



The Role of Nonstructural Carbohydrates Storage in Forest Resilience under Climate Change

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Abstract

Purpose of Review Nonstructural carbohydrates (NSC) promote tree survival when photosynthesis is impeded by factors whose impact is expected to increase under climate change, like droughts, herbivory, and fires. Nonetheless, it remains unclear whether NSC are depleted under natural conditions and if they mediate tree recovery. To determine if there is a general pattern of NSC variation, we reviewed the recent (2008–2018) literature reporting NSC changes in response to droughts, insect herbivory, and fires, in woody species under natural conditions.

Recent Findings We found 25 cases in 16 studies examining NSC dynamics post-drought, most of them conducted in species of Pinaceae or Fagaceae in Mediterranean Europe. Drought-affected trees had lower NSC, starch, and sugars concentrations than unaffected counterparts, although these results were entirely driven by roots and trunks of Pinaceae. We found only six studies examining NSC responses to herbivory, which indicate both increases and decreases in NSC concentrations inconsistently related to changes in growth or survival. Fire led to consistent decreases in NSC that mediated a successfully regrowth in absence of drought.

Summary NSC decrease related equivocally to the occurrence of drought, fire, and herbivory and also to post-disturbance recovery, indicating no clear pattern of decreasing forest resilience under current climate change. An exception seems to be Pinaceae, which showed decreased NSC and performance in response to drought or herbivory. We suggest that a more water conservative strategy and smaller NSC pools in gymnosperms relative to angiosperms underlie these results.

Keywords Drought · Fire · Outbreaks · Sugars · Starch · Tree mortality

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Introduction

In woody species, a significant proportion of the carbon (C) gained by photosynthesis is stored as nonstructural carbohydrates (NSC) [1–3], although lipids may be quantitatively important in some species [4, 5]. Low molecular weight sugars and starch are the main NSC compounds in woody species, while fructans have also been described as reserve compounds in woody Neotropical Asteraceae [6, 7]. Starch is osmotically inert and has no other function than storage, the latter defined as those resources that build up in the plant and can be mobilized in the future to support biosynthesis for growth or other plant functions [2]. In contrast to starch, sugars are osmotically active, and thus, additionally to storage, they play immediate roles including the maintenance of the cellular integrity (e.g., osmoprotection, osmoregulation) and vascular functioning [8, 9••]. NSC play a central role in plant life, as storage can provide energy for respiration and regrowth during periods of negative C balance (i.e., when photosynthesis is lower than demands of respiration and growth) via remobilization (i.e.,

hydrolysis, translocation, and use). However, storage may not be available for remobilization [10, 11••]. Also, some C-limiting conditions (e.g., drought) may limit remobilization and/or cause transitory NSC increases due to sink limitations which eventually offset higher NSC remobilization occurring after such increases [12]. In this sense, the extent to which stored NSC are reduced during C-limiting conditions affecting natural populations is unclear.

There is a current debate on whether storage could compete for C with growth, since for competition to occur C must be a limiting resource. Under the current atmospheric CO₂ concentrations of 400 ppm, which have no precedents in the last 60,000 years, C limitation has been counterargued [13]. Also, several studies have found no significant growth response to CO₂ fertilization experiments [14, 15]. Nonetheless, although growth is rarely C limited under natural conditions, tree survival could be. For example, disturbances that involve the removal of photosynthetic tissues, like folivory or fire, reduce C storage by reducing the C returns of the removed leaf cohort and by supporting regrowth before stores had achieved full C replenishment [16–18]. Additionally, regrowth after severe folivory is often sparse and characterized by smaller and nutritionally poorer leaves than the foliage lost to herbivores [19, 20], in turn rendering low C return. Since the severity and frequency of both insect herbivory and fires are expected to increase in response to climate change [21–23], the reliance on C storage could increase as well. Thus, many species could be pushed to a tipping point by reaching levels of C storage insufficient to survive, even under a richer CO₂ atmosphere. Droughts, which are also expected to become more severe and frequent under climate change, can also force plants to survive longer periods at the expense of their C stores [24, 25], eventually leading to insufficient C availability for survival [26•, 27].

Several recent studies have examined responses of NSC concentrations and performance (e.g., growth, survival, tree vigor) to drought, herbivory, and fire in seedlings or saplings under experimental conditions (e.g., [26•]). Although such experiments are helpful (and sometimes the only way) to understand physiological mechanisms of plant stress responses, they may fail to predict responses of trees under natural conditions. For example, in contrast to pot experiments, the soil volume explored by a large tree in the forest might provide sufficient water availability to maintain photosynthesis and hence prevent C starvation under severely reduced precipitation [28•]. Likewise, seedlings and saplings could be much more susceptible than large trees to NSC reductions because they need to incur larger NSC concentration changes to cover a given C demand (e.g., regrowth after herbivory or fire) due to their reduced storage capacity [29, 30]. Also, responses to natural herbivory may differ from those experimental defoliation [16, 20], because herbivores elicit defensive responses that manual defoliation does not [31]. Field studies also have

been conducted to evaluate the variation in NSC concentration in face of climate change-related disturbances, but a quantitative analysis of the recent literature is lacking. Therefore, the role and effectiveness of NSC remobilization to mediate forest resilience under climate change remain unclear.

Here, we systematically reviewed empirical studies published during the last 10 years examining NSC responses to droughts, herbivory, fires, or the combinations of them, under natural conditions. Using meta-analysis techniques, we quantified NSC concentration changes and their relationship to tree performance in woody species. Specifically, we aimed at determining (i) whether, and in which organs, NSC concentrations of trees under natural conditions are reduced by droughts, insect herbivory and, fires, (ii) whether such potential reductions are linked to post-disturbance tree recovery, and (iii) which is the main NSC fraction – starch and/or sugars – available for growth and metabolic activity during periods of negative C balance. We hypothesized that decreasing NSC concentrations or pools following drought, herbivory, and/or fire are indicative of faster rates of recovery and hence improves survival potential.

Literature Search and Analyses

By January 8, 2019, we conducted a series of literature searches in Web of Science with different combinations of keywords and criteria (Table S1) for the period 2008–2019. We first defined three keyword sets (#1, #2, and #3, Table S1) which were then included (AND) or excluded (NOT) in subsequent searches that generated nine libraries with a number of studies that ranged from 8 to 238 (Table S1). Libraries #4, #5, and #6 are related to fire; libraries #7, #8, and #9 are related to drought; and libraries #10, #11, and #12 are related to herbivory. Additionally, we included four studies that were not picked by the criteria search but that were relevant for our analysis [32, 33•, 34, 35].

We considered only those studies that fulfilled the following requirements: data on NSC and performance provided for the same species by the same study, for single or several dates (in the last case only data from the same dates were considered and then averaged for both controls and stressed individuals), and for trees naturally or experimentally established under natural field conditions (field experiments like rain exclusions, watering treatments, or fire simulations were included). We discarded studies that did not distinguish between phenology and disturbance effects on NSC ([e.g., [28•, 36•]). From each study, we extracted data of NSC, starch, and sugar (SS) concentrations for two categories of stress: no stressed (controls) and stressed (generally defined as a categorical variable, e.g., degree of defoliation, crown dieback, crown health appearance, etc., Table 1). Only two drought-related studies reported NSC concentrations before drought [39, 45]. For study 45, these NSC concentrations were treated as the controls since

Table 1 Details on studies (published between 2008 and 2018) included in the metaanalysis examining drought effects on NSC concentrations

Ref.	Species (individuals per species)	Geographic area	Severity	Elapsed time (months)	Organs analyzed	Stress criteria	Performance response
Drought							
[37]	<i>Pinus sylvestris</i> (10)	41°19'N, 01°00'E	High	271–278	R, T _s , B, L	Defoliation level	BAI (cm ²)
[38]	<i>Populus tremuloides</i> (7–14)	37°33'N, 107°40'W	High	128	R, T _s , T _b , L	Dieback presence	—
[39]	<i>Abies alba</i> (26–16)	42°45'N, 00°52'W	High	5–7	T _s	Declining appearance	—
[39]	<i>Pinus sylvestris</i> (13–24)	40°26'N, 00°58'W	High	5	T _s	Declining appearance	—
[39]	<i>Pinus halepensis</i> (19–14)	41°47'N, 00°44'W	High	5	T _s	Declining appearance	—
[40]	<i>Quercus ilex</i> (10)	40°18'N, 00°52'W	High	30	L, T _s , S	Defoliation level	—
[40]	<i>Quercus faginea</i> (10)	40°18'N, 00°52'W	High	30	L, T _s , S	Defoliation level	—
[41]	<i>Pinus mugo</i> (8)	46°40'N, 46°40'N	—	290	L	Declining appearance	—
[42]	<i>Quercus frainetto</i> (5)	40°00'N, 16°23'E	—	81–166	T _s	Declining appearance	—
[43]	<i>Pinus halepensis</i> (5)	38°24'N, 00°27'W	High	8	T _s	Declining appearance	—
[44]	<i>Fagus sylvatica</i> (5)	48°22'N, 02°36'E	Moderate	0–18	B, T _s , T _b	Declining appearance	—
[45]	<i>Pseudotsuga menziesii</i> (18)	39°28'N, 121°13'W	Moderate	–12–0	T _s	Drought occurrence	Ring width index
[45]	<i>Pinus ponderosa</i> (18)	39°28'N, 121°13'W	Moderate	–12–0	T _s	Drought occurrence	Ring width index
[45]	<i>Pinus lambertiana</i> (16)	39°28'N, 121°13'W	Moderate	–12–0	T _s	Drought occurrence	Ring width index
[27]	<i>Pinus sylvestris</i> (26, 16)	48°22'N, 01°06'E	High	68	T _s	Defoliation level	Survival
[46]	<i>Fagus sylvatica</i> (8, 10)	48°37'N, 7°03'E	High	64	T _s	Defoliation level	—
[47]	<i>Pinus halepensis</i> (5)	31°20'N, 35°20'E	Moderate	53–59	B, R	Foliage vitality	—
[48]	<i>Pinus sylvestris</i> (15, 15)	41°19'N, 01°00'E	High	235	T _s	Defoliation level	—
[49]	<i>Pinus sylvestris</i> (8, 8)	41°19'N, 01°00'E	—	272	B, L	Defoliation level	—
[32]	<i>Quercus ilex</i> (16)	42°8'N, 02°27'E	High	90	lignotuber	Dieback presence	—
[50]	<i>Acer saccharum</i> (12)	44°44'N, 73°41'W	Mild	0–12	B	Drought occurrence	—

R, T_s, T_b, B, L, and S stands for roots, trunk sapwood, trunk bark, branches and twigs, leaves, and shoots, respectively. Dash indicates unavailable information

the study lacked true controls. For study 39, they were not considered because controls were reported and in turn had similar values to pre-drought. Only one drought-related study reported tree performance after drought [37]; therefore, it was not possible to quantitatively determine the role of NSC in tree recovery. Data were directly extracted from tables or digitized with DataThief III (V. 1.7), and the effect size was calculated using OpenMEE [51]. The same software was used to examine the influence of the plant family, organ, and their interaction, by meta-regression analyses using mixed-effects models.

Results and Discussion

Drought and NSCs

We found 25 cases (species–study–organ combinations) in 16 studies fulfilling the search criteria. Most drought-related studies (libraries 7, 8, 9) were excluded from our analysis because they were pot experiments (Table S1). Most studies

compatible with our meta-analysis criteria represented a snapshot of categorical conditions assumed to represent drought stress and non-drought stress and are largely concentrated in one single geographical area (Mediterranean Europe) and two plant families (Pinaceae and Fagaceae) (Table 1). Also, most studies determined trunk sapwood NSC concentrations, with branches (including twigs), leaves, and roots, less represented (in that order). From the complete data set, we found that NSC, starch, and sugars concentrations were all significantly lower in drought stressed than in control trees (NSC-All Data, Table 2). These results thus indicate that drought caused decreases in NSC concentrations (question i) and that both sugars and starch were remobilized (question iii). However, these trends were entirely driven by Pinaceae and mostly by NSC in trunks and roots (Table 2). Additionally, we found a significant interaction between “family” and “organ” for NSC ($Q_{3, 65} = 19.27, P < 0.001$), as differences in trunk NSC concentrations between control and drought-affected trees were detected only in Pinaceae (Table 2). For sugars, no interaction was found ($Q_{2, 41} = 0.716, P = 0.699$), while for starch, it was

Table 2 Effect sizes (as standardized mean difference), upper and lower confidence intervals, and *p* values of the difference in NSC, starch, and soluble sugars (SS) concentration of control vs. drought-stressed trees calculated by continuous random-effects models using standard meta-analysis techniques

	Effect size	Lower limit	Upper limit	Tau ²	Q (df)	<i>P</i> value
NSC-All data	−0.683	−1.014	−0.353	0.430	65.37 (24)	<0.001
Fagaceae	−0.396	−0.962	0.170	0.708	39.88 (11)	0.170
Pinaceae	−0.932	−1.243	−0.622	0.079	16.00 (12)	<0.001
NSC-Roots	−1.790	−3.243	−0.337	1.324	10.44 (2)	0.016
NSC-Trunks	−0.801	−1.208	−0.394	0.207	18.78 (10)	<0.001
Fagaceae	−0.186	−0.660	0.287	0.000	2.34 (4)	0.441
Pinaceae	−1.183	−1.569	−0.796	0.031	5.75 (5)	<0.001
NSC-Branches	−0.236	−0.673	0.200	0.033	5.62 (5)	0.289
NSC-Leaves	−0.192	−0.948	0.566	0.369	7.88 (3)	0.620
Starch-All data	−0.392	−0.645	−0.138	0.192	46.39 (25)	0.002
Fagaceae	−0.296	−0.746	0.154	0.224	15.34 (8)	0.198
Fagaceae, Sapindaceae, Salicaceae	−0.406	−0.825	0.012	0.436	39.58 (14)	0.057
Pinaceae	−0.444	−0.710	−0.177	0.000	6.36 (10)	<0.001
Starch-roots	−0.406	−1.103	0.290	0.038	2.21 (2)	0.253
Starch-trunks	−0.471	−0.775	−0.168	0.077	15.23 (11)	0.002
Fagaceae, Sapindaceae, Salicaceae	−0.532	−1.184	0.120	0.377	11.81 (5)	0.110
Pinaceae	−0.486	−0.799	−0.174	0.000	3.42 (5)	0.002
Starch-branches	−0.623	−1.535	0.289	1.025	24.75 (5)	0.181
Starch-leaves	−0.048	−0.503	0.406	0.000	0.36 (3)	0.834
SS-All data	−0.434	−0.759	−0.108	0.388	62.38 (22)	0.009
Fagaceae-Sapindaceae	0.068	−0.226	0.362	0.000	6.90 (9)	0.650
Pinaceae	−0.849	−1.296	−0.402	0.421	36.71 (12)	<0.001
SS-trunks	−0.732	−1.149	−0.315	0.356	34.04 (12)	<0.001
Fagaceae-Sapindaceae	−0.187	−0.639	0.264	0.000	3.86 (4)	0.415
Pinaceae	−1.071	−1.595	−0.546	0.368	22.49 (7)	<0.001
SS-branches	0.064	−0.351	0.480	0.000	1.66 (4)	0.761
SS-leaves	0.255	−0.210	0.719	0.000	0.504 (3)	0.282

not possible to test for the interaction due to insufficient organ x family combinations.

The aforementioned results are consistent with Adams et al. 2017 [26•], who found that only in gymnosperms NSC concentration of extremely drought-stressed seedlings was significantly lower than control (well-watered) seedlings. Both our study and that of Adams et al. (2017) suggest that gymnosperms are more sensitive than angiosperms in terms of NSC responses to drought. However, since angiosperms were mostly represented by Fagaceae in both Adams et al. (2017) and our analysis, it remains unclear whether the lack of drought effect on NSC concentrations of Fagaceae can be generalized to all angiosperms.

Our analysis revealed that NSC concentration reductions due to drought occurred mainly in trunks and roots; trunks are also the organ where starch and SS reductions are observed (Table 2). Decreases in NSC belowground could be related to increased root metabolism associated with the search of water [52] or to the maintenance of ectomycorrhizal symbiosis [53]. Severe reductions in root NSC along with minor or no reductions in leaf NSC concentrations have been found in seedlings subjected to dry-down experiments [54•, 55] and may indicate little use of branch carbohydrates to meet root demands because long-distance transport of carbohydrates gets impaired by drought [1, 56–58]. The consistent decrease in NSC, starch, and sugar concentrations in trunks is unexpected, because trunks represent a large NSC pool in trees due to their higher biomass relative to other organs [59]. Nevertheless, a recent study found that, in temperate trees, trunk NSC pools were generally as low as root NSC pools and that both were lower than branch pools [60]. Thus, for a given C demand, trunks and roots would need to remobilize a higher NSC proportion than branches. On the other hand, it has been hypothesized that the maintenance of an adequate hydraulic integrity represents a significant C demand for trees during drought [61, 62]. Although the steep decrease in NSC, starch, and sugar concentration found in our study in trunks are consistent with the previous idea, conclusive evidence for this premise is still lacking.

Whether drought-induced reductions in NSC concentration are transitory or chronic, it remains largely uncertain as NSC concentrations are generally not reported both during and after drought (for a same phenological stage). However, in the only study where this comparison was found, the trunk sapwood and phloem NSC concentrations in *Fagus sylvatica* were similar between a warmer year with a moderately lower than historical precipitation records (84%) and a climatically normal year [44•]. The same study found that branch NSC concentrations were lower in the drier year and more so for apparently drought-stressed trees than for healthy ones, but both healthy and stressed trees increased their NSC concentrations up to similar levels in the normal year [44•]. Similar results are being observed in forests of *Araucaria araucana* (i.e.,

monkey puzzle, Araucariaceae) in Southern Chile, where tree mortality has occurred after a severe drought during the 2010–2015 period [63, 64]. Right after the drought period (early summer 2016), NSC concentration (averaged for roots and needles) was significantly lower in unhealthy trees compared to healthy ones (5 and 8%, respectively, $p = 0.004$, no difference among tissues); however, after the following year, when precipitation was back to historical “normal” values, unhealthy trees increased their concentrations up to levels closer (but still different) to healthy trees (7 and 9%, for unhealthy and healthy, respectively; $p = 0.015$ for health status) (M. Jiménez-Castillo, unpublished data). The NSC recovery of unhealthy trees was accompanied by a healthier appearance of trees (defined by the levels of regrowth and greenness), which after the rainy year looked more similar to healthy ones (Fig. 1). The cases of *F. sylvatica* and *A. araucana* suggest that the use of NSC stores promotes tree recovery after moderate drought, in support of our hypothesis. Nevertheless, it remains uncertain whether NSC concentrations can be recovered after more severe droughts than those considered by these cases.



Fig. 1 *Araucaria araucana* juvenile trees at Reserva Nacional Conguillio, Southern Chile, 2 years after a 5-year long drought (2010–2015). Notice the dead branches in the lower crowns (corresponding to old branch cohorts) and the vigorous regrowth in the upper crown (corresponding to branches formed after drought). Photo credit Alex Fajardo

Whether drought-induced NSC reductions (i.e., NSC concentrations in apparently unhealthy trees) led to mortality or rather reflect a successful mechanism mediating recovery and eventually leading to survival (question ii) could not be quantitatively answered because very few studies report survival status after NSC sampling. In one of the studies that did report post-drought mortality, only 4 out of 16 drought-stressed trees of *P. sylvestris* (defined by having 50% less leaves and reduced NSC concentrations) died 1 year after NSC records [27]. In this study, the reduction of NSC *per se* seems to account for mortality only partially and, rather, appears as a successful mechanism to prolong survival under drought. Similarly, drought-induced defoliation or dieback could reflect modular responses like leaf shedding or hydraulic segmentation, which increase survival by mediating the stabilization of branch water potential with decreasing soil water potential [36, 65, 66]. If so, what is defined as “drought-affected” trees could be actually the most drought-resistant ones. As such, comparisons of NSC concentrations between trees belonging to categorical stress conditions defined from vigor appearance, as done by most studies (Table 2), should be interpreted with caution. Tree appearance seems a good predictor of the NSC status, but the validity of tree appearance to predict tree survival responses to drought remains unclear.

NSC and Herbivory

We found six studies reporting herbivory effects on NSC in five woody species. Results show both NSC decreases and increases and no change in diverse performance responses, providing mixed evidence for question i (Table 3). In only one study, defoliated individuals had transitory NSC decreases along with similar survival to undefoliated individuals [71] (Table 3). Thus, we found little support for the premise that NSC reductions are linked to post-disturbance tree recovery; most often, NSC concentration and performance varied independently in response to herbivory. Also, a conspicuous decrease in both NSC and survival was found in the only conifer species that our search included, where both surviving and dead *Pinus contorta* trees reduced their NSC concentrations across organs 3–11 months after a bark beetle attack, but surviving trees recovered their NSC concentrations 16 months after the attack (Table 3) [70]. Although this result suggests that the NSC and performance responses depend on the lineage (like for drought), caution must be taken since this is also the only study where the herbivore was a phloem borer. As such, tree mortality was suggested to be driven by a loss of hydraulic conductance [70]. The number of studies included precludes us from making robust inferences on the availability of starch and sugars for remobilization in response to herbivory (question iii); however, in one study, leaf sugars were available for remobilization, while in two studies, starch was the available NSC (from roots and trunk).

Since most insect herbivores are under suboptimal temperatures in temperate latitudes, it has been predicted that warmer conditions will trigger higher insect abundance [23]; this could lead to higher herbivory. However, evidence that herbivory is really increasing under climate change is equivocal, since global warming occurs concomitantly with other global changes detrimental for insects, such as pollution-induced forest disturbances [74]. For *Ormiscodes amphimone*, an outbreak insect causing massive defoliations in the Southern Andes [75, 76], warmer winter temperature correlated positively with outbreak occurrence [77]. However, the main tree target species – *Nothofagus pumilio* – is extremely well-adapted to current levels of defoliation [20]. Juveniles of this species showed 100% survival following three seasons of complete defoliation [16], something never reported to occur naturally. Such impressive tolerance to defoliation relies on C and nutrient conservative allocation at the expense of growth, which allow a fast regrowth of secondary leaves *c.* 2–3 weeks after complete defoliation [16, 78]. Secondary leaves are highly efficient to refill the C stores, thanks to their high nitrogen concentration (related to high photosynthetic rates) and herbivory resistance, which impede the defoliation of secondary leaves when they are formed before the outbreak declines [78]. Although *Nothofagus pumilio* appears to be well-adapted to current severity of defoliation by *Ormiscodes amphimone*, the resilience of *N. pumilio* forests to more severe defoliations remains uncertain. For example a defoliation experiment on juveniles of *N. pumilio* showed an extremely high regrowth capacity and survival; however, recurrent defoliations by the caterpillar could have different effects. In fact, the outbreaks of *O. amphimone* occur much more frequently in some stands than in others [75, 76], and a previous study found that leaf resistance to *O. amphimone* was similar between trees from a stand without outbreak history and counterparts from a recurrently outbreak-affected stand [79]. However, it remains unknown if *N. pumilio* populations without outbreak history are as tolerant to defoliation as populations recurrently affected by outbreaks.

Although potentially more severe herbivory induced by global climate change will occur along with other stresses, we only found one published study examining concomitant effects of herbivory and fire [67]. In this case, fire and herbivory enhanced mortality and reduced the root starch concentrations in comparison to trees that were affected by herbivory only [67]. However, the effects of fire and herbivory were highly dependent on the time of fire, and fires occurring in summer had stronger negative effects compared to fall fires. Herbivory alone or combined with fire led to significant root starch decreases (likely associated with regrowth), while summer fire led to a starch reduction regardless the degree of herbivory [67].

Table 3 Details of studies published between 2008 and 2018 examining effects of herbivory, herbivory, and fire (and its interaction with drought, when available) on NSC concentrations of woody species and on the corresponding post-disturbance plant performance

Ref.	Species	Geographic area	Stress type	severity	Elapsed time (months)	Organs analyzed ⁶	NSC response ⁷	Performance response ⁸
[20]	<i>Nothofagus pumilio</i>	46°06'S, 72°14'W	Folivory ¹	High	12, 24	L, B, T _s , R	[NSC] _{leaf} undef = [NSC] _{leaf} def [NSC] _{branch} undef > [NSC] _{branch} def [NSC] _{root} undef = [NSC] _{root} def	<BAI, =Survival
[67]	<i>Tamarix ramosissima</i>	40.07°N, 118.5°W	Herbivory ¹ + fire	Gradient	0	R	[starch] _{undef} pre-burn Aug > [starch] _{def} pre-burn Aug [starch] _{undef} unburned Dec = [starch] _{def} unburned Dec [starch] _{undef} fall-burn Dec > [starch] _{def} fall-burn Dec [starch] _{undef} summer-burn Dec = [starch] _{def} summer-burn Dec	Survival _{unburned} def. > Survival _{fall burn} def. > Survival _{summer burn} def
[68]	<i>Tamarix ramosissima</i>	36–38°N, 109–114°W	Herbivory ¹	Gradient	12– > 48	T _s	[starch] _{branch} def. > [starch] _{branch} undef.	shoot growth _{def} = shoot growth _{undef}
[69]	<i>Betula pubescens</i>	69°45'N, 27°01'E	Folivory ¹	High	24–48	L, T _s ²	[GFS] _{def} < [GFS] _{undef} .	
[70]	<i>Pinus contorta</i>	51°36' N 123°45' E	Phloem borer	High	16	R	[GFS] _{def} > [GFS] _{undef} .	survival/BAI _{control} > survival/BAI _{alive} attacked > survival/BAI _{dead} attacked
[71]	<i>Populus tremuloides</i>	52°58'N, 114°59'W	Folivory ¹	High		L, B, T _s , T _b	[NSC] _{control} = [NSC] _{alive} attacked > [NSC] _{branch} undef = [NSC] _{branch} def	100% resprouting capacity
[72]	<i>Acacia karroo</i> ²	28°12'S, 32°3°E	Fire	High	4, 6, 10	R	[NSC] _{root} undef > = [NSC] _{root} def	72% resprouting capacity
[73]	<i>Celastrus orbicularis</i>	41°37'N, 87°50'W	Fire	Mid ³	10	R	4–6 mo: [starch] _{unburnt} > [starch] _{burnt}	62% resprouting capacity; 27% final survival
[35]	<i>Adenostoma fasciculatum</i>	34°8'N, 118°52'W	Fire + drought	High	12	L	12 mo: [starch] _{unburnt} = [starch] _{burnt}	95% resprouting capacity; 36% final survival
[35]	<i>Ceanothus spinosus</i>	34°8'N, 118°52'W	Fire + drought	High	12	L	[starch] _{unburnt} > [starch] _{burnt}	100% resprouting capacity; 73% final survival ⁵
[18]	<i>Erica arborea</i>	36°20'N, 5°33'W	Basal clipping	Mid	6	R	[starch] _{unclipped} > [starch] _{clipped}	100% resprouting capacity
[18]	<i>Erica scoparia</i>	36°20'N, 5°33'W	Basal clipping	Mid	6	R	[starch] _{unclipped} > [starch] _{clipped}	100% resprouting capacity
[18]	<i>Erica australis</i>	36°20'N, 5°33'W	Basal clipping	Mid	6	R	[starch] _{unclipped} > [starch] _{clipped}	100% resprouting capacity
[73]	<i>Celastrus orbicularis</i>	41°37'N, 87°50'W	Basal clipping	Mid	< 1	R	[NSC] _{unclipped} > [NSC] _{clipped}	72% resprouting capacity
[34]	<i>Quercus ilex</i>	41°13' N, 0°55'E	Basal clipping	Low ⁴	3, 6, 9, 12	stump	[starch] _{unclipped} > [starch] _{clipped}	100% resprouting capacity; DBH growth _{unclipped} < DBH growth _{clipped} ⁶
[33]	<i>Eucalyptus obliqua</i>	37°25'S, 144°11'E	Basal clipping	Mid	10	R, L	R: [starch] _{preclipping} > > [starch] _{postclipping} R: Mass(starch) _{unclipped} > Mass(starch) _{clipped} L: [starch] _{preclipping} > [starch] _{postclipping} L: Mass(starch) _{unclipped} > Mass(starch) _{clipped} R: [SS] _{preclipping} = [SS] _{postclipping} L: [SS] _{preclipping} = [SS] _{postclipping}	100% resprouting capacity

¹ caused by insects

² saplings

³ dormant experimental fire

⁴ 80% reduction in basal area

⁵ final survival measured 1.5 years after fire (drought started 0.5 years after burning)

⁶ R, T_s, T_b, B, L, S, and Li stands for roots, trunk sapwood, trunk bark, branches, twigs, leaves, shoots, and lignotuber, respectively

⁷ def: defoliated; undef: undefoliated DBH diameter at breast height

⁸ Resprouting capacity was defined as the percentage of disturbed plants that resprout after the removal of most of its above-ground biomass

NSC and Fire

We only found three recent studies evaluating the effect of fires on NSC (Table 3), precluding us to perform a formal metaanalysis. However, a review on the role of NSC after catastrophic disturbances could be performed if three studies of basal clipping experiments were also included (Table 3). This type of experiment traditionally constituted an alternative approach to study NSC dynamics associated to recovery after disturbances like fire [80–82]. The higher severity of fires compared to other disturbances removing most of the above-ground biomass is mainly explained by the deleterious effect of the heat released by fires on the meristematic tissues [6•]; but it is not expected that fires affect the belowground NSC reserves in a different way than basal clipping would. Two studies relating pre-clipping NSC with post-clipping performance were also included in this review since they contribute to directly answering our hypothesis, despite NSC levels after recovery not being provided [83, 84]. Therefore, this review considers a total of eight studies (references 69 and 70, and those included in Table 3).

Root NSC concentrations after clipping or burning were significantly reduced in three of the five species evaluated for fire effects (plants resprouting after fire vs. undisturbed plants) [35, 72] and in the six species evaluated for basal clipping effects (compared to unclipped plants) [18, 33, 34, 73]. In all cases, the percentage of plants recovering after the removal of most the aboveground biomass (i.e., resprouting capacity) was always higher to c. 60% (Table 3). Consistently, pre-disturbance NSC levels were correlated to post-clipping performance in four species [83, 84]. Therefore, there is a strong support for the role of NSC in post-fire resprouting (question i and ii). However, some exceptions were detected (Table 3). The first one was *Celastrus orbicularis*, a liana for which fires did not affected the NSC root concentrations compared to unburnt plants [73]. Nevertheless, fire treatments were applied during the dormant seasons, when the metabolic demands are low, and thus, the NSC levels are high. In fact, the same study found that basal clipping during summer (as a surrogate of growing season fires) did produce a fast decrease in the root starch concentration of *C. orbicularis* [73]. The second exception was reported for the shrub *Ceanothus spinosus*, for which no differences in the lignotuber starch concentration were found between resprouting and control plants during a severe drought episode [35] (Table 3). Within the *Ceanothus* genus, resprouters have higher root NSC concentration than non-resprouters [85], as expected if NSC constitute the carbon fuel that supply resprouting. Therefore, the NSC lignotuber dynamics in burned plants of *C. spinosus* (unchanged compared to undisturbed plants) do not diminish the relevance of NSC as the resprouting fuel.

Apart from the exceptions mentioned above, NSC reserves are severely reduced after resprouting. Even a total depletion

(i.e., concentrations close to zero) of the root starch shortly after resprouting (6 months old) has been reported in *Erica* spp., independently of the clipping frequency [18]. This non-conservative use of the NSC reserves was explained as a strategy to maximize the initial resprouted biomass in order to ensure a rapid replenishment of C reserves through photosynthesis [86]. In fact, the slow recovery rate of the starch reserves after resprouting explained the population decline of *E. australis* under high slashing frequency [18].

Only one study evaluated NSC changes associated to resprouting in different organs (Table 3). This was conducted in *Eucalyptus obliqua* trees (14 years old) subjected to basal clipping, where starch concentration during resprouting was more reduced in the roots than in the lignotuber [33•]. When considering the starch pool size, the percentage reduction was quite similar for the two organs (82 and 85% for the lignotuber and the roots, respectively). It is noticeable that, in this species, only 9% of the total starch mass was stored in the lignotuber compared to 35% in the roots. Altogether, these results indicate that the lignotuber starch supply to resprouting is much lower compared to that of the roots, supporting the role of the roots as the main NSC storage organ in basal resprouters within woody plants (question i) [87].

Studies evaluating changes of different fractions of NSC during resprouting clearly identify starch as the main NSC compound used to feed post-disturbance resprouting. For instance, soluble sugars did not change during resprouting in *Eucalyptus obliqua*, neither in the roots nor the lignotuber, whereas starch concentration did [33•]. Consistently, pre-clipping root starch concentrations were positively related to resprouting success (i.e., initial resprouting, resprouting vigor, and post-resprouting survival) in three Mediterranean shrubs; however, soluble sugar concentrations were related to post-resprouting survival in only one of the studied species [83]. Previous studies on NSC dynamics in undisturbed resprouters have shown lower interannual variability in root starch concentration than in soluble sugars [e.g., [88], but see [89]]. In summary, different evidence points toward starch as the main C reserve stored to fuel post-disturbance resprouting (question iii).

The relationship between resprouting vigor and pre-disturbance NSC has been detected when carbohydrates were expressed in terms of pool size [83, 84], but not when the analyses were based on NSC concentration [84]. These results corroborate the key role of the carbohydrate pool size rather than carbohydrate concentration in resprouting [2]. Both variables tend to be related, but this relationship varies interspecifically with the size and density of the reserve organ [90]. This explains why the NSC concentration co-varies with resprouting vigor in some cases but not always ([e.g., [81]).

Increasing temperatures and decreasing rainfall will probably lead to severe fires concurrent with intense drought [22]. Drought-induced stomatal closure will reduce NSC reserves

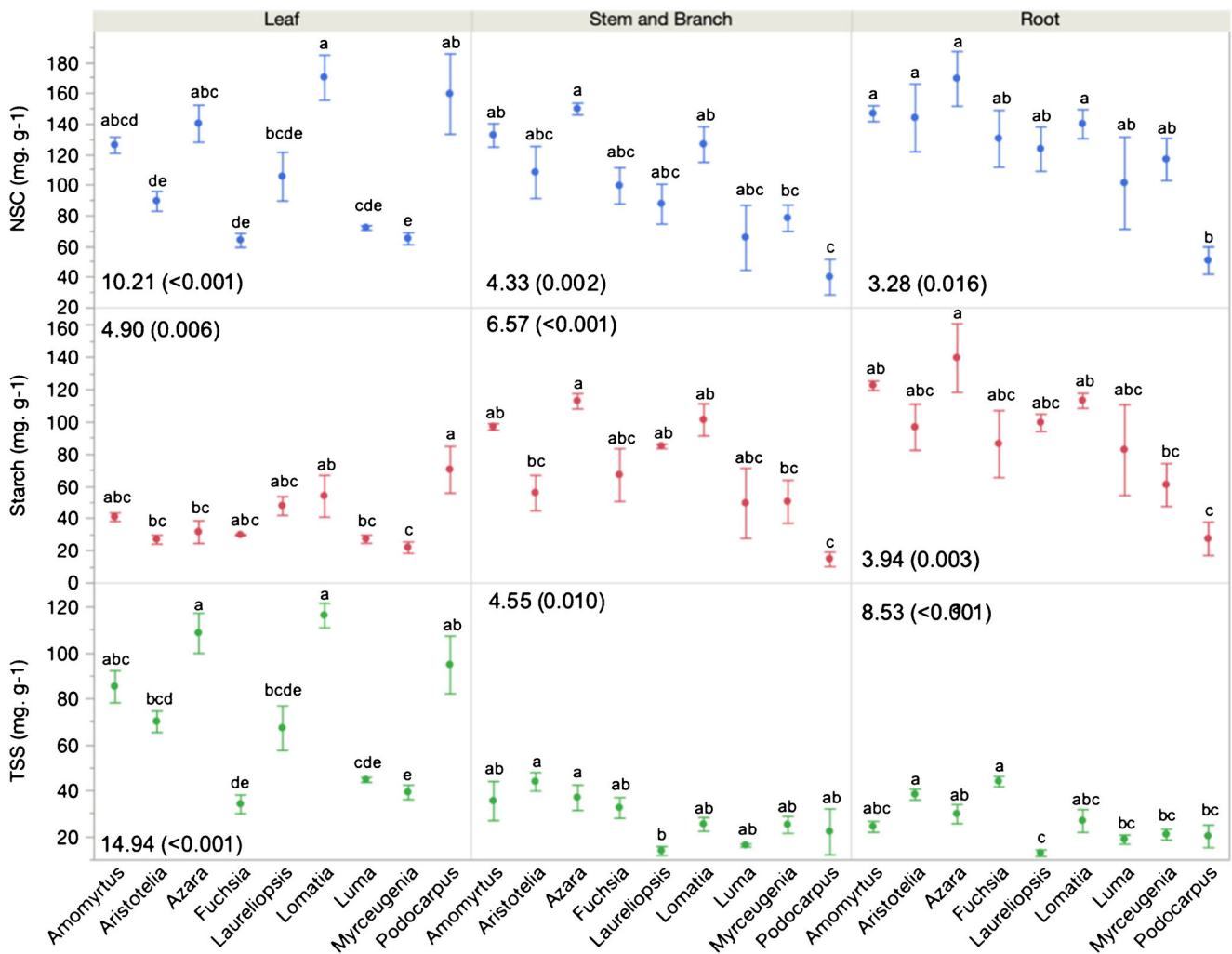


Fig. 2 Mean concentrations (± 1 SE, $n = 2-10$) of nonstructural carbohydrates (NSC = starch + total soluble sugars), starch, and total soluble sugars in late spring for seedlings of nine co-occurring evergreen species of cold-temperate rainforests in Southern Chile: *Amomyrtus luma*, *Aristotelia chilensis*, *Azara lanceolata*, *Fuchsia magellanica*, *Laureliopsis philippiana*, *Lomatia ferruginea*, *Luma apiculata*, *Myrceugenia planipes*, and *Podocarpus nubigena*. Insets

show F ratio (with 3 and 38 degrees of freedom) and P values (in parentheses) of ANOVAs testing the effect of “species.” Species with same letters are statistically similar ($P > 0.05$). Methods and study site as described in a previous study [97]. Note the relatively low NSC and starch concentrations of *Podocarpus nubigena*, the only gymnosperms included in this study

[12], jeopardizing the ability to resprout after a fire event [91••]. In addition, resprouts tend to be more susceptible to embolism due to their higher transpiration rates, stem vessel diameters, and inter-vessel pit density compared to the shoots of undisturbed plants [72, 92, 93]. In fact, runaway cavitation was proposed as the cause of the high mortality reported in resprouting plants during the severe drought affecting the Californian chaparral in 2007 [35].

Conclusions

A role of NSC mediating stress resilience was partly supported for drought and herbivory and strongly supported for fire.

Burning is often a more severe stress than drought or folivory, due to both the deleterious effect of extreme heating during tissue scorching and the negative C balance as consequence of the removal of much of the photosynthetic biomass [6•, 91••]. Thus, the relationship between NSC reserves and post-disturbance recovery was clearer for fire than for herbivory and drought due to the higher disturbance severity of the former. Additionally, our analytical review revealed a strong influence of the lineage on current patterns of NSC reductions and their relationships to tree performance. Conifers are clearly a group where the strongest NSC reductions are being observed in response to drought and herbivory and where such reductions also impact tree growth and/or survival. Several factors inherent to a review could have influenced this result.

For example, different species were examined under different environmental conditions and under a variety of stress or disturbance intensities and durations; this may affect the C pools and fluxes and hence determine the magnitude of NSC reductions and the post-disturbance tree performance. Nevertheless, the consistent evidence of NSC reductions and poor performance showed by Pinaceae species in response to drought and herbivory deserves some analysis.

Gymnosperms appeared on earth earlier than angiosperms, when CO₂ levels were *c.* 2–3 fold higher than current levels and climate was unseasonally warm [94]. By contrast, the angiosperm radiation coincided with a drastic decline in atmospheric CO₂ concentrations [95]. It has been proposed that the higher photosynthetic capacity of angiosperms compared with gymnosperms was a response to this climatic change [95]. Gymnosperms also store much less carbohydrates than angiosperms [60, 96] (Fig. 2), and this pattern could be a consequence of their lower capacity of C assimilation [95]. Although some gymnosperms store lipids, the levels are generally much lower than those of NSC, and they seem less readily available than carbohydrates [4, 5]. Constitutively low NSC concentrations could determine a lower resilience of gymnosperm species to drought and herbivory. Additionally, Pinaceae and Araucariaceae species are characterized by a high stomatal conductance sensitivity to drought [98], which may leave these species particularly vulnerable to drought-induced C starvation.

A major caveat in the current understanding of the role of NSC in forest resilience under drought is the uncertainty regarding the implications of reduced NSC levels in terms of tree performance. Contrary to studies on NSC changes associated to herbivory or fire, most studies on NSC and drought consider a single date of sampling, which impedes robust predictions over time. Measurements of NSC and tree performance not only in the dry period, but also during the recovery phase (e.g., during a wetter year following the dry period), or monitoring the NSC and performance dynamics over several dry years, could help to more comprehensively understand the role of NSC in forest resilience under drought.

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Compliance with Ethical Standards

Frida I. Piper and Susana Paula declare that they have no conflict of interest

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