:443–458.

Muhr J, Messier C, Delagrange S, Trumbore S, Xu X, Hartmann H (2016) How fresh is maple syrup? Sugar maple trees mobilize carbon stored several years previously during early springtime sap-ascent. New Phytol 209:1410–1416.

Muller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, Gibon Y (2011) Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. J Exp Bot 62:1715–1729.

Mystakidis S, Davin EL, Gruber N, Seneviratne SI (2016) Constraining future terrestrial carbon cycle projections using observation-based water and carbon flux estimates. Glob Chang Biol 22:2198–2215.

Nie M, Lu M, Bell J, Raut S, Pendall E (2013) Altered root traits due to elevated CO_2: a meta-analysis. Glob Ecol Biogeogr 22:1095–1105.

Niinemets U, Tenhunen JD, Canta NR, Chaves MM, Faria T, Pereira JS, Reynolds JF (1999) Interactive effects of nitrogen and phosphorus on the acclimation potential of foliage photosynthetic properties of cork oak, Quercus suber, to elevated atmospheric CO_2 concentrations. Glob Chang. Biol 5:455–470.

Norby RJ, Zak DR (2011) Ecological lessons from free-air CO_2 enrichment (FACE) experiments. Annu Rev Ecol Evol Syst 42:181–203.

O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A (2014) Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. Nat Clim Change 4:710–714.

Olszyk DM, Johnson MG, Tingey DT et al. (2003) Whole-seedling biomass allocation, leaf area, and tissue chemistry for Douglas-fir exposed to elevated CO_2 and temperature for 4 years. Can J Forest Res 33:269–278.

Palacio S, Hoch G, Sala A, Körner C, Millard P (2014) Does carbon storage limit tree growth? New Phytol 201:1096–1100.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Piper FI (2011) Drought induces opposite changes in the concentration of non-structural carbohydrates of two evergreen Nothofagus species of differential drought resistance. Ann. Forest Sci 68:415–424.

Piper FI, Fajardo A (2016) Carbon dynamics of Acer pseudoplatanus seedlings under drought and complete darkness. Tree Physiol. 36: 1400–1408.

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193: 30–50.

Quentin AG, Pinkard EA, Ryan MG et al. (2015) Non-structural carbohydrates in woody plants compared among laboratories. Tree Physiol 35:1146–1165.

Reay DS, Dentener F, Smith P, Grace J, Feely RA (2008) Global nitrogen deposition and carbon sinks. Nat Geosci 1:430–437.

Reich P, Walters M, Tjoelker M, Vanderklein D, Buschena C (1998) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct Ecol 12:395–405.

Reichstein M, Bahn M, Ciais P et al. (2013) Climate extremes and the carbon cycle. Nature 500:287–295.

Rennie EA, Turgeon R (2009) A comprehensive picture of phloem loading strategies. Proc Natl Acad Sci USA 106:14162–14167.

Rey A, Jarvis PG (1998) Long-term photosynthetic acclimation to increased atmospheric CO_2 concentration in young birch (Betula pendula) trees. Tree Physiol 18:441–450.

Richardson AD, Carbone MS, Huggett BA, Furze ME, Czimczik CI, Walker JC, Xu X, Schaberg PG, Murakami P (2015) Distribution and mixing of old and new nonstructural carbon in two temperate trees. New Phytol 206:590–597.

Roden JS, Ball MC (1996) The effect of elevated CO_2 on growth and photosynthesis of two eucalyptus species exposed to high temperatures and water deficits. Plant Physiol 111:909–919.

Rodriguez-Calcerrada J, Shahin O, del Rey MdC, Rambal S (2011) Opposite changes in leaf dark respiration and soluble sugars with drought in two Mediterranean oaks. Funct Plant Biol 38: 1004–1015.

Rosenberg MS, Adams DC, Gurevitch J (2000) MetaWin: statistical software for meta-analysis. Sinauer Associates, Sunderland, MA, USA.

Rothstein DE, Zak DR, Pregitzer KS, Curtis PS (2000) Kinetics of nitrogen uptake by Populus tremuloides in relation to atmospheric CO_2 and soil nitrogen availability. Tree Physiol 20:265–270.

Rowe DB, Blazich FA, Weir RJ (1999) Mineral nutrient and carbohydrate status of loblolly pine during mist propagation as influenced by stock plant nitrogen fertility. Hortscience. 34:1279–1285.

Runion GB, Entry JA, Prior SA, Mitchell RJ, Rogers HH (1999) Tissue chemistry and carbon allocation in seedlings of Pinus palustris subjected to elevated atmospheric CO_2 and water stress. Tree Physiol 19: 329–335.

Sala A, Hoch G (2009) Height-related growth declines in ponderosa pine are not due to carbon limitation. Plant Cell Environ 32:22–30.

Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: feast or famine? Tree Physiol 32:764–775.

Sallas L, Luomala E-M, Utriainen J, Kainulainen P, Holopainen JK (2003) Contrasting effects of elevated carbon dioxide concentration and temperature on Rubisco activity, chlorophyll fluorescence, needle ultrastructure and secondary metabolites in conifer seedlings. Tree Physiol 23:97–108.

Savi T, Casolo V, Luglio J, Bertuzzi S, Trifilo P, Lo Gullo MA, Nardini A (2016) Species-specific reversal of stem xylem embolism after a prolonged drought correlates to endpoint concentration of soluble sugars. Plant Physiol Bioch 106:198–207.

Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO_2 atmosphere. New Phytol 139:395–436.

Sevanto S (2014) Phloem transport and drought. J Exp Bot 65: 1751–1759.

Sitch S, Huntingford C, Gedney N et al. (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Glob Chang Biol 14:2015–2039.

Smith AM, Stitt M (2007) Coordination of carbon supply and plant growth. Plant Cell Environ 30:1126–1149.

Smith SE, Smith FA (2011) Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. Annu Rev Plant Biol 62:227–250.

Sperry JS, Tyree MT (1988) Mechanism of water stress-induced xylem embolism. Plant Physiol 88:581–587.

Susiluoto S, Hilasvuori E, Berninger F (2010) Testing the growth limitation hypothesis for subarctic Scots pine. J Ecol 98:1186–1195.

Tissue DT, Lewis JD, Wullschleger SD, Amthor JS, Griffin KL, Anderson OR (2002) Leaf respiration at different canopy positions in sweetgum (Liquidambar styraciflua) grown in ambient and elevated concentrations of carbon dioxide in the field. Tree Physiol 22: 1157–1166.

Tjoelker MG, Oleksyn J, Reich PB (1998) Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. Tree Physiol 18:715–726.

Turnbull MH, Tissue DT, Murthy R, Wang XZ, Sparrow AD, Griffin KL (2004) Nocturnal warming increases photosynthesis at elevated CO_2 partial pressure in Populus deltoides. New Phytol 161: 819–826.

Ülo N (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. For Ecol Manage 260: 1623–1639.

Villar-Salvador P, Planelles R, Oliet J, Penuelas-Rubira JL, Jacobs DF, Gonzalez M (2004) Drought tolerance and transplanting performance of holm oak (Quercus ilex) seedlings after drought hardening in the nursery. Tree Physiol 24:1147–1155.

Vizoso S, Gerant D, Guehl JM, Joffre R, Chalot M, Gross P, Maillard P (2008) Do elevation of CO_2 concentration and nitrogen fertilization alter storage and remobilization of carbon and nitrogen in pedunculate oak saplings? Tree Physiol 28:1729–1739.

Vu JC, Newman YC, Allen LH, Gallo-Meagher M, Zhang M-Q (2002) Photosynthetic acclimation of young sweet orange trees to elevated growth CO_2 and temperature. J Plant Physiol 159:147–157.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395.

Wiley E, Helliker B (2012) A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. New Phytol 195: 285–289.

Williams R, Lincoln D, Thomas R (1994) Loblolly pine grown under elevated CO_2 affects early instar pine sawfly performance. Oecologia. 98: 64–71.

Williams RS, Lincoln DE, Norby RJ (2003) Development of gypsy moth larvae feeding on red maple saplings at elevated CO_2 and temperature. Oecologia. 137:114–122.

Williams RS, Norby RJ, Lincoln DE (2000) Effects of elevated CO_2 and temperature-grown red and sugar maple on gypsy moth performance. Glob Chang. Biol 6:685–695.

Williams AP, Allen CD, Macalady AK et al. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. Nat Clim Change 3:292–297.

Wu S, Liang D, Ma F (2014) Leaf micromorphology and sugar may contribute to differences in drought tolerance for two apple cultivars. Plant Physiol Bioch 80:249–258.

Yue K, Fornara DA, Yang W, Peng Y, Peng C, Liu Z, Wu F (2017) Influence of multiple global change drivers on terrestrial carbon storage: additive effects are common. Ecol Lett 20:663–672.

Zha T, Ryyppö A, Wang K-Y, Kellomäki S (2001) Effects of elevated carbon dioxide concentration and temperature on needle growth, respiration and carbohydrate status in field-grown Scots pines during the needle expansion period. Tree Physiol 21:1279–1287.

Zha T, Wang K-Y, Ryyppö A, Kellomäki S (2002) Impact of needle age on the response of respiration in Scots pine to long-term elevation of carbon dioxide concentration and temperature. Tree Physiol 22: 1241–1248.

Zhang Y, Duan B, Qiao Y, Wang K, Korpelainen H, Li C (2008) Leaf photosynthesis of Betula albosinensis seedlings as affected by elevated CO_2 and planting density. Forest Ecol Manag 255: 1937–1944.

Zhang H, Li W, Adams HD, Wang A, Wu J, Jin C, Guan D, Yuan F (2018) Responses of woody plant functional traits to nitrogen addition: a meta-analysis of leaf economics, gas exchange, and hydraulic traits. Front Plant Sci 9:683.

Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. Glob Chang Biol 12:27–41.