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1 ***Running Head: Dynamics of NSC in terrestrial plants***

2

3 **Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis**

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24 **ABSTRACT**

25

26 Plants store large amounts of non-structural carbohydrates (NSC). While multiple functions of
27 NSC have long been recognized, the interpretation of NSC seasonal dynamics is often based on
28 the idea that stored NSC is a reservoir of carbon that fluctuates depending on the balance
29 between supply via photosynthesis and demand for growth and respiration (the source-sink
30 dynamics concept). Consequently, relatively high NSC concentrations in some plants have been
31 interpreted to reflect excess supply relative to demand. An alternative view, however, is that
32 NSC accumulation reflects the relatively high NSC levels required for plant survival; an
33 important issue that remains highly controversial. Here, we assembled a new global database to
34 examine broad patterns of seasonal NSC variation across organs (leaves, stems and
35 belowground), plant functional types (coniferous, drought deciduous angiosperms, winter
36 deciduous angiosperms, evergreen angiosperms, and herbaceous) and biomes (boreal, temperate,
37 Mediterranean and tropical). We compiled data from 123 studies, including seasonal
38 measurements for 179 species under natural conditions. Our results showed that, on average,
39 NSC account for ~10% of dry plant biomass and are highest in leaves and lowest in stems,
40 whereas belowground organs show intermediate concentrations. Total NSC, starch and soluble
41 sugars (SS) varied seasonally, with a strong depletion of starch during the growing season and a
42 general increase during winter months, particularly in boreal and temperate biomes. Across
43 functional types, NSC concentrations were highest and most variable in herbaceous species and
44 in conifer needles. Conifers showed the lowest stem and belowground NSC concentrations.
45 Minimum NSC values were relatively high (46% of seasonal maximums on average for total
46 NSC) and, in contrast to average values, were similar among biomes and functional types.

47 Overall, although starch depletion was relatively common, seasonal depletion of total NSC or SS
48 was rare. These results are consistent with a dual view of NSC function: whereas starch acts
49 mostly as a reservoir for future use, soluble sugars perform immediate functions (e.g.,
50 osmoregulation) and are kept above some critical threshold. If confirmed, this dual function of
51 NSC will have important implications for the way we understand and model plant carbon
52 allocation and survival under stress.

53

54

55 **Keywords:** carbon storage, global synthesis, non-structural carbon compounds, NSC,
56 osmoregulation, plant carbon economy, seasonal dynamics, soluble sugars, starch, source-sink
57 imbalances, stress responses, terrestrial plants.

58 **INTRODUCTION**

59

60 Plants acquire carbon via photosynthesis and use most of it as substrate for metabolism (e.g.
61 respiration) and to build structural biomass. A smaller fraction is retained in the form of non-
62 structural carbon compounds (NCC), including non-structural carbohydrates (NSC: starch,
63 soluble sugars and, in some herbs and grasses, fructans), and neutral lipids, which occur in large
64 quantities only in some taxa. NCC pools are broadly referred to as storage because they support
65 metabolism at night and a variety of plant functions during stressful periods when carbon
66 assimilation is insufficient to meet demand (Chapin et al. 1990, Kozlowski 1992, Dietze et al.
67 2014). At any given point in time, carbon assimilation may be greater or lower than demand for
68 plant functions (respiration, growth, etc.), resulting in periods of carbon surplus and deficit,
69 respectively. Accordingly, the NCC pool (biomass x concentration) may increase or decrease. In
70 the long term, plants will not survive if carbon supply via photosynthesis does not meet overall
71 demands, and periods of carbon surplus must necessarily offset periods of carbon deficit. Despite
72 their critical role in the plant carbon balance, our understanding of the dynamics, role and
73 regulation of NCC storage in perennial wild plants remains limited (Dietze et al. 2014, Hartmann
74 and Turmbore 2016) and, in many respects, it has not advanced much since the classical reviews
75 by Chapin (1990) and Kozlowski (1992).

76

77 Although on an annual basis net carbon flux to storage may be small relative to allocation to
78 respiration and growth (but see Klein and Hoch 2015), storage is a critical plant function. On a
79 daily basis, starch storage during the day supplies carbon for growth and respiration at night
80 (Walter et al. 2005, Smith and Stitt 2007). In plants that seasonally shed their leaves,

81 maintenance during leafless seasons necessarily relies on stored carbon (e.g. Barbaroux et al.
82 2003, Crone et al. 2009). In long-lived plants, storage is also important to cope with conditions
83 that reduce carbon input via photosynthesis relative to demand, including shade, drought and
84 disturbances such as herbivory and fire (e.g. Canadell and López-Soria 1998, Bréda et al. 2006,
85 Myers and Kitajima 2007, Palacio et al. 2008, Hartmann et al. 2013a, O'Brien et al. 2014, Piper
86 and Fajardo 2014, Dickman et al. 2015).

87

88 Climate change is predicted to increase the frequency and severity of drought and the incidence
89 of related biotic stress factors, such as insect pests and pathogens (McDowell et al. 2008, 2011,
90 Paritsis and Veblen 2011, Gaylord et al. 2013, Oliva et al. 2014). Not surprisingly, due to the
91 critical role of storage for survival under stress, these predicted changes have led to a recent
92 renewed interest in NCC storage (particularly NSC), which is increasingly acknowledged as a
93 key component in tree and ecosystem models (Sala et al. 2012, McDowell et al. 2013,
94 Richardson et al. 2013, Dietze et al. 2014). Progress, however, is hampered by our limited
95 understanding of the dynamics, role and regulation of carbon storage. For instance, there is
96 evidence that NSC concentrations in mature plants from very contrasted biomes, including arctic
97 (Chapin and Shaver 1988), temperate (Hoch et al. 2003) and tropical (Würth et al. 2005)
98 climates, tend to remain relatively high year round regardless of seasonal fluctuations in climatic
99 conditions, with minimum values being typically 30-60% of the seasonal maxima, at least in
100 perennial organs (cf. previous references). Several, non-exclusive hypotheses have been
101 proposed to explain this pattern: a) plants at current atmospheric conditions store surplus carbon
102 and are not carbon-limited (Körner 2003); b) a significant fraction of storage becomes
103 sequestered over time and is not accessible (Millard et al. 2007); c) relatively high NSC levels

104 are required to ensure long term survival and result from NSC storage being a strong sink in
105 itself (relative to alternative demands) (Wiley and Helliker 2012, Sala et al. 2012, Dietze et al.
106 2014). These alternative views underlie the broader question as to whether plant growth is
107 limited by carbon availability (Palacio et al. 2014, Körner 2015) and have profound
108 consequences on how we understand and model growth and productivity (Fatichi et al. 2013).

109

110 Several aspects may contribute to the limited progress in our understanding of carbon storage
111 dynamics in plants, besides the inherent complexity of the topic. Although intuitive, the
112 definition of storage is difficult (Chapin et al. 1990). In the broadest sense, carbon storage may
113 be defined as carbon that builds up in the plant and can be mobilized in the future to support
114 biosynthesis for growth or other plant functions (Chapin et al. 1990). This definition includes all
115 compounds that serve any cell function but that can be converted (recycled) to provide additional
116 carbon sources. Therefore, with the exception of highly immobile carbon compounds such as
117 cellulose and lignin, any other compound in a plant that can be degraded is, in theory, a storage
118 compound, and any living tissue within the plant can be considered a storage organ (Spicer
119 2014). Although recycling of carbon (i.e., the reutilization of compounds that were initially
120 invested in growth or defense) was thought to be unimportant relative to that of nitrogen or
121 phosphorous (Chapin et al. 1990), there is some evidence that hemicellulose in cell walls may be
122 recycled and used as storage (Hoch 2007, Schädel et al. 2009).

123

124 NSC, including starch (and/or fructans) and soluble sugars, is often used as a measure of storage.
125 However, this use of NSC is problematic for several reasons (Hoch 2015). Firstly, it ignores the
126 storage role of lipids (e.g., Hoch et al. 2003), which along with starch are the only compounds

127 synthesized exclusively for storage, with no other metabolic function. Secondly, and related to
128 the first, NSC is a mixture of two fractions (starch and soluble sugars) with contrasted functions,
129 whose inter-conversion at different time scales (Dietze et al. 2014) make their roles difficult to
130 separate in practice. While starch is a purely storage compound for future use, soluble sugars
131 perform a variety of immediate functions besides supporting new growth and demands for
132 respiration and defense, including their role as intermediary metabolites, osmolytes and
133 substrates for transport (e.g. sucrose) (Fig. 1). Indeed, together with other low molecular carbon
134 compounds and inorganic ions, soluble sugars are involved in signaling (Gibson 2005), cold
135 tolerance (Graham and Patterson 1982), turgor maintenance (Morgan 1984, Hummel et al. 2010),
136 phloem transport (Savage et al. 2016) and, possibly, xylem repair (Salleo et al. 2004, Secchi and
137 Zwieniecki 2011). While some of these functions may be associated with particular stresses (e.g.
138 drought or cold tolerance), others may be critical under any situation. The distinction between
139 immediate vs. future needs is important for predictions of seasonal dynamics of NSC and its
140 components. While the starch fraction may become severely depleted, the immediate metabolic
141 functions of the soluble fraction require this pool to remain above the threshold necessary to
142 carry these functions. The magnitude of this threshold is unknown, but if significant it could help
143 explain the relative abundance of NSC. To the extent that strictly storage compounds also serve
144 as a source of soluble sugars to perform immediate plant functions, plants are likely to prevent
145 acute depletions of the NSC pool at all times.

146

147 NSC seasonal dynamics have often been interpreted in a context of source-sink activity, derived
148 from the idea that “plants accumulate carbohydrates during periods of excess production and
149 deplete them when demand for growth and respiration exceeds the rate of production” as

150 proposed by Mooney (1972) and later by Kozlowski (1992). Although the nuances and
151 complexities of source-sink relationships and multiple functions of NSC have been duly
152 acknowledged (e.g., the fact that many carbon compounds or activities, including storage, can be
153 sources and sinks, depending on the organ and the specific conditions when they occur; Chapin
154 et al. 1990, Hoch 2007), over time the use of a simplified source-sink framework to interpret
155 NSC dynamics has become common among plant ecologists and forest modelers. According to
156 this framework, plants have a source (photosynthesis) and a number of sinks (growth,
157 respiration, export, etc., but excluding storage), and NSC pools grow and shrink purely as a
158 function of the balance between them (i.e., storage is not a regulated process in itself; see Dietze
159 et al. 2014).

160

161 This simplified source-sink framework has led to some predictions. For instance, because
162 deciduous species experience greater asynchrony between supply (restricted to the growing
163 season) and demand (throughout the year and particularly strong during leaf flushing in early
164 spring), seasonal fluctuations of NSC should be stronger in deciduous relative to evergreen
165 species (Kramer and Kozlowski 1979, Chapin et al. 1990, Piispanen and Saranpää 2001).
166 Likewise, seasonal NSC fluctuations should be stronger in seasonal climates, where
167 accumulation during favorable periods supports carbon demands during less favorable times
168 (Chapin et al. 1990, Piispanen and Saranpää 2001). However, data in the literature is not always
169 consistent with these predictions. For instance, fluctuations of NSC are not necessarily stronger
170 in deciduous than in evergreen species (Hoch et al. 2003, Palacio et al. 2007a, Richardson et al.
171 2013). These inconsistencies point towards the need to carefully evaluate NSC seasonal
172 dynamics in the context of all potential functions of its components.

173
174 The large variability in NSC seasonal dynamics in plants was captured in Kozlowski's seminal
175 review over 20 years ago (Kozlowski 1992), which provided invaluable insight on when and
176 where organs in woody plants acted as sources and sinks. However, a quantitative synthesis of
177 patterns of seasonal variation among organs, plant functional types and climate was lacking,
178 perhaps reflecting limited data (most available data were for temperate tree species) and
179 statistical tools at the time. This leaves us with a voluminous case-specific literature from which
180 it is difficult to draw general patterns of variation and their possible biological significance. Here
181 we assembled a global data base on seasonal dynamics of NSC concentrations in plants to
182 examine patterns of variation as a function of organ (leaves, stems and belowground), plant
183 functional type (coniferous, drought deciduous angiosperms, winter deciduous angiosperms,
184 evergreen angiosperms, and herbaceous) and biome (boreal, temperate, Mediterranean and
185 tropical). We refer specifically to total NSC (NSC_T) as the sum of starch, fructans (when
186 present), and soluble sugars, whereas we use NSC to refer generically to any of the fractions
187 analyzed (NSC_T , starch or soluble sugars). These are the most commonly reported NCC in the
188 literature and for which most data is available. However, we recognize that other organic
189 compounds (e.g. sugar alcohols, lipids) are important in some species (see Discussion).

190
191 Our main goal is to explore broad patterns of seasonal NSC dynamics and their potential
192 biological significance in the general context of source-sink relationships but explicitly
193 considering the potential functions of different NSC components (cf. Fig. 1). We hypothesize
194 that:

195

196 1) The concentrations of NSC in different plant organs reflect their respective function and their
197 role in whole-plant C dynamics (Fig. 1). Specifically, we expect: a) high concentrations of NSC
198 (particularly soluble sugars) in leaves, where the proportion of lignified tissue is lower and where
199 soluble sugars are important for osmoregulation, phloem loading and the sustained maintenance
200 of metabolism; b) generally higher concentrations of starch in roots than in leaves reflecting a
201 greater long-term storage role in the former, and c) lower concentrations of NSC in stems, where
202 the relative proportion of lignified and non-living tissues tends to be highest.

203

204 2) Average NSC concentrations and its fractions vary according to plant functional type and
205 biome, although some of this variation may average out at relatively long (e.g., annual) time
206 scales due to contrasted seasonal dynamics (cf. next paragraph). Specifically, a) NSC
207 concentrations will be higher in herbaceous than woody species, reflecting their higher
208 proportion of living, metabolically active tissues. Among woody species, we expect b) higher
209 overall concentrations of NSC in conifer foliage, in agreement with its known role in storage and
210 cold tolerance (Kozlowski 1992). Among biomes, we expect c) generally lower NSC
211 concentrations in tropical ecosystems (Körner 2003), as relatively lower climatic stress levels
212 and high competition for light may result in proportionally higher C allocation to growth.

213

214 3) The concentration of NSC in plants varies seasonally showing consistent patterns within
215 biomes and functional types. Seasonal oscillations (regular changes) may occur in all organs, but
216 a) their magnitude, particularly in woody plants, will be lower in stems due to their generally
217 larger pools (relative to demands) (Körner 1994). Ultimately, NSC oscillations reflect the
218 underlying environmental seasonality under which species live and, in particular, the temporal

219 imbalance between assimilation, growth and stress responses (at different temporal scales). Thus,
220 we expect: b) NSC levels to decline at the beginning of the growing season due to higher
221 demand than supply, and increase towards the end of the growing season. In addition, c) high
222 levels of soluble sugars and low levels of starch will occur during particularly stressful periods
223 (e.g., winter in boreal ecosystems, summer in the Mediterranean) and will be preceded by starch
224 accumulation. In general, we expect d) greater starch oscillations under situations with greater
225 source-sink asynchronies such as in more seasonal environments (e.g., boreal).

226

227 4) Plants keep relatively high minimum NSC concentrations at all times. Specifically, we expect:
228 a) relatively high and similar seasonal NSC minimums relative to maximums across biomes and
229 functional types; and b) lower minimum levels (relative to seasonal maximums) for starch than
230 for soluble sugars, reflecting the longer-term storage role of starch but multiple, immediate
231 functions of soluble sugars.

232

233 **METHODS**

234 *Literature searches*

235 The literature on NSC is vast and covers many fields (plant ecology, food industry, forage,
236 biofuels, to name just a few). In a first phase we conducted a search on the Web of Science
237 (WoS, accessed 27 May 2012) looking for the following combination of words in any field of the
238 papers: “(NSC OR TNC OR starch OR carbohydrate*) AND (plant* OR shrub* OR tree* OR
239 seedling* OR sapling*) AND (seasonal* OR temporal*)”. To target papers that emphasized NSC
240 dynamics, from the 2143 references obtained we selected only those containing the words
241 “(seasonal* OR temporal*) AND (NSC OR TNC OR starch OR carbohydrate*)” in the abstract

242 or title, which reduced the number of references to 1226. We reviewed the abstracts of these
243 1226 papers and selected only those including seasonal NSC data on wild species measured
244 under natural, field conditions. We included forest plantations but not orchard trees or cultivated
245 plants because the latter have been subjected to centuries of artificial selection, with potential
246 consequences on their carbon dynamics. These criteria resulted in a final list of 296 papers.

247

248 All individual NSC data points were extracted from the text, tables or figures of each study, in
249 the latter case using the software TechDig (Version 2.0, Ronald B. Jones). In most studies NSC
250 concentrations were expressed as % or mg g^{-1} dry mass directly. Otherwise, whenever possible,
251 values were converted to mg g^{-1} . When reported results were not in mg g^{-1} and conversion was
252 not possible with the information in the paper, we attempted to contact the original authors for
253 proper conversions. Ultimately, data that could not be expressed in mg g^{-1} dry mass was not
254 included in the analyses. The exact composition of the soluble sugar component varies
255 depending on the method (Chow and Landhäusser 2004), although glucose, fructose and sucrose
256 are often the dominant sugars and are those most commonly measured. However, these potential
257 differences did not alter our results (see *Data analyses* section). Reported values of starch (and or
258 fructans) and soluble sugars were added up to estimate total NSC (thereafter NSC_T) in studies in
259 which this latter variable was not reported or where components other than starch (or fructans),
260 and soluble sugars were measured.

261

262 ***Database construction***

263 Whenever available, additional information was extracted from the original studies regarding
264 their location (latitude, longitude, altitude, climate, community type, biome), type of study

265 (observational or experimental), study duration, species, ontogenetic state (seedling, sapling,
266 mature, cutting), organ (root, stem, leaves, buds, reproductive, mixed aboveground), organ type
267 (fine or coarse roots, lignotuber, main or terminal stem, current or older leaves), tissue (bark,
268 sapwood, heartwood, phloem, cortex, all), sampling month and year, measured NSC component
269 (NSC_T, soluble sugars, starch, other compounds) and detailed methods used during sample
270 processing, extraction and quantification. For studies involving experimental manipulations we
271 only considered results from un-manipulated controls, which were identified in experimental
272 treatment categories. In addition, to ensure good temporal coverage and reduce unwanted
273 variability due to specific characteristics of the sampled material that were not well represented
274 in our data set, we selected only data that fulfilled the following criteria: (1) study duration was
275 at least four months, (2) the same individuals or populations were measured at least three times
276 spanning the length of the study, (3) plants were mature, (4) measurements were taken on leaves,
277 stems, or belowground organs, (5) tissue was not bark, phloem or cortex, (6) values reported
278 were NSC_T, starch/fructans or soluble sugars, and (7) species were land plants (i.e., saltwater and
279 freshwater species were not included). While the original data base contained samples from
280 seedlings, saplings and adults, seedling and sapling data did not sufficiently cover the range of
281 variation among organs, functional types and biomes, and were not included in the final
282 analyses.

283

284 All species names were checked against standard taxonomical nomenclature and species were
285 assigned to broad functional types (coniferous, drought deciduous angiosperms, winter
286 deciduous angiosperms, evergreen angiosperms, and herbaceous) using the information provided
287 in the original articles and searches in mainstream web databases, including The Plant List

288 (<http://www.theplantlist.org/>), Encyclopedia of Life (<http://eol.org/>), Global Species
289 (<http://www.globalspecies.org/>), Integrated Taxonomic Information System
290 (<http://www.itis.gov/>), and Global Biodiversity Information Facility (<http://www.gbif.org/>). We
291 verified that all herbaceous plants in the data base are perennial. From the 296 studies identified
292 in the initial search, 123 studies (including 179 species) matched our final criteria and were
293 subsequently used for all analyses. These studies covered boreal (12 studies), temperate (78
294 studies), Mediterranean (15 studies) and tropical biomes (18 studies), and included at least 21
295 species from each of the considered functional types (Appendix S1: Table S1; Appendix S2: Fig.
296 S1). We only considered biomes for which we had sufficient data (e.g., the two studies in desert
297 biomes were not considered). All grasses from grasslands in mid latitudes were included in the
298 temperate biome.

299
300 Our final analysis included three main explanatory variables: organ, functional type and biome.
301 The variable organ had three basic levels: leaves, aboveground stems, thereafter referred to as
302 stems, and belowground organs (including roots, bulbs, rhizomes and lignotubers). In some
303 analyses belowground organs were split between roots and primarily reserve organs. Although
304 any living tissue in a plant can store starch and SS (i.e. serves as a storage organ to some degree)
305 some belowground organs such as bulbs and lignotubers become specialized to primarily serve a
306 ‘reserve’ function (Chapin et al. 1990). For simplicity, we refer to these as ‘belowground reserve
307 organs’ throughout the text. All belowground organs (including reserve organs) were merged
308 into a single ‘belowground’ category in more complex models when the low sample size for
309 belowground reserve organs did not allow testing for interactions with other variables (cf. *Data*
310 *analyses* section). For grasses and some herbaceous plants, data is often reported for

311 aboveground tissues rather than separately for leaves or stems. In these cases, we evaluated each
312 case individually from visual images of each species. For rosette-like plants and tussock-like
313 grasses, values for aboveground biomass were taken as leaves. A new aggregation variable,
314 ‘context’, was created to include all different combinations of study, site, different levels of
315 environmental conditions within a study or site (e.g., altitude), and organ type (e.g., different leaf
316 cohorts or stem types). This variable was used in statistical analyses to account for additional
317 sources of variability that could affect the absolute value of reported NSC concentrations (cf.
318 *Data analyses* section).

319
320 Before conducting the analyses, the month of the year for data pertaining to the Southern
321 hemisphere was changed to match the seasons in the Northern hemisphere. Note that we use the
322 term season in a general sense, using a mid-latitude meteorological definition in which spring
323 begins on 1 March, summer on 1 June, autumn on 1 September, and winter on 1 December (or
324 the complementary dates for Southern hemisphere locations). This definition is used mainly as a
325 reference to describe general temporal patterns, and it is not necessarily related to the local
326 phenological development of the study species at each site, which was not available for most
327 studies.

328

329 *Data analyses*

330 We carried out three different types of analyses, all of them on three main response variables:
331 soluble sugars (SS) concentration, starch concentration, and their sum (NSC_T). Note that, for
332 simplicity, we refer to starch, but the starch fraction includes fructans for species where this
333 compound was reported.

334

335 *Hypotheses 1 and 2 (average NSC differences across organs, biomes and functional types) –*336 In a first set of analyses we focused on the absolute values of SS, starch and NSC_T

337 concentrations. Data for different months were averaged by different combinations of species,

338 study, context, organ, biome and functional type, and these combinations constituted the smallest

339 experimental unit in our analyses. Three mixed effects linear models (GLMM) were conducted

340 for each response variable: the first model included only organ as fixed factor, the second

341 included organ, functional type and their interaction, and the third included organ, biome and

342 their interaction. Our dataset did not allow for simultaneously testing functional type and biome

343 effects (and their interaction), as many combinations of functional type and biome were not

344 represented (Appendix S2: Fig. S2), reflecting the covariance between these two variables at the

345 global scale. Species identity, study and context, the latter nested within study, were included as

346 random factors in all models.

347

348 Our analysis of NSC concentrations and its fractions relies on available published data.

349 However, a recent study on the comparability of NSC measurements across laboratories

350 concludes that NSC estimates for woody plant tissues may not be directly comparable (Quentin

351 et al. 2015), which could affect our analyses of average NSC concentrations. We therefore tested

352 whether methods used for starch and SS extraction and quantification (largely following the

353 classification by Quentin et al. 2015) confounded our results (Appendix S3). Note, however, that

354 results regarding methodological comparisons per se have to be interpreted with caution because

355 our study was not designed to test them.

356

357 Including a methodological variable improved the fit of the base model explained above in only
358 four out of twenty seven cases (Table 1; see Appendix S3 for details). In each of these four cases,
359 starch was the only response variable affected, and only by extraction methods (SS extraction in
360 one case and starch extraction in three cases). The effect of starch extraction was always in the
361 same direction, with acid extractions resulting in higher starch concentrations than enzymatic
362 methods ($P < 0.05$ in all three cases; Appendix S3: Fig. S2). Although including SS extraction
363 improved the biome model for starch, individual SS extraction methods did not significantly
364 affect starch estimates ($P > 0.05$ for all pairwise comparisons; only water extractions of SS
365 produced marginally higher starch estimates, $P = 0.082$; Appendix S3: Fig. S1). When including
366 methodological effects improved the base model fit, we assessed whether results differed in any
367 meaningful way from the base model. In three out of the four cases, model results were identical.
368 Only in one case (the starch model including organ, functional type and starch extraction as fixed
369 factors) there was a minor difference (Appendix S3). In summary, results remained nearly
370 identical when methodological variables were accounted for (i.e., they are not confounded by
371 methodological effects) and, for simplicity, we opted to present the results using the base model
372 while noting any minor significant differences in the results when accounting for methods.

373

374 ***Hypothesis 3 (seasonal dynamics)*** – In another set of analyses we aimed at describing the
375 seasonal dynamics of SS, starch and NSC_T concentrations using generalized additive mixed
376 models (GAMM). These models expand the GLMM structure to include semi-parametric terms
377 so that the linear predictor incorporates non-linear smooth functions of at least one covariate
378 (Wood 2006). These models were applied to the raw measurements including all the individual
379 data points from all selected studies meeting the criteria specified in the *Database construction*

380 section (i.e., data were not averaged) and included a smooth term describing the temporal
381 dynamics of the response variable as a function of month (using cubic splines as the smooth
382 function; Wood 2006). The (approximate) P -value of this smooth term measures how likely it is
383 that the splines that make up the term equal zero and, hence, can be used to assess the
384 significance of seasonal variations. Two different GAMM models were fitted to each of the
385 response variables. In the first one organ, functional type and their interaction were included as
386 fixed factors, and a different temporal smooth function was fitted for each combination of organ
387 and functional type (factor smooth interaction). In the second model, organ, biome and their
388 interaction were included as fixed factors, and a different temporal smooth function was also
389 fitted for each combination of organ and biome. In all cases, the random part of the models
390 included species identity, study and context (the latter nested within study).

391

392 ***Hypothesis 4 (minimum NSC)*** – Finally, a last set of GLMM analyses was aimed at
393 characterizing the minimum seasonal NSC values as a function of organ, functional type and
394 biome. Minimum values were calculated as a percentage of seasonal maximums for each NSC
395 fraction and for each combination of species, study, context, organ, biome and functional type.
396 Three models were fit to each response variable (SS, starch and NSC_T), with the exact same
397 structure as the models for mean NSC described above (i.e., including organ or organ x
398 functional type or organ x biome as fixed factors and with the same random structure). In
399 addition, minimum NSC concentrations (absolute values) were modeled as a function of
400 maximum NSC and functional type for each organ and NSC fraction, to assess whether the
401 relationship between minimum and maximum NSC varied with functional type. A different

402 model was fitted for each combination of NSC fraction and organ, using the same random
403 structure as before (species crossed with context nested within study).

404

405 All analyses were conducted with the software R (v. 3.1, the R Foundation for Statistical
406 Computing) using the packages *lme4* (GLMM) and *gamm4* (GAMM). NSC, starch and soluble
407 sugars concentrations were not normally distributed and were square root-transformed before
408 conducting the analyses. Percentage minimum values required normalization (square root-
409 transformation) only for starch. In all cases, random effects were assumed to follow a normal
410 distribution with zero mean. The residuals of all reported models were approximately normally
411 distributed and showed no obvious pattern. Significance for all statistical analyses was accepted
412 at $\alpha = 0.05$. Linear hypothesis testing in GLMM was conducted using the function *glht* in
413 package *multcomp*. Coefficients of determination (marginal and conditional R^2) were calculated
414 using the *r.squaredGLMM* function (*MuMIn* package; Nakagawa and Schielzeth 2013).

415

416 **RESULTS**

417 ***Hypothesis 1: Mean NSC variation among organs***

418 On average, NSC_T concentrations were higher in leaves ($144 \pm 10 \text{ mg} \cdot \text{g}^{-1}$; model estimated mean
419 \pm standard error) than belowground ($106 \pm 8 \text{ mg} \cdot \text{g}^{-1}$) and in belowground organs than in stems
420 ($70 \pm 7 \text{ mg} \cdot \text{g}^{-1}$) ($P < 0.05$ in both cases). Starch concentrations were similar in leaves (64 ± 6
421 $\text{mg} \cdot \text{g}^{-1}$) and belowground ($71 \pm 7 \text{ mg} \cdot \text{g}^{-1}$) and significantly higher in these two organs than in
422 stems ($33 \pm 5 \text{ mg} \cdot \text{g}^{-1}$; $P < 0.05$). Finally, results for SS concentrations were similar to those for
423 NSC_T, with leaves ($70 \pm 5 \text{ mg} \cdot \text{g}^{-1}$) $>$ belowground ($42 \pm 4 \text{ mg} \cdot \text{g}^{-1}$) $>$ stem ($34 \pm 3 \text{ mg} \cdot \text{g}^{-1}$) ($P <$
424 0.05 in both cases). These mixed models explained a large fraction of the overall variance in the

425 data (conditional $R^2 = 0.88, 0.83$ and 0.90 for NSC_T , starch and SS, respectively), but the
426 contribution of organ, the fixed factor, was relatively small (marginal $R^2 = 0.10 - 0.16$), implying
427 that a large fraction of the variance was explained by the random part of the models (attributable
428 to differences among species, sites, and conditions within sites).

429

430 When belowground reserve organs, such as bulbs and lignotubers, were considered as a separate
431 category instead of being included in the belowground class (see *Database construction* section
432 above), the results illustrated high NSC_T concentrations in these reserve organs, particularly for
433 starch (Fig. 2). Note that starch and soluble sugars do not necessarily add up to NSC_T because
434 not all studies report the three components (cf. Appendix S2: Fig. S2).

435

436 ***Hypothesis 2: Mean NSC variation among functional types and biomes***

437 The variance explained by the fixed part of the model increased substantially when including the
438 interaction organ x functional type (marginal $R^2 = 0.22 - 0.27$, Appendix S2: Table S1). For all
439 organs, NSC_T and its fractions were generally higher in herbaceous than in woody species (Fig.
440 3; Appendix S2: Table S1). In leaves and belowground, starch concentrations were higher in
441 herbaceous species than in any other functional type, but no significant difference was found
442 between other functional types. In stems, starch concentrations were lower in conifers than in
443 any other functional type (with the exception of herbaceous species when methodological effects
444 were explicitly accounted for; cf. Appendix S3). Soluble sugar concentrations belowground were
445 higher in herbaceous species than in any other functional type, whereas no significant difference
446 was found between other functional types. In leaves and stems, SS concentrations were again
447 highest in herbs, but the differences were only significant with respect to leaves of evergreen and

448 drought deciduous species and to conifer stems. Among woody species, conifers had the highest
449 starch, SS and NSC_T concentrations in leaves, although the differences with other functional
450 types were not statistically significant. In general, differences in NSC_T mirrored the main
451 patterns observed for starch and SS, with conifers having significantly lower NSC_T values than
452 any other functional type in stems and belowground organs (Fig. 3; Appendix S2: Table S1).

453

454 The explanatory power of biome was lower than for functional type (marginal $R^2 = 0.12 - 0.24$
455 for the model including organ x biome interactions; Appendix S2: Table S2). Consistent with
456 this, differences in average starch and SS concentrations were greater among functional types
457 than among biomes (Fig. 4). Mean starch concentrations did not differ among biomes for any
458 organ. Soluble sugars in leaves were higher in boreal and temperate biomes than in tropical ones,
459 whereas Mediterranean systems showed intermediate values. In stems and belowground, SS
460 were similar among biomes. Differences in NSC_T among biomes were similar to those reported
461 for SS (Fig. 4; Appendix S2: Table S2). Because herbaceous species show distinctive patterns
462 and different representation across biomes, we repeated the analyses by excluding herbaceous
463 species. Results remained similar in most cases, with the following exceptions: starch
464 concentrations in stems were significantly higher in tropical than in boreal or temperate
465 ecosystems; and NSC_T concentrations in stems and belowground were higher in tropical than in
466 temperate biomes ($P < 0.05$, results not shown), whereas all other biomes showed intermediate
467 values.

468

469 In the tropical biome, where sample size was similar for evergreen and drought deciduous
470 species (Appendix S2: Table S2), we conducted a separate analysis to compare these two

471 functional types. The results of the corresponding models showed similar concentrations of SS in
472 the three studied organs between the two functional groups. However, relative to evergreen
473 species, drought deciduous species had higher NSC_T and starch concentrations belowground, and
474 higher NSC_T in stems ($P < 0.05$, results not shown).

475

476 ***Hypothesis 3(i): Seasonal NSC patterns across functional types***

477 All functional types considered in this study showed significant seasonal oscillations in at least
478 one organ for NSC_T, starch and SS (Fig. 5). The largest seasonal variations were observed for
479 starch concentrations in leaves and belowground organs for herbaceous and conifer species.
480 Although the amplitude of seasonal variations of the three NSC fractions was generally lower in
481 stems relative to leaves and belowground organs, such lower variation was highly consistent,
482 resulting in statistically significant seasonal variations in stems for all functional types, which
483 were not observed for the other two organs.

484

485 In conifers, seasonal patterns of starch and SS were distinctly different from those of other
486 functional groups, and were characterized by opposite temporal dynamics for starch and SS in
487 leaves: a very sharp starch peak in late spring-early summer coincided with the seasonal
488 minimum for SS (Fig. 5). The temporal dynamics of NSC_T in leaves were similar to those of
489 starch. Starch levels in conifers peaked belowground first (~early spring), then in stems (mid
490 spring) and finally in leaves (late spring-early summer). Soluble sugars belowground and in
491 stems were less variable, with a hint of a seasonal minimum around late spring-early summer in
492 stems.

493

494 Evergreen angiosperm species showed a maximum in starch levels in leaves around late-spring
495 and a minimum belowground later in the season (late summer-early fall). Soluble sugars only
496 showed seasonal variation in stems, with a minimum around late spring-early summer, which
497 was also mirrored in the NSC_T patterns. Drought deciduous species showed low seasonal
498 variation in starch levels, with a seasonal minimum apparent only in stems (~late spring-early
499 summer). Similar temporal patterns were observed for SS and NSC_T in stems, although the
500 minimum occurred slightly earlier, roughly coinciding with a NSC_T peak belowground. In
501 leaves, a clear peak in SS concentrations was observed around midsummer, which was mirrored
502 in the NSC_T patterns. Very similar temporal patterns were obtained when the few non-tropical,
503 drought deciduous species were excluded from the analyses (results not shown). Comparisons of
504 seasonal dynamics for evergreen and drought deciduous species in tropical systems, where
505 sample sizes for the two groups were similar (Appendix S2: Table S2), were also generally
506 consistent with the previous patterns, although there were slightly more pronounced seasonal
507 oscillations in drought deciduous species, particularly for SS in leaves (Appendix S2: Fig. S3).
508

509 Winter deciduous species showed a maximum in starch concentrations around late summer for
510 belowground organs and stems (Fig. 5). Soluble sugars increased during spring and early
511 summer in leaves, when values were lowest in stems and belowground. The seasonal patterns for
512 NSC_T concentrations in winter deciduous species were broadly similar to those for SS, except
513 that the variation of NSC_T in leaves was not significant, and the respective maximum and
514 minimum peaks were somewhat offset in stems and belowground. Note that the presence of
515 leaves' data in the summer and winter for drought- and winter-deciduous species, respectively, is
516 due to the pooling of different studies with slightly different phenologies that end up covering

517 the whole season. Model predictions for these months are thus based on limited data and should
518 be considered with caution.

519

520 Finally, herbaceous species showed a marked peak in starch concentrations belowground around
521 late summer-early fall, and a minimum in SS around late spring-early summer in this same
522 organ, which was reflected in NSC_T levels (Fig. 5). Soluble sugar levels followed a two-peak
523 pattern (~spring and ~fall) in leaves and stems. In leaves, this pattern was accompanied by large
524 and opposite oscillations in starch.

525

526 *Hypothesis 3(ii): Seasonal NSC patterns across biomes*

527 Seasonal oscillations of starch and SS were significant for all organs only in boreal and
528 temperate biomes. The amplitude of the oscillations in these biomes was largest for starch, and
529 particularly noticeable in leaves. In cases where Mediterranean or tropical biomes had also
530 significant oscillations, the magnitude of such oscillation was generally lower than those
531 observed for boreal and temperate ecosystems (Fig. 6).

532

533 Boreal ecosystems showed contrasting temporal dynamics for starch and SS, consistent with the
534 patterns for conifers (Fig. 6). In leaves, stems and belowground organs, starch peaked around late
535 spring-early summer, mid spring to late summer, and midsummer, respectively; whereas SS were
536 lowest around late spring to midsummer in all organs. Temperate biomes were characterized by
537 maximum starch concentrations towards late spring-early summer, particularly in leaves,
538 coinciding with minimum levels of SS in all organs (Fig. 6). These patterns resulted in NSC_T
539 peaking around late-spring in leaves, and showing a minimum around the same time in stems and

540 belowground. Starch in belowground organs of temperate species showed a complex pattern with
541 three peaks around early spring, midsummer and autumn, probably due to the combination of
542 different functional types.

543

544 Mediterranean ecosystems were characterized by low seasonal variability in starch and SS (Fig.
545 6). Soluble sugars showed significant patterns in all organs, with a peak around midsummer.
546 NSC_T also showed seasonal variability belowground, with a minimum in spring and a maximum
547 in late summer. Finally, tropical systems showed relatively low seasonal variability, although not
548 as low as Mediterranean ones (Fig. 6). The most notable patterns were an increase of SS from
549 early to late spring in leaves, a U-shaped seasonal pattern for all fractions belowground and for
550 starch and soluble sugars in stems, and a minimum NSC_T peak in late spring-early summer in
551 stems. Overall, seasonal patterns for all biomes remained qualitatively similar if herbs were
552 excluded from the analyses (i.e., only woody species were considered), except for a conspicuous
553 early spring peak of NSC_T in belowground organs of tropical species (Appendix S2: Fig. S4).

554

555 ***Hypothesis 4: Minimum NSC values***

556 Seasonal minimum and maximum concentrations of NSC_T , starch and SS were positively
557 related, regardless of the organ or NSC fraction being considered, and this relationship was
558 generally similar among functional types (Fig. 7). The only exceptions were NSC_T and SS in
559 leaves and SS in stems of drought deciduous species, where there was no relationship between
560 minimum and maximum concentrations (Fig. 7). Despite substantial seasonal variation in NSC
561 concentrations (cf. previous section), minimum NSC values, defined as a percentage of the
562 seasonal maximum, were relatively high, in most cases between 30 and 50% of seasonal maxima

563 (Figs. 8-10). A histogram of minimum NSC values as a function of organ and fraction showed
564 clearly that starch was the only fraction for which seasonal depletion was common (particularly
565 in leaves and stems, where a substantial proportion of $\min(\text{starch}) \sim 0$ was observed; Fig. 8).

566

567 Mixed models indicated similar minimum NSC_T across organs (overall average = $46 \pm 2\%$),
568 regardless of whether belowground reserve organs were considered a different category or were
569 included in the belowground class. Minimum starch was higher in belowground reserve organs
570 ($40 \pm 6\%$) than in stems ($22 \pm 3\%$) or leaves ($19 \pm 3\%$) ($P < 0.05$), whereas roots showed
571 intermediate values. For SS, minimum values were highest in leaves ($47 \pm 2\%$), although
572 differences were only significant with regards to stems ($37 \pm 2\%$) ($P < 0.05$).

573

574 In general, minimum NSC (NSC_T , starch or SS) values varied much less among functional types
575 and biomes than mean NSC, and the variance explained by mixed models was always lower for
576 minimum NSC (compare Appendix S2: Tables S3-S4 with Tables S1-S2; and Figs. 9-10 with
577 Figs. 3-4). Minimum starch did not differ among functional types for any organ (Fig. 9). Across
578 biomes, minimum starch only differed in stems, being higher in tropical than in temperate
579 ecosystems, whereas Mediterranean and boreal biomes had intermediate values (Fig. 10).

580 Minimum SS did not differ among functional types or biomes for any organ. Finally, minimum
581 NSC_T did not differ among biomes. Among functional types, only stems of winter deciduous and
582 evergreen species had significantly higher minimum NSC_T than herbaceous species (Fig. 9).

583

584 **DISCUSSION**

585 Overall, our results indicate that NSC seasonal dynamics respond to temporal imbalances

586 between carbon uptake (photosynthesis) and demands for growth and respiration. However, they
587 also show that these imbalances are most likely not sufficient to explain seasonal patterns of
588 NSC concentrations in different organs, plant functional types and biomes (Sala et al. 2012,
589 Dietze et al. 2014). Predictions from a simplified source-sink framework that does not account
590 for storage (in itself) as a potentially regulated process and for multiple functions of NSC were
591 not fully met (see INTRODUCTION for a detailed account of this framework). For instance,
592 seasonal oscillations of NSC concentrations were not necessarily greater in deciduous relative to
593 evergreen woody species (Fig. 5), or in more seasonal climates relative to less seasonal ones
594 (Fig. 6). Importantly, we found relatively high and consistent minimum seasonal NSC levels
595 (relative to maximums) regardless of biome and functional type (Figs. 9-10). The reservoir
596 function of storage was supported by frequent starch depletion. In contrast, soluble sugars were
597 seldom depleted (Fig. 8), suggesting that this NSC fraction serves important immediate
598 physiological functions other than long-term carbon storage. Although the multiple functions of
599 different NSC fractions and the regulation of NSC levels beyond a simple balance between
600 carbon uptake and demands for growth and respiration have been acknowledged in the past (e.g.,
601 Chapin et al. 1990), our study evidences that such functions occur across organs, functional types
602 and biomes. These ideas are yet to be fully integrated into our interpretation and modeling of
603 NSC dynamics (Dietze et al. 2014).

604

605 *Caveats/limitations*

606 Although we specifically tested that differences in average NSC and its fractions among organs,
607 functional types and biomes were not confounded by methodological artifacts (see Appendix
608 S3), the quantification of NSC and its fractions remains highly problematic (Quentin et al. 2015).

609 Therefore, the average values given here should be taken with caution until future tests can be
610 done with a resolved and reliable methodology that reduces experimental variability. However,
611 and most importantly, Quentin et al. (2015) showed that relative differences among samples are
612 reasonably consistent within and between laboratories (more so for starch). Since we analyzed
613 relative values within individual studies (see *Data Analyses* section), results pertaining to
614 seasonal dynamics and seasonal minima should also be robust against methodological artifacts
615 related to different extraction or quantification techniques, as well as more subtle laboratory
616 effects. In addition, ‘study’ was included as a random factor in all GLMM and GAMM models,
617 thus accounting for methodological variability among studies.

618

619 Another important consideration is that the compounds analyzed in this study (starch, fructans,
620 and soluble sugars) are those most routinely measured, but they are not the only carbon storage
621 compounds in plants. For instance, in some members of the Pinaceae and some angiosperm tree
622 species like *Tilia*, neutral lipids can comprise almost half of the total non-structural mobile
623 carbon pool (Hoch et al. 2003, Hoch and Körner 2003). These compounds are equivalent to
624 starch in the sense that they are synthesized primarily for storage purposes, with no other known
625 function (Chapin et al. 1990). In addition, certain species accumulate large quantities of other
626 compounds not assessed in this study (e.g., sugar alcohols; Hoch et al. 2003, Arndt et al. 2008).
627 Therefore, interpretation of the results pertains to NSC, measured only as soluble sugars and
628 starch (or fructans). The degree to which seasonal patterns across functional types and biomes
629 would change if all storage compounds were included in the analysis is not known, although
630 previous research in temperate trees suggests that this effect may be relatively small, at least for

631 lipids (Hoch et al. 2003). Unfortunately, storage compounds other than NSC have not been
632 studied for most plant species.

633

634 Our criterion for selection of studies was that they reported at least three measurements over a
635 minimum period of four months. Such criterion was used as a compromise to capture as much
636 temporal variability and data as possible. However, the degree to which seasonal minimums in
637 our analysis reflect a true seasonal (or longer term) minimum is not known, particularly
638 considering that NSC might show very fast changes (e.g., Schädel et al. 2009, Landhäuser
639 2010). Despite this, it is reasonable to expect that studies interested in the seasonal dynamics of
640 NSC capture the most significant periods for the target species based on their phenology.

641 Further, 50 % of the studies considered provided data for at least seven different months (mean =
642 7.3 months per study), and the average study duration was 14.4 months (median = 12 months).

643 Therefore, while the true seasonal minimum may not be strictly captured, we feel confident that
644 seasonal patterns are indicative of approximate times when minimums and maximums occur, and
645 that the estimated minimum magnitudes are reasonable approximations over relatively long and
646 representative periods of time.

647

648 The link between NSC and phenology is at the core of our understanding of NSC dynamics in
649 plants (e.g., source-sink activity; Kozlowski 1992). However, phenology may differ substantially
650 between and within biomes (Pau et al. 2011) and even for different species within sites (e.g.,
651 Palacio et al. 2007a). Unfortunately, detailed phenological information for most studies included
652 in our analyses was not available, which greatly limited our capacity to interpret in depth the
653 temporal NSC dynamics in different biomes and functional types. In addition, since our analyses

654 are restricted to available data, the generality of our conclusions regarding differences among
655 organs, biomes and functional types depends on how representative the data is in a global
656 context. Although our overall sample size is large (more than 15,000 individual NSC
657 measurements covering 179 species), numbers decrease rapidly when data is split by
658 combinations of study factors (Appendix S2: Fig. S2).

659
660 Finally, our analysis is based on concentrations and not pools, and it is limited to most
661 commonly measured tissues in plants. Although absolute pool sizes are desirable in some
662 contexts (Ryan 2011, Martínez-Vilalta 2014), they must be weighted by the biomass of the plant
663 to give an idea of the availability of NSC per unit tissue. Since carbon allocation between tissues
664 and organs with different NSC concentrations may differ across species and sites, pools weighted
665 by biomass may provide a better measure to compare with overall sources and sinks. However,
666 to the extent that seasonal changes in biomass partitioning are likely smaller than changes in
667 concentrations (particularly in woody tissues), changes in concentrations likely reflect, to a large
668 extent, changes in pools. With a few exceptions (e.g., Gholz and Cropper Jr. 1991, Barbaroux et
669 al. 2003, Hoch et al. 2003, Würth et al. 2005, Gough et al. 2009), total NSC pools (and their
670 seasonal dynamics) in woody plants are rarely reported in the literature. In fact, an analysis
671 focusing on seasonal pool dynamics would require repeated and simultaneous measurements of
672 biomass fractions, including roots, which is practically unfeasible in mature woody plants.

673
674 ***Hypothesis 1: Average NSC concentrations are higher in leaves and belowground organs***

675 Although our models explained a large proportion of the variance in average NSC values, the
676 variability explained by fixed factors (organ, functional type, biome) was relatively low. Among

677 those, organ had the highest contribution to explained variance and biome the lowest. In
678 agreement with our initial hypothesis, the concentration of NSC and its fractions in different
679 organs (Fig. 2) was consistent with their respective functions. Concentrations were highest in
680 leaves and belowground reserve organs, and lowest in stems, with intermediate values in roots.
681 High concentrations of NSC_T and, particularly, SS in leaves are consistent with their role as the
682 main sources of carbohydrates, and likely reflect their high metabolic rates, high concentrations
683 of intermediary metabolites, and high proportion of living cells requiring turgor maintenance
684 (Sala et al. 2012, Sala and Mencuccini 2014). Both leaf and root NSC concentrations were high
685 relative to stems, where a higher proportion of tissue is lignified or non-living. In roots, whose
686 osmotic and metabolic demands are intermediate, SS and NSC_T concentrations were also
687 intermediate. Note, however, that differences in SS between leaves, stems and roots also reflect
688 the fact that phloem tissue, where the SS component is likely high, is included in leaves but not
689 necessarily in roots and stems. The results of our global synthesis show that starch
690 concentrations were as high in roots as in leaves, and highest in belowground reserve organs
691 such as bulbs and lignotubers, generalizing previous results from specific case studies (e.g.,
692 Brocklebank and Hendry 1989, Canadell and López-Soria 1998, Pratt et al. 2014).

693

694 ***Hypotheses 2: Highest NSC is found in herbaceous species and conifer needles, with little***
695 ***variation across biomes***

696 As hypothesized, herbaceous species generally showed higher concentrations of NSC_T, SS and
697 starch than woody species, although differences were not always statistically significant (Fig. 3).
698 This result probably reflects the lower proportion of lignified tissue in herbs and it is consistent
699 with studies comparing herbs, graminoids and shrubs from the Arctic tundra (Chapin and Shaver

700 1988) and herbs, shrubs and trees from cold temperate to tropical forests in China (Li et al.
701 2016). In our case, differences were particularly high in belowground organs, likely because in
702 many herbs, roots are the only organ that remains during unfavorable periods. On average,
703 herbaceous plants tend to have higher leaf mass fraction (Poorter et al. 2012) and higher SLA,
704 nitrogen concentration in leaves, assimilation and respiration rates (in leaves and roots) than
705 woody species (Wright et al. 2004, Reich et al. 2008, Kattge et al. 2011). Larger supply
706 (assimilation) and demand (growth, respiration) relative to total pools of stored carbon (smaller
707 in herbs relative to woody plants) likely also explain why seasonal NSC oscillations are larger in
708 herbs than in woody species (Fig. 5).

709

710 Along with herbs, conifer foliage exhibited the highest average NSC concentration, even though
711 differences were not statistically significant with respect to all other functional types (Fig. 3).
712 The role of evergreen conifer foliage as an important storage organ has been recognized
713 previously (Li et al. 2002, Hoch et al. 2003). The fact that conifer stems and belowground organs
714 have lower NSC compared to other functional types is likely associated with the lower amount of
715 parenchyma in conifer sapwood relative to angiosperm species (Spicer et al. 2014, Morris et al.,
716 2016, Plavcová et al. 2016). It has been hypothesized that these lower NSC concentrations in
717 conifer sapwood may result in lower capacity to refill embolized xylem conduits (Johnson et al.
718 2012) and, thus, explain the wider hydraulic safety margins in conifers (Choat et al. 2012).
719 However, xylem refilling remains a highly controversial issue (Cochard and Delzon 2013) and
720 further research is needed to elucidate the link (if any) between low NSC and wide hydraulic
721 safety margins in conifer xylem.

722

723 Overall, we found few significant differences in average NSC, starch and SS concentrations
724 among biomes (Fig. 4). NSC values, however, were significantly higher in leaves of temperate
725 species relative to Mediterranean or tropical ones. This result may reflect the fact that temperate
726 species include many conifers and herbs, whose foliage is NSC rich, while there were no
727 conifers and few herbaceous species in Mediterranean or tropical biomes in our data base. In
728 addition, differences in biomass allocation among biomes and functional types may also help to
729 explain patterns of NSC variation. For instance, the generally lower NSC concentrations in
730 Mediterranean species compared to boreal or temperate ones may be compensated at the plant
731 level by higher relative biomass allocation to roots and leaves in the former (Poorter et al. 2012).
732 Finally, some combinations of biome by functional type were not well represented in our
733 database (e.g., temperate evergreens from the Southern hemisphere), which limits our capacity to
734 draw general conclusions.

735

736 When considering woody plants only, tropical species tended to have higher starch
737 concentrations in stems than boreal and temperate plants, and higher NSC_T concentrations in
738 stems and belowground relative to temperate species. This result is contrary to our prediction
739 that relatively higher C allocation to growth in tropical systems would result in overall lower
740 NSC concentrations (Körner 2003). It is also in contrast with a recent study reporting lower NSC
741 concentrations in the stem sapwood of tropical compared to temperate tree species, where all
742 samples were analysed using the same protocol for NSC (Plavcová et al. 2016). This latter study,
743 however, is based on only four tropical species sampled at a single date during the wet season. If
744 confirmed, relatively high NSC levels in tropical species may indicate an adaptation to high
745 levels of disturbance from herbivory (Coley and Barone 1996) and/or shade, consistent with

746 previous results on saplings (Myers and Kitajima 2007, Poorter and Kitajima 2007, Poorter et al.
747 2010).

748

749 ***Hypothesis 3: NSC seasonal dynamics cannot be explained solely by imbalances between***
750 ***supply and demand for growth and respiration***

751 Seasonal variations in NSC and its fractions were detected in all organs from most functional
752 types and biomes (Figs. 5 and 6). As hypothesized, the amplitude of these seasonal oscillations
753 was generally larger in leaves and belowground than in stems, again highlighting the higher
754 metabolic activity in the former organs. These patterns are consistent with previous results from
755 individual studies (e.g., Hoch et al. 2003, Woodruff and Meinzer 2011), which also suggest that
756 differences among organs may be less marked in smaller plants (e.g., sub-shrubs, Palacio et al.
757 2007b). Although the absolute variation in stems was low, the seasonal variation of NSC_T, starch
758 and SS was consistently significant in stems but not so in leaves or belowground organs. Because
759 stem biomass can be very large (particularly in trees) small oscillations in concentration may
760 represent significant amounts of mobilized carbon, suggesting an important role of stems on the
761 overall seasonal plant carbohydrate dynamics, at least in trees. For instance, Hoch et al. (2003)
762 reported that the amount of non-structural carbon stored in stems and branches would be
763 sufficient to rebuild the whole leaf canopy more than four times in temperate deciduous species,
764 whereas it was ~60% of the amount of carbon contained in foliage for evergreen species. Along
765 the same lines, Barbaroux et al. (2003) found similar total NSC pools in stems and roots of adult
766 *Quercus petraea* and *Fagus sylvatica*, despite much higher concentrations in their roots. Similar
767 results were obtained by Piper & Fajardo (2014) studying *Nothofagus betuloides* and *N. pumilio*.

768 The importance of stem pools may be even larger in tropical trees, where stems plus branches
769 have been found to store 80% of the total tree NSC pool (Würth et al. 2005).

770

771 The strongest seasonal variation in woody plants occurred in leaves and belowground organs of
772 conifers (Fig. 5), despite the fact that conifers tend to have lower rates of assimilation and
773 biomass production per unit of leaf mass than angiosperms (Enquist 2003, Carnicer et al. 2013).
774 As opposed to other woody forms, where seasonal NSC variation in leaves was driven by SS,
775 seasonal variation of NSC_T in conifer foliage was driven by starch, which showed an opposite
776 pattern to that of SS. These results are consistent with the well-known role of sugars promoting
777 cold tolerance and the corresponding conversion of starch to SS in winter (Kozłowski 1992,
778 Amundson et al. 1992, Gruber et al. 2011). High osmotic needs in winter associated with cold
779 acclimation (Graham and Patterson 1982) could also explain the decline in starch levels
780 belowground in autumn and winter in perennial herbs, concurrent with maximum SS
781 concentrations.

782

783 In agreement with a simplified source-sink framework that accounts only for imbalances
784 between supply via photosynthesis and demand for growth and respiration, dynamics of NSC
785 concentrations in most organs and functional types showed maximums prior to or at the onset of
786 the growth season and subsequent declines (at least in mid latitudes, where the correspondence
787 between months and meteorological seasons is clearer; Fig. 5). Our results showed that, among
788 woody forms, seasonal fluctuations were not always greater in deciduous species, in agreement
789 with previous research (Hoch et al. 2003, Palacio et al. 2007a, Richardson et al. 2013). Rather,
790 NSC oscillations were most pronounced in conifers which, with the exception of *Larix decidua*,

791 are all evergreen species. In addition, seasonal oscillations belowground and in stems were
792 similar in drought deciduous and evergreen angiosperms (winter deciduous showed more
793 pronounced variation), although among tropical species seasonal fluctuations were greater in
794 drought deciduous than in evergreen species (Appendix S2: Fig. S3). The fact that deciduous
795 species do not necessarily show higher seasonal variation than evergreen species may indicate (i)
796 that shoot growth is largely supplied by current assimilates and independent of stored carbon
797 reserves (Keel and Schädel 2010, Landhäusser 2010), (ii) that growth demands are lower in
798 deciduous species (e.g., Tomlison et al. 2012) or (iii) that storage is strongly regulated in all
799 species, as reported for herbaceous plants (Smith and Stitt 2007; see also McDowell et al. 2011,
800 Sala et al. 2012, Stitt and Zeeman 2012, Dietze et al. 2014). Additional research is needed to
801 resolve these contrasting (and, to some extent, compatible) interpretations.

802

803 The simplified source-sink framework also predicts stronger NSC oscillations in more seasonal
804 climates, where accumulation during favorable periods supports carbon demands during less
805 favorable times (Kramer and Kozlowski 1979, Piispanen and Saranpää 2001). Our results
806 partially support this prediction. Seasonal variation was most pronounced in boreal and
807 temperate biomes (more seasonal) and lower in relatively less seasonal, tropical biomes (note,
808 however, that species from rainforests and seasonal tropical forests were pooled together in our
809 analysis). At the same time, however, we observed higher minimum starch in stems of tropical
810 relative to temperate species (Fig. 10), which may reflect the relatively high pressure from
811 defoliators in tropical systems (Coley and Barone 1996, Poorter and Kitajima 2007). In addition,
812 our results show that seasonal oscillations were surprisingly low for Mediterranean biomes,
813 which are characterized by a strong seasonality (mild to cold winters and hot, dry summers).

814 These results contrast with other studies showing substantial seasonality of NSC in
815 Mediterranean species (Körner 2003, Palacio et al. 2007b, Rosas et al. 2013, Pratt et al. 2014).
816 Our results, however, are averages for all species within a biome, and seasonal patterns may
817 differ markedly between Mediterranean species, which frequently encompass diverse plant
818 functional types (even within a site, cf. Palacio et al. 2007a). In addition, Mediterranean climates
819 and their seasonality are more variable in time and space than other climates (Lionello et al.
820 2006). As a result, temporal patterns may average out when data from different sites, including
821 species with contrasted leaf habits and growth forms, are combined, which could mask
822 individual seasonal variations. It should also be noted that differences in seasonal variation
823 among biomes likely reflect, to some extent, the uneven distribution of functional types across
824 biomes (particularly herbs and conifers).

825

826 ***Hypothesis 4: Plants rarely deplete their NSC***

827 As initially hypothesized, seasonal depletion of total NSC was rare, and seasonal NSC
828 minimums remained above 40% of the maximum in most cases (average of 46%; Figs. 9-10).
829 This is consistent with positive associations between seasonal minimums and maximums across
830 studies for all NSC fractions (except for some instances in drought deciduous species; Fig. 7),
831 and also agrees with previous studies showing that woody plants rarely completely deplete their
832 NSC pools unless when they are under (natural or artificial) extreme conditions leading to death
833 (Bonicec et al. 1987, Hoch et al. 2002, 2003, Körner 2003, Galiano et al. 2011, Hartmann et al.
834 2013b, Sevanto et al. 2014).

835

836 In a purely passive view of carbon storage (i.e., storage in itself is not regulated and cannot be a
837 competing sink), fluctuations of NSC concentrations should be driven exclusively by
838 phenological changes in assimilation vs. growth and respiration. In this case, the magnitude of
839 NSC fluctuations would depend on the relative magnitude and temporal dynamics of different
840 carbon flows and the observed high levels of minimum NSC concentrations (relative to
841 maximums) would be interpreted as a surplus of carbon at all times (Körner 2003, Fatichi et al.
842 2013, Palacio et al. 2014). Alternatively, if NSC serve multiple functions (in addition to a
843 reservoir of carbon to buffer periods of stress), it would be reasonable to expect that selection has
844 favored perennial species that keep sufficient NSC reserves at all times (Wiley and Helliker
845 2012, Sala et al. 2012, Dietze et al. 2014) and, therefore, complete NSC depletion under field
846 conditions should also be rare. Unfortunately, these two alternative views of carbon storage
847 frequently predict similar NSC temporal dynamics and this critical issue remains difficult to
848 resolve using purely descriptive approaches (as the one used here).

849

850 Although most of our results are consistent with the two previous interpretations, some lines of
851 evidence suggest that the view of NSC storage as purely an overflow of carbon may need re-
852 evaluation. Firstly, NSC seasonal dynamics cannot be explained solely by imbalances between
853 supply and demand for growth and respiration (see above). Secondly, the variability of minimum
854 values (as % of maximums) was much smaller than that of average values, and seasonal
855 minimums remained relatively high and constant among functional types and biomes (Figs. 9-
856 10). Determining what can be considered a high (or low) minimum NSC value is somewhat
857 arbitrary because we lack a biologically meaningful reference. However, there is a growing body
858 of literature relating NSC levels with tree mortality, particularly in the context of drought stress.

859 Only a few of these studies report temporal data (at least three points over time) that allows
860 estimating minimum NSC that are comparable to our values. For these studies, average
861 minimum NSC_T (as % of maximums) in dying trees relative to the maximum value for the
862 corresponding control treatment were 30 - 32% for *Pinus edulis* leaves (Adams et al. 2013,
863 Dickman et al. 2015), ca. 31% for *Sequoia sempervirens* (average between leaves and roots,
864 Quirk et al. 2013), ca. 44% for *Pinus sylvestris* (average across organs; Aguadé et al. 2015) and
865 ca. 48% for *Pinus radiata* (whole-plant level; Mitchell et al. 2014). Similarly, *Pinus edulis* trees
866 experimentally subjected to shade but kept watered died when their leaf and twig NSC_T were ca.
867 35% relative to pre-treatment conditions (Sevanto et al. 2014), and in *Pinus ponderosa* mortality
868 of seedlings subjected to darkness started when whole-plant NSC_T concentrations approached
869 40% of their initial value (A. L. Bayless and A. Sala, unpublished results). Overall, these values,
870 albeit limited and for gymnosperms only (mostly *Pinus*), correspond well with our overall
871 estimate of 46% minimum NSC, supporting the notion that NSC levels are maintained above a
872 minimum critical threshold except during extremely stressful conditions (Sala et al. 2012, Wiley
873 and Helliker 2012, Dietze et al. 2014).

874

875 Finally, and most important, whereas depletion of SS or NSC was very rare, starch depletion was
876 relatively common in all organs (Fig. 8). These results are consistent with a dual NSC function:
877 whereas starch (and fructans) act mostly as reservoirs for future use, soluble sugars perform
878 immediate functions (e.g., osmotic) and, therefore, their concentration has to be kept above some
879 critical threshold (McDowell et al. 2011, Sala et al. 2012, Dietze et al. 2014, Sala and
880 Mencuccini 2014). This view is supported by several studies showing that starch is more
881 depleted than SS under lethal drought (Adams et al. 2013, Mitchell et al. 2013, Sevanto et al.

882 2014, Dickman et al. 2015, Garcia-Forner et al. 2016), and by modeling and empirical results
883 indicating that NSC has two distinct pools with different turnover times (Richardson et al. 2013,
884 2015). These immediate vs. long term functions of NSC are connected by the mutual conversion
885 between starch and SS (Fig. 1), which involves highly regulated biochemical pathways (Dietze et
886 al. 2014). Mutual conversion between starch and sugars commonly results in relative stable NSC
887 levels, compared to larger seasonal oscillations of starch and SS (Fischer and Höll 1991, Terziev
888 et al. 1997, Hoch et al. 2003, Richardson et al. 2013; Figs. 5 and 6 in this study). The
889 requirement to keep relatively high SS concentrations seems to be most pressing for woody
890 species subjected to cold periods, for which the soluble sugar fraction increases during winter
891 months, often at the expense of starch (Figs. 5 and 6), in agreement with previous studies (Sauter
892 1988, Kozłowski 1992, Amundson et al. 1992, Schrader and Sauter 2002, Reyes-Díaz et al.
893 2005, Deslauriers et al. 2009, Gruber et al. 2011).

894

895 ***Conclusion: there is more to NSC than storage (and vice versa)***

896 Despite the inherent limitations of this study (see above), our results confirm many long-held
897 views on the role and dynamics of NSC in terrestrial plants and, at the same time, call for a more
898 careful evaluation of seasonal NSC dynamics. Specifically, the reserve function of NSC,
899 particularly of starch, was clear. Maximum starch values occurred in belowground reserve
900 organs and their seasonal dynamics (e.g., accumulation prior to the growing season in conifer
901 and evergreen angiosperms from mid latitudes) suggests that starch accumulates to support later
902 growth or metabolism when plants remain dormant. At the same time, however, our results show
903 that imbalances between supply and demand for growth and respiration alone are insufficient to
904 explain the observed NSC patterns and their seasonal dynamics. All the patterns we report can be

905 explained if we account for additional roles of NSC (e.g., metabolic, osmotic) and for the fact
906 that performing these roles requires maintaining relatively high concentrations of soluble sugars
907 at all times. If the general dual function of NSC as reservoir (starch) and in performing
908 immediate physiological functions (SS) is confirmed, NSC concentrations at a single point in
909 time may not be a good measure of storage (*sensu* Chapin et al. 1990), which would call for a
910 better definition of what carbon storage is and how it should be measured.

911

912 Further research combining experimental approaches and field studies for a wide range of plant
913 species and environmental conditions is needed to confirm the dual role (immediate vs. future
914 use) and multiple functions of NSC, including their role in plant water relations. We stress the
915 need for concurrent assessment of NSC dynamics with phenology and physiology (e.g., gas
916 exchange, water potential, turgor and hydraulic performance) in different organs to allow for a
917 better integration of whole-plant carbon and water economy. Isotopic techniques combined with
918 modelling of carbon allocation (Richardson et al. 2013; Hartmann et al. 2015; Hartmann and
919 Trumbore 2016), new methodologies to quantify cambial growth at short timescales (Chan et al.
920 2016; Deslauriers et al. 2016) and molecular approaches to decipher gene expression and
921 metabolic profiling (Stitt and Zeeman 2012) offer promising avenues to measure the fluxes into
922 and out of NSC pools and disentangle the roles of different NSC fractions and how they vary
923 over time.

924

925 Our results suggest that plants exhibit relatively high NSC thresholds to support immediate
926 metabolic functions, which could help explain the general abundance of NSC in plants. If so,
927 mortality should occur when NSC fall below these thresholds, even in non-stressed plants.

928 Experiments to confirm these thresholds and whether and how they vary across functional types
929 and physiological strategies are needed. If confirmed, the dual function of NSC, together with
930 the fact that SS are mobile within the plant and can be interconverted to starch in all plant organs
931 (Fig. 1), will have to be accounted for explicitly in models of NSC dynamics in plants and in
932 studies of plant survival under stress.

933

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944

945 **LITERATURE CITED**

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1285 **TABLES**

1286

1287 TABLE 1. *P*-values of the comparison between the base models of NSC as a function of organ, biome and
 1288 functional type (without explicitly considering methodological effects) and the same models including a
 1289 methodological variable as fixed effect. Different columns correspond to different methodological
 1290 variables. $P < 0.05$ (marked with an asterisk) indicates a significant improvement due to the inclusion of
 1291 the corresponding methodological variable (see Appendix S3 for further details).

Model	+ SS extraction	+ SS quantification	+ Starch extraction	+ Starch quantification
NSC _T Organ	0.095	0.177	0.157	0.063
NSC _T Organ x Biome	0.159	0.082	0.146	0.051
NSC _T Organ x FT	0.156	0.218	0.209	0.055
SS Organ	0.079	0.161	NA	NA
SS Organ x Biome	0.236	0.075	NA	NA
SS Organ x FT	0.290	0.064	NA	NA
Starch Organ	0.077	NA	0.011*	0.754
Starch Organ x Biome	0.029*	NA	0.041*	0.911
Starch Organ x FT	0.129	NA	0.009*	0.659

1292 SS: Soluble sugars; FT: Functional type; NA: not evaluated.

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1299 **FIGURES**

1300

1301 FIG. 1. Conceptual diagram showing the main roles and functions of different NSC fractions in
1302 different plant organs. SS designates soluble sugars, and SS_{New} indicates those soluble sugars
1303 that correspond to recently assimilated carbon.

1304

1305 FIG. 2. Box and whiskers plot of NSC concentrations as a function of organ and fraction (soluble
1306 sugars, starch and total NSC). 'Reserve' refers to belowground reserve organs such as bulbs and
1307 lignotubers. Thick horizontal bars (black) show the median, whereas fine dashed lines indicate
1308 the mean. The upper and lower "hinges" correspond to the first and third quartiles (the 25th and
1309 75th percentiles), and whiskers extend from the hinge to the highest (or lowest) value that is
1310 within $1.5 * IQR$ of the hinge. All these statistics are computed across species by context
1311 combinations (context corresponds to different combinations of study, site and specific
1312 measurement conditions; see text). Different letters indicate significant differences between
1313 organs for a given NSC fraction (GLMM models).

1314

1315 FIG. 3. Box and whiskers plot of NSC concentrations as a function of functional type, organ and
1316 fraction (soluble sugars, starch and total NSC). Thick horizontal bars (black) show the median,
1317 whereas fine dashed lines indicate the mean. The upper and lower "hinges" correspond to the
1318 first and third quartiles (the 25th and 75th percentiles), and whiskers extend from the hinge to the
1319 highest (or lowest) value that is within $1.5 * IQR$ of the hinge. All these statistics are computed
1320 across species by context combinations (context corresponds to different combinations of study,
1321 site and specific measurement conditions; see text). Different letters indicate significant

1322 differences between functional types for a given organ and NSC fraction (GLMM models). Note
1323 that when the effect of starch extraction was included, starch concentrations in the stems of
1324 herbaceous species were no longer significantly different from those of conifer stems; that is, the
1325 letter code corresponding to herbaceous species in the central panel of the figure would be 'AB'
1326 instead of 'B' (cf. Appendix S3). Abbreviations: C, conifer; E, evergreen; DD, drought
1327 deciduous; WD, winter deciduous; H, herbaceous.

1328

1329 FIG. 4. Box and whiskers plot of NSC concentrations as a function of biome, organ and fraction
1330 (soluble sugars, starch and total NSC). Thick horizontal bars (black) show the median, whereas
1331 fine dashed lines indicate the mean. The upper and lower "hinges" correspond to the first and
1332 third quartiles (the 25th and 75th percentiles), and whiskers extend from the hinge to the highest
1333 (or lowest) value that is within $1.5 * \text{IQR}$ of the hinge. All these statistics are computed across
1334 species by context combinations (context corresponds to different combinations of study, site
1335 and specific measurement conditions; see text). Different letters indicate significant differences
1336 between biomes for a given organ and NSC fraction (GLMM models). Abbreviations: Bor,
1337 Boreal; Tem, Temperate; Med, Mediterranean; Tro, Tropical.

1338

1339 FIG. 5. Seasonal variation (centered smooths) of NSC concentrations as a function of month for
1340 different functional type (columns) and organ (rows) combinations, according to the fitted
1341 GAMM models (see text). Three NSC fractions (total NSC, starch, soluble sugars (SS)) are
1342 shown in each panel. Shaded areas around the contour plot for each estimate correspond to ± 1
1343 SE. In each panel, asterisks indicate that the smooth term is significant (at $P < 0.05$ (*), $P < 0.01$
1344 (**), or $P < 0.001$ (***) for NSC_T / Starch / SS, in this order). Seasons are indicated by a colored

1345 bar in the x axis of each panel: blue, winter; green, spring; yellow; summer; orange, autumn. For
1346 Southern hemisphere data the month of the year was changed to match the seasons in the
1347 Northern hemisphere. Abbreviations: C, conifer; E, evergreen; DD, drought deciduous; WD,
1348 winter deciduous; H, herbaceous.

1349

1350 FIG. 6. Seasonal variation (centered smooths) of NSC concentrations as a function of month for
1351 different biome (columns) and organ (rows) combinations, according to the fitted GAMM
1352 models (see text). Three NSC fractions (total NSC, starch, soluble sugars (SS)) are shown in
1353 each panel. Shaded areas around the contour plot for each estimate correspond to ± 1 SE. In each
1354 panel, asterisks indicate that the smooth term is significant (at $P < 0.05$ (*), $P < 0.01$ (**), or $P <$
1355 0.001 (***) for NSC_T / Starch / SS, in this order). Seasons are indicated by a colored bar in the x
1356 axis of each panel: blue, winter; green, spring; yellow; summer; orange, autumn. For Southern
1357 hemisphere data the month of the year was changed to match the seasons in the Northern
1358 hemisphere.

1359

1360 FIG. 7. Minimum NSC concentration as a function of the seasonal maximum values, for different
1361 organs and fractions (soluble sugars, starch and total NSC). Each dot corresponds to a different
1362 species by context combination (context corresponds to different combinations of study, site and
1363 specific measurement conditions; see text). Colors indicate different functional types. Simple
1364 linear regressions are shown for each functional type. All values are square-root transformed to
1365 ensure normality. Abbreviations: C, conifer; E, evergreen; DD, drought deciduous; WD, winter
1366 deciduous; H, herbaceous.

1367

1368 FIG. 8. Histogram of minimum NSC (as a % of seasonal maximum values) for different organs
1369 and NSC fractions (soluble sugars, starch and total NSC). Counts correspond to the number of
1370 different species by context combinations in each bin.

1371

1372 FIG. 9. Box and whiskers plot of minimum NSC (as a % of seasonal maximum values) as a
1373 function of functional type, organ and fraction (soluble sugars, starch and total NSC). Thick
1374 horizontal bars (black) show the median, whereas fine dashed lines indicate the mean. The upper
1375 and lower "hinges" correspond to the first and third quartiles (the 25th and 75th percentiles), and
1376 whiskers extend from the hinge to the highest (or lowest) value that is within $1.5 * IQR$ of the
1377 hinge. All these statistics are computed across species by context combinations (context
1378 corresponds to different combinations of study, site and specific measurement conditions; see
1379 text). Different letters indicate significant differences between functional types for a given organ
1380 and NSC fraction (GLMM models). Abbreviations: C, conifer; E, evergreen; DD, drought
1381 deciduous; WD, winter deciduous; H, herbaceous.

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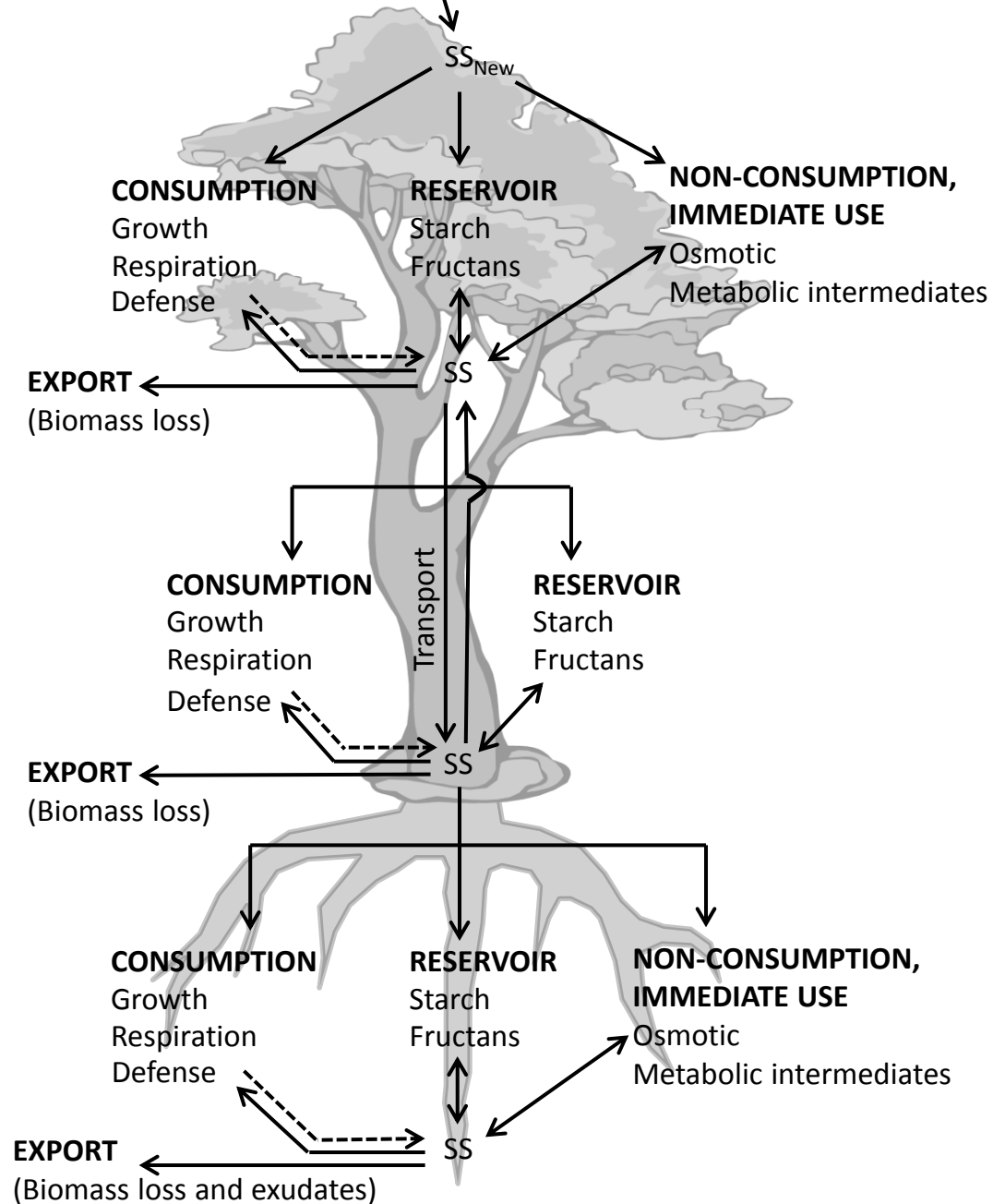
1383 FIG. 10. Box and whiskers plot of minimum NSC (as a % of seasonal maximum values) as a
1384 function of biome, organ and fraction (soluble sugars, starch and total NSC). Thick horizontal
1385 bars (black) show the median, whereas fine dashed lines indicate the mean. The upper and lower
1386 "hinges" correspond to the first and third quartiles (the 25th and 75th percentiles), and whiskers
1387 extend from the hinge to the highest (or lowest) value that is within $1.5 * IQR$ of the hinge. All
1388 these statistics are computed across species by context combinations (context corresponds to
1389 different combinations of study, site and specific measurement conditions; see text). Different
1390 letters indicate significant differences between biomes for a given organ and NSC fraction

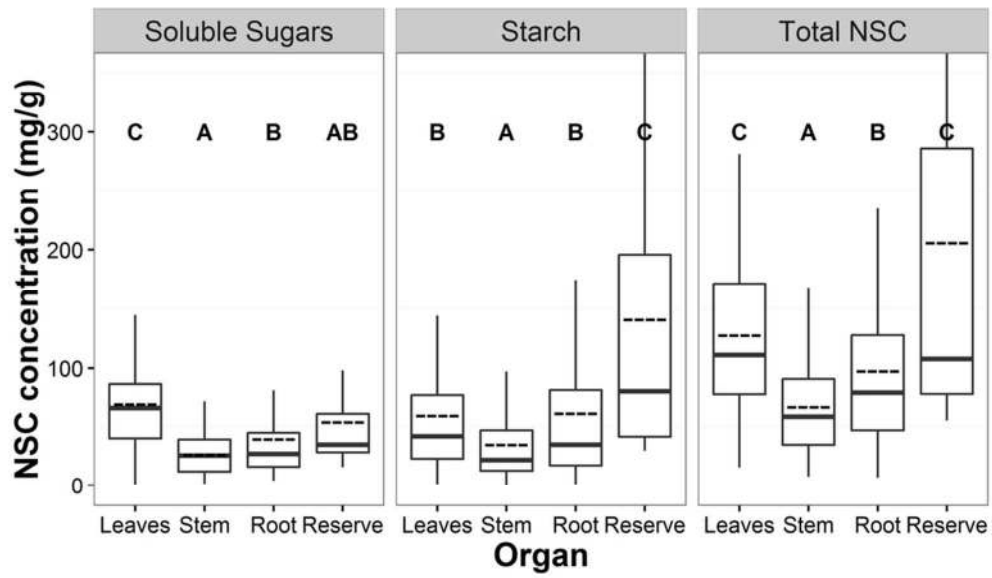
1391 (GLMM models). Abbreviations: Bor, Boreal; Tem, Temperate; Med, Mediterranean; Tro,

1392 Tropical.

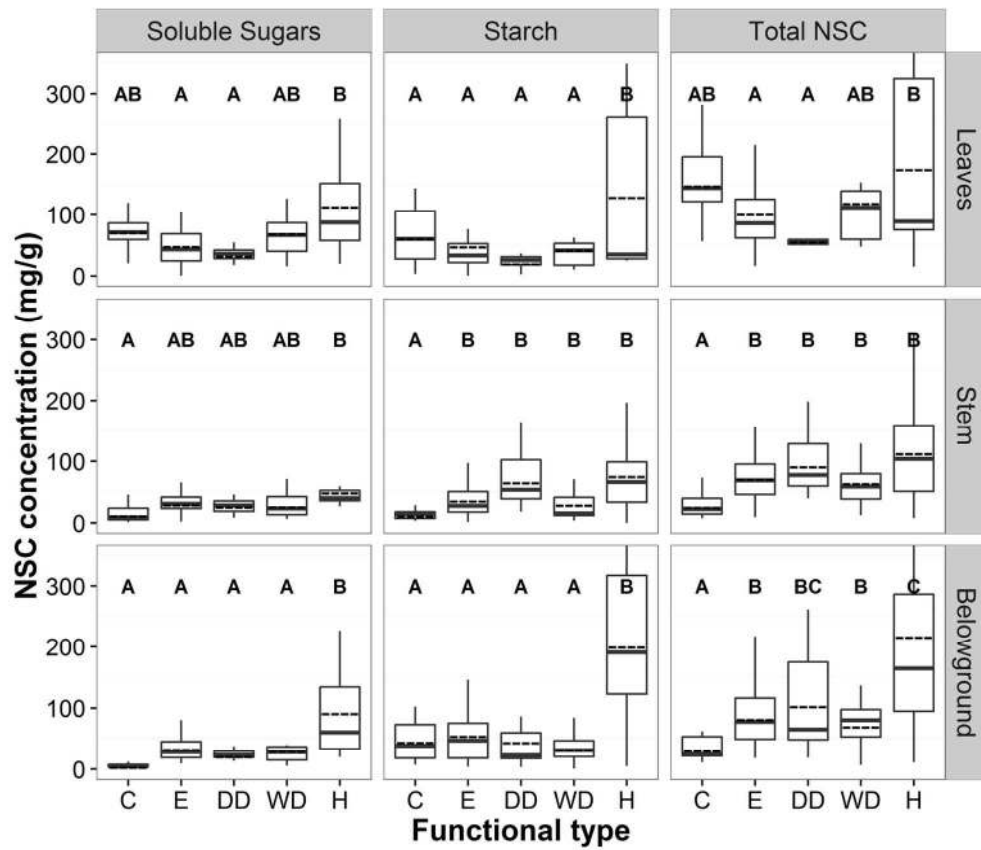
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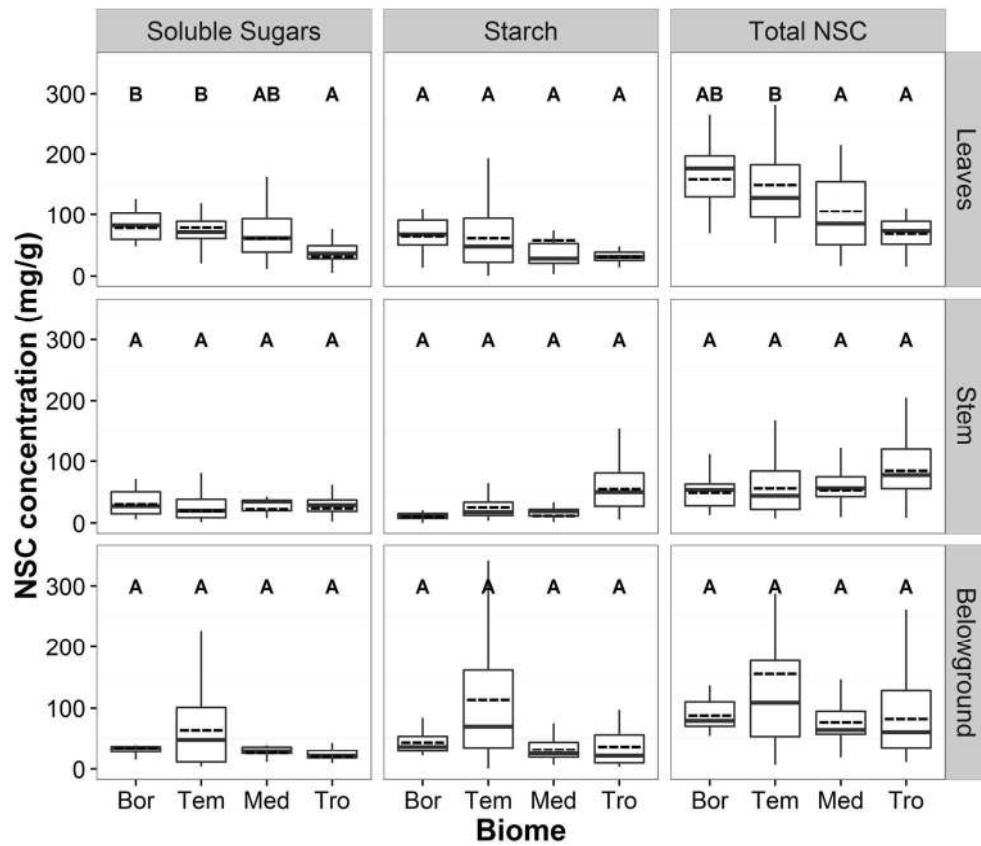




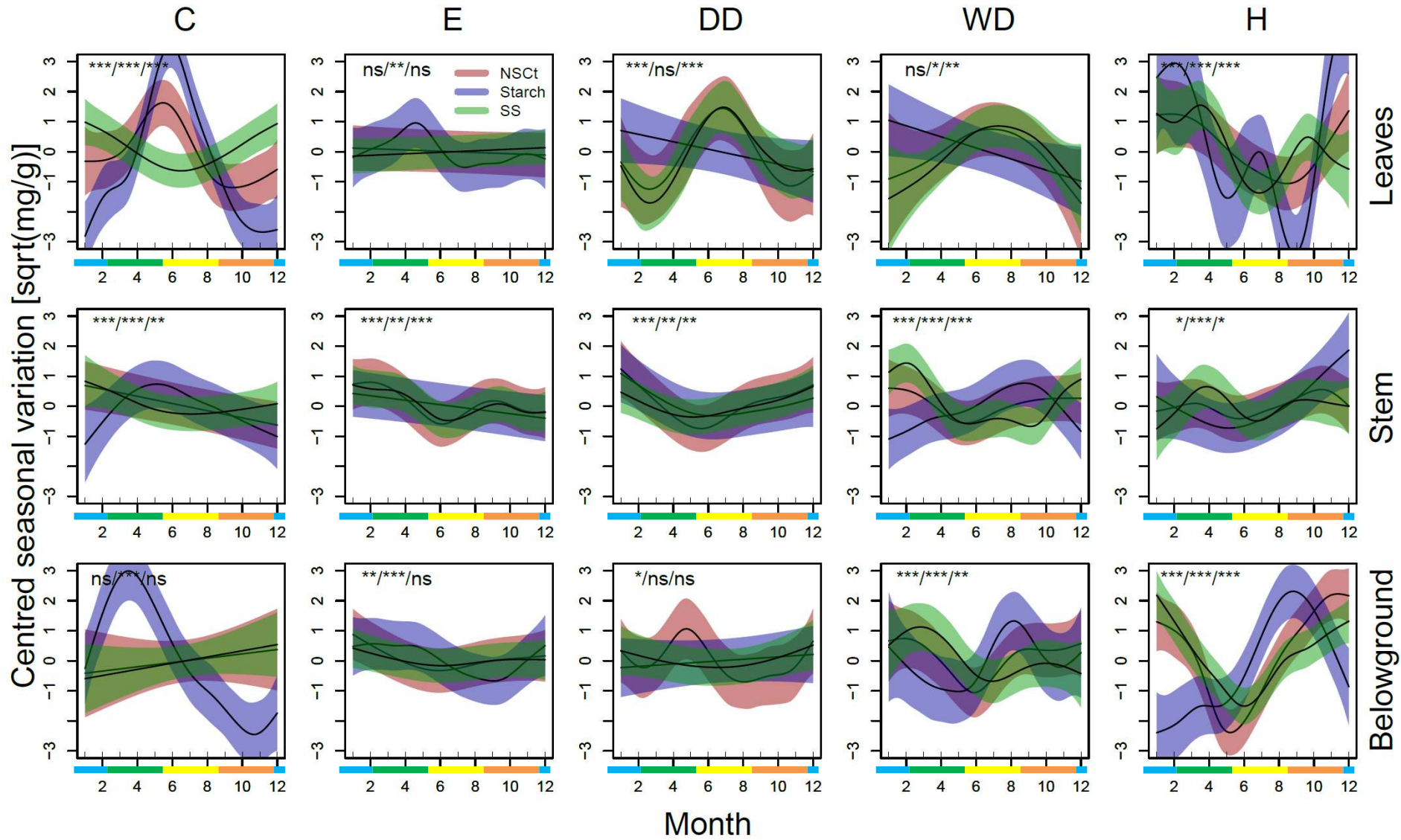
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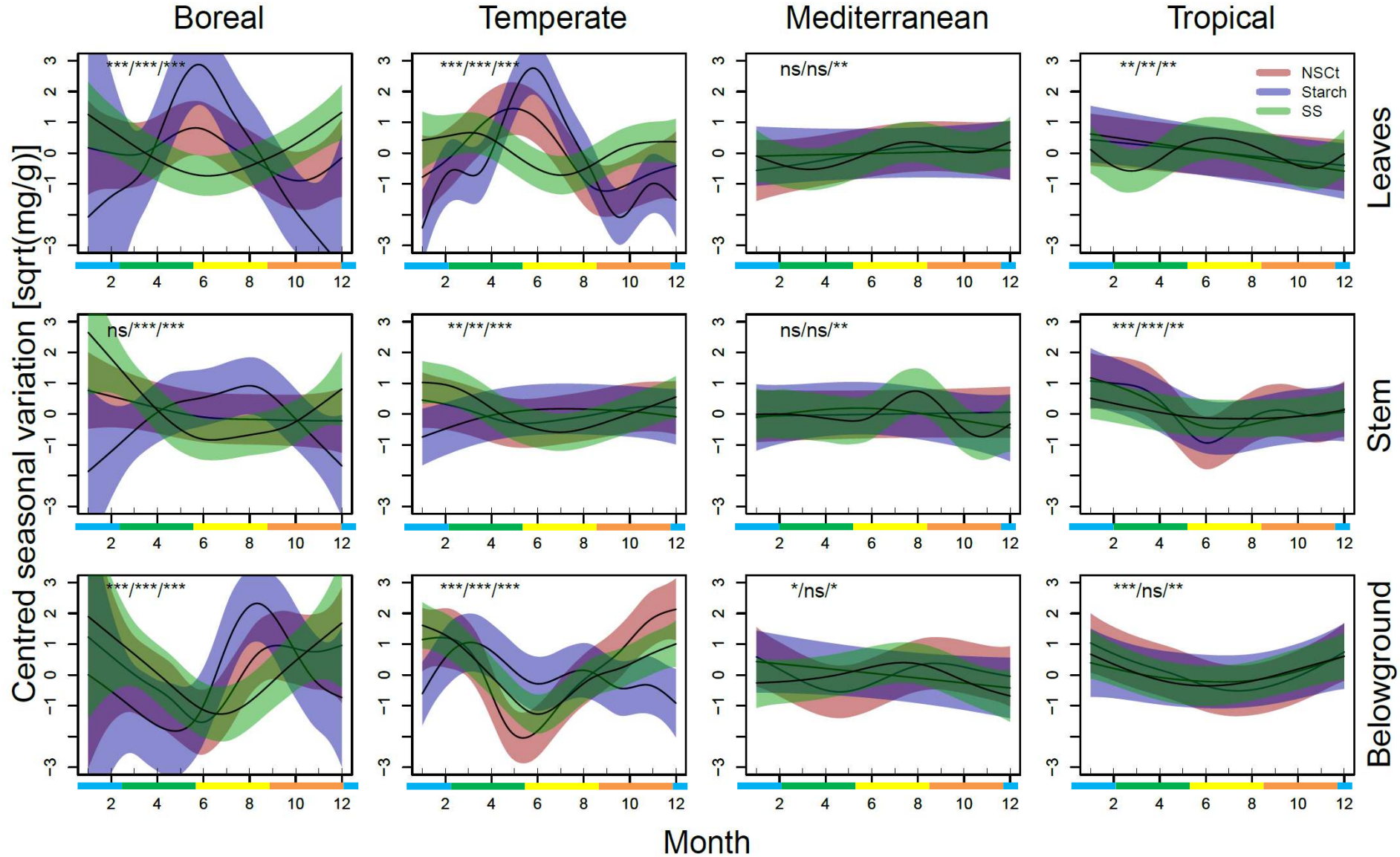


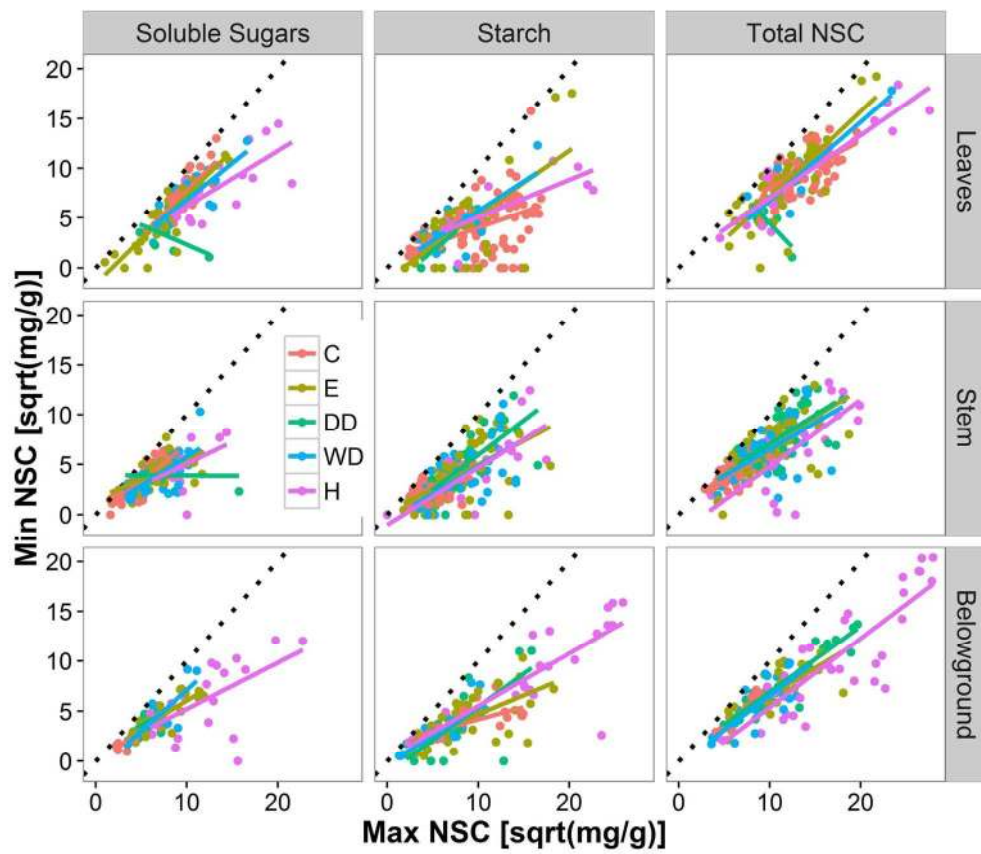
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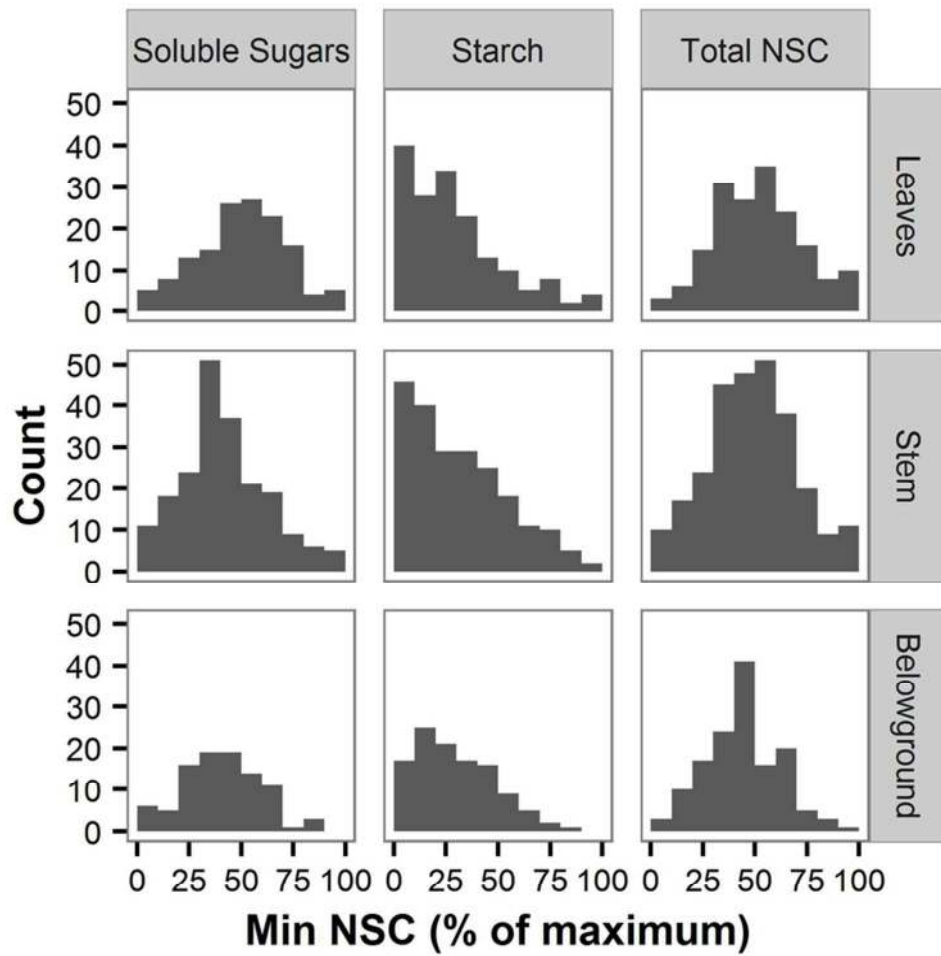
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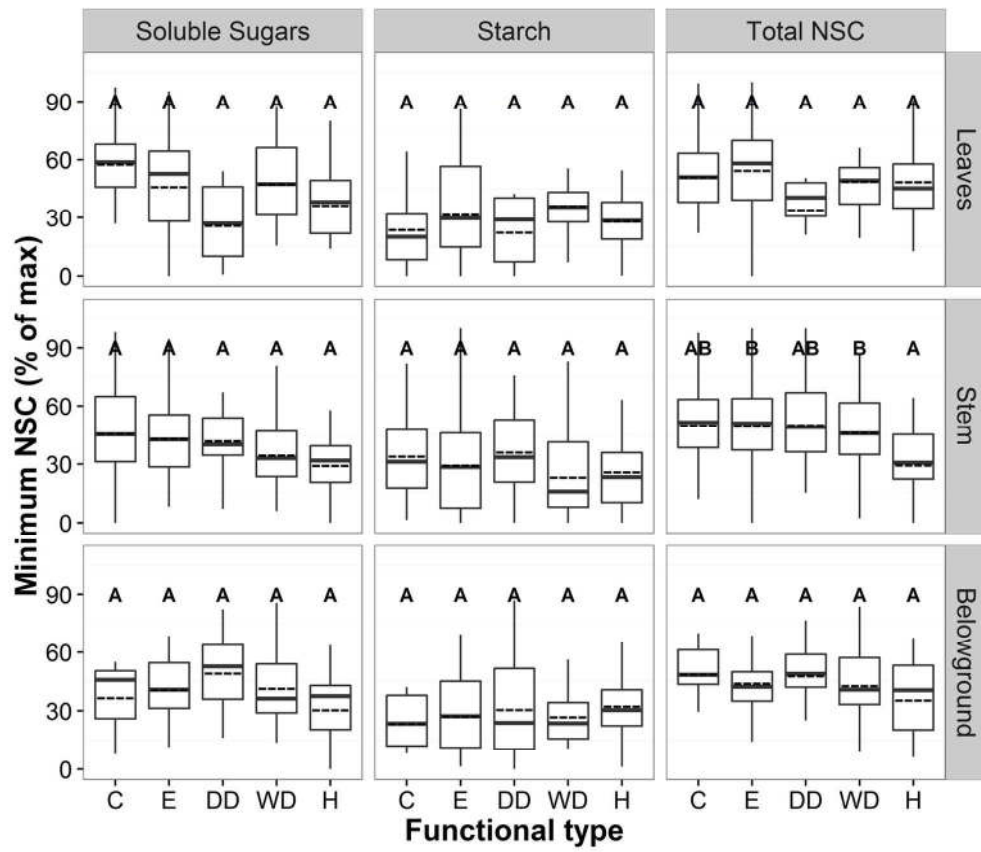




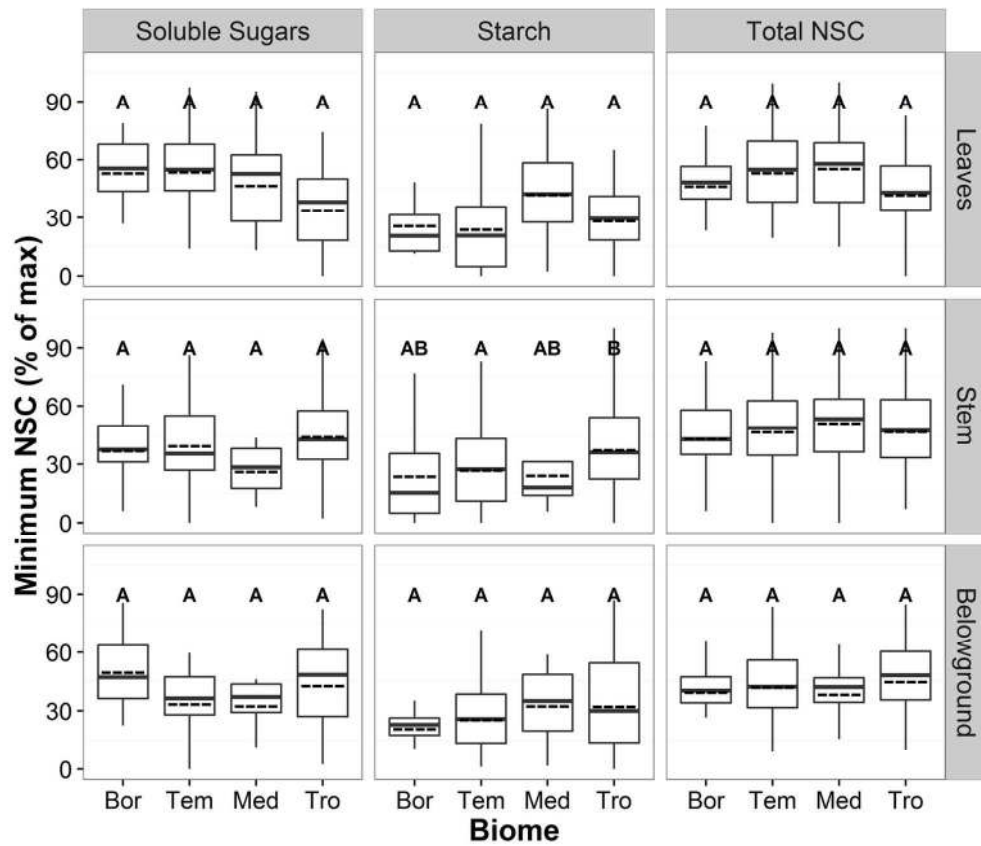
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