

1 **Does carbon storage limit tree growth?**

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21 **Introduction**

22 Storage is a fundamental process that allows organisms to meet variable demand for
23 resources during their development and buffer environmental fluctuations in resource
24 supply. Storage of non-structural carbohydrates (NSC) such as starch and sugars or
25 other carbon C compounds that can be mobilized (sugar alcohols, lipids, proteins) are
26 thought to be critical for survival under stress and disturbance, particularly for long-
27 lived trees. Our view of tree physiology often assumes that, as the availability of CO₂
28 limits photosynthesis, growth is in turn C limited (implying a C source limitation).
29 However, for trees growing under environmental constraints such as nutrient limitation,
30 cold or drought, direct restrictions on tissue formation can occur before a C shortage
31 comes into play (C sink limitation, Körner, 2003). Recent attempts at explaining C
32 limitation under stress suggest that priority allocation to storage could compete with
33 growth and, thus, make assimilated C a limiting resource (e.g., McDowell, 2011; Sala *et*
34 *al.*, 2012; Wiley & Helliker, 2012). These considerations imply that under limiting
35 availability of assimilates, (1) C storage is given priority over growth, because
36 ultimately survival depends more on C demands for metabolism than for growth (Sala *et*
37 *al.*, 2012), and (2) such prioritization is a conservative strategy that occurs frequently
38 regardless of environmental stress (Wiley & Helliker, 2012). The latter implies that
39 most storage by trees occurs at the expense of growth and the frequently observed
40 build-up of NSC in trees under cold and dry conditions reflects a precautionary measure
41 by plants, compatible with (or even indicative of) C limitation for growth (Wiley &
42 Helliker, 2012). These concepts, particularly (2), build on theories that are, so far, not
43 supported empirically, in contrast to the known empirical evidence of greater stress
44 sensitivity of growth over photosynthesis.

45 The questions remain whether (i) C storage by trees is under most circumstances
46 a priority over growth, and (ii) whether growth restriction under stress is the result of a
47 direct impact on meristems or plant-internal tradeoffs of C utilization. Here we argue
48 that there is substantial experimental and observational evidence that growth limitation
49 of plants under environmental stress like critically low temperature or drought is not
50 driven by a limited supply of photo-assimilates, except perhaps for extreme situations
51 when severe constraints on carbon assimilation prevail over several months. We also
52 review the literature dealing with a C-based growth-storage tradeoff in woody plants
53 and conclude that current evidence in support of such a tradeoff is equivocal.
54 Consequently, although a storage-growth tradeoff for C could occur under certain

55 circumstances when C supply becomes indeed limiting (such as after severe
56 defoliation), we conclude that caution should be taken when generalizing such results.

57

58 **Does C availability ever limit tree growth?**

59 One way to test whether carbon limitation plays a role in tree growth is to expose trees
60 to elevated CO₂. After a decade of CO₂ fertilization experiments, growth stimulation
61 has only been documented under high nutrition (e.g. fertilized sites or on former
62 agricultural land) or over short periods of time (i.e. transitorily; see reviews by Körner,
63 2006; Millard *et al.*, 2007; Norby & Zak, 2011, and new data by Bader *et al.* 2013,
64 Sigurdsson *et al.* 2013). For example, the continued response of trees at the Duke FACE
65 site has been explained by a combination of high nutrient availability (at least in one of
66 the three FACE rings) and priming effects through which nutrients were released
67 (Phillips *et al.* 2011). Consequently, so far, there is no empirical evidence for a long-
68 term, sustained stimulation of tree growth by elevated CO₂ in natural undisturbed
69 settings with a natural steady state nutrient cycle.

70 Cell division and expansion are more sensitive to drought and cold stress than
71 photosynthesis (Boyer, 1970; Hsiao & Acevedo, 1974; Körner, 2003; Muller *et al.*,
72 2011; Dosio *et al.* 2012; Galvez *et al.*, 2013). Similarly, the growth reduction found in
73 trees when they reach their maximum height is related to hydraulic constraints directly
74 affecting meristematic growth, rather than C availability (Sala *et al.*, 2010; Woodruff &
75 Meinzer, 2011). The capacity for tissue formation in cold-adapted plants becomes
76 marginal below 5 °C, as shown for xylogenesis (Rossi *et al.*, 2008) and for root growth
77 (Alvarez-Uria & Körner, 2007). Leaf photosynthesis, in contrast, reaches 30-50 % of
78 maximum rates under light saturation at 0 °C and 50-70 % at 5 °C in cold adapted plants
79 (Körner, 2012). Hence, under low temperature or drought, growth ceases long before C-
80 gain does.

81 Situations leading to long-lasting negative C balance could, however, lead to C
82 limitation (Quirk *et al.*, 2013). For instance, trees fully and repeatedly defoliated over
83 11 years, and left to recover for 6 years, had lower growth, but similar NSC
84 concentrations and higher starch concentrations in their stems relative to undefoliated
85 trees (Palacio *et al.*, 2012). However, while these results are consistent with a C
86 limitation of growth induced by preferential allocation to storage, the conditions in this
87 study were quite extreme. Further, they could also be explained by a sink limitation to
88 growth due to bud (Palacio *et al.*, 2008) or nutrient limitation (Millard *et al.*, 2001) after

89 sustained, severe defoliation, or by the lack of a demand-signal from the canopy for
90 cambial activity. Similar to root growth, the cambium may not produce xylem if there is
91 no demand, i.e. no terminal branch growth and transpiring foliage (Zimmermann &
92 Brown, 1974). Detailed investigations on the growth and C allocation processes of long-
93 term defoliated trees and their response to increased C-availability are needed to
94 ascertain which explanation is more plausible. If defoliation systematically leads to C-
95 limitation of growth, then elevated CO₂ should ameliorate growth of defoliated trees.
96 However, results from previous studies are inconsistent with this prediction (e.g.
97 Lovelock *et al.* 1999; Handa *et al.* 2005; Huttunen *et al.* 2007) indicating that growth in
98 defoliated trees is not necessarily C-limited.

99

100 **A closer look at the literature: does increased storage ever reduce tree growth?**

101 Does allocation of C to storage systematically incur a cost in terms of tree growth in the
102 long term, as argued by Wiley and Helliker (2012)? A closer look at the studies cited in
103 support for a competition between C allocation to storage and growth in trees (i.e.
104 Chapin *et al.*, 1990; Kobe, 1997; Canham *et al.*, 1999; Lacointe *et al.*, 2004; Myers &
105 Kitajima, 2007; Poorter & Kitajima, 2007; Silpi *et al.*, 2007; Genet *et al.*, 2010) reveals
106 inconclusive evidence. For example, Chapin *et al.* (1990) cited studies on wild herbs
107 and sugar beet but none on trees and concluded that C allocation to storage over growth
108 “has been critically demonstrated in only a few studies, making it difficult to detect any
109 broad-scale ecological pattern”. Lacointe *et al.* (2004) compared growth and
110 carbohydrate allocation in the branches of young walnut trees in shade or full sunlight.
111 Shaded branches grew less but had similar NSC concentrations in sun or shade. They
112 concluded that reserve levels were maintained in shaded branches “possibly at the
113 expense of growth”. However, this assumes that maximizing growth in the shade is an
114 efficient alternative, which is not necessarily the case. Even so, their results also showed
115 that shaded branches allocated slightly more labeled C to growth than to storage, thus
116 casting some doubt on their assertion that allocation to storage occurred at the expense
117 of growth. Further, growth in the shade could be regulated to prevent excessive self-
118 shading without invoking competition with storage.

119 Adaptation to disturbance such as fire can lead to differences in C allocation and
120 growth. Resprouter species or ecotypes generally show greater allocation to NSC (i.e.
121 larger NSC concentrations and pools) than seeders (Bell, 2001; Verdaguer & Ojeda,
122 2002), and generally exhibit overall slower growth (Bell, 2001). However, results are

123 not consistent across families and species (e.g. Knox & Clarke, 2005; Clarke & Knox,
124 2009). For instance, Chew & Bonser (2009) analyzed differences in growth rate and
125 allocation to NSC of seedlings of eight pairs of species, each including a resprouter and
126 a seeder. They found no differences in growth rate or starch content between
127 regeneration strategies of comparable lifespans, and concluded that differences in life
128 history, rather than in NSC allocation, were controlling their respective growth rates.

129 Finally, the majority of studies that evaluated the existence of a tradeoff between
130 C allocation to NSC (measured as change in NSC pools or concentrations) and growth
131 in trees used correlation analyses. We note however, that while some studies document
132 a negative correlation between growth and NSC allocation (Myers & Kitajima, 2007;
133 Silpi *et al.*, 2007; Chantuma *et al.*, 2009; Genet *et al.*, 2010), others do not (Canham *et*
134 *al.*, 1999; Poorter & Kitajima, 2007; Imaji & Seiwa, 2010; Piper, 2011; Palacio *et al.*
135 2012). Overall, results are species-specific (Genet *et al.*, 2010) or vary through
136 ontogeny (Myers & Kitajima, 2007). Furthermore, correlation does not imply causation,
137 and negative correlations between NSC concentrations or pools and growth do not
138 provide unequivocal evidence of a tradeoff between the two. Alternatively, direct
139 constraints on growth (sink limitation) could lead to increased NSC availability for
140 storage (Genet *et al.*, 2010; Hoch & Körner, 2012; Palacio *et al.*, 2012). For example
141 Silpi *et al.* (2007) and Chantuma *et al.* (2009) showed that rubber gum trees tapped or
142 treated to increase latex production had higher NSC concentrations, but grew less than
143 control trees. Because latex is rich in C, this was interpreted as evidence of active C
144 allocation to storage in response to tapping, thereby limiting growth. However, other
145 factors, such as turgor maintenance or nutrient supply, could limit growth and enhance
146 C availability for storage and latex production (Junjittakarn *et al.*, 2012). One would
147 expect that elevated CO₂ would enhance latex production, but when tested, the opposite
148 was found, namely a reduction in latex production while NSC concentrations rose in
149 response to elevated CO₂ (Häring & Körner 2004). To evaluate the potential
150 consequences of increased C allocation to storage on tree growth we need to move
151 beyond correlative studies and experimentally determine if tree growth is limited by C-
152 availability and the mechanisms leading to the observed increases in C-storage pools.

153

154 **Why results from *Arabidopsis* cannot be directly extrapolated to trees**

155 To date, the only evidence of plant growth being limited by preferential C allocation to
156 NSC storage comes from light-limited, C-starved *Arabidopsis* plants (Smith & Stitt,

157 2007; Gibon *et al.*, 2009). However, up to which point can results from *Arabidopsis* be
158 extrapolated to trees? Trees are long-lived plants with a complex structure, composed of
159 multiple, semi-autonomous modules (Sprugel *et al.*, 1991). C and nutrients are allocated
160 to storage in specialized organs and tissues over many years. In contrast, the
161 monocarpic senescence exhibited by *Arabidopsis* plants relies on NSC stored largely in
162 foliage (assimilatory starch in chloroplasts) and short-lived axial tissue, for seed
163 production. In essence, most of the C-storing tissue of *Arabidopsis* photosynthesizes,
164 while the majority of C-storage organs in woody species do not. When C becomes
165 limiting in herbaceous plants it is hence possible that *all* stores within the plant are
166 mobilized and consumed (Smith & Stitt, 2007). Also, because of the monocarpic
167 senescence, C invested in starch in leaves might contribute directly to reproductive
168 fitness. In trees, C-starvation may be found at the leaf or even the branch level without
169 depletion of NSC pools at the whole tree level (Würth *et al.*, 2005). In contrast to
170 *Arabidopsis*, it is probable that a large proportion of the C found in NSC pools in large
171 trees is actually sequestered (and hence not functional), rather than stored (Millard &
172 Grelet, 2010). Also, if starch serves as a source of compatible solutes for hydraulic
173 functions (Sala *et al.*, 2012), plants may prevent falling below certain minimum levels
174 of stored NSC. If so, not all *measured* NSC may be available for growth and respiration
175 and starch pools do not need to be completely exhausted before trees have no NSC
176 storage left available for growth and respiration. Consequently, measuring NSC pools
177 may inform about the overall C-supply status of trees (particularly when used in
178 comparative terms, e.g. Hoch and Körner, 2005), but cannot estimate the size of the
179 readily available C stock. The different dynamism of NSC pools in trees as compared to
180 annual plants leaves some leeway for the occurrence of a tradeoff between C allocation
181 to storage vs. growth in trees, even when starch pools are present. It also illustrates the
182 difficulties in translating results from *Arabidopsis* to trees.

183

184 **Conclusions and open questions for future research**

185 There is experimental evidence showing that: (1) closed tree stands on undisturbed
186 forest soil do not show a sustained stimulation of growth by CO₂ fertilization and, (2)
187 cell growth processes are commonly more sensitive to stress than processes related to C
188 gain. This suggests that growth of mature trees is seldom limited by C availability. In
189 contrast, evidence in support for a tradeoff between C storage and growth in trees is, to
190 date, inconclusive. Under cold or drought stress, there are physiological limitations to

191 tissue formation, such as a critical cell turgor, that prevent structural growth irrespective
192 of C supply. However, during certain developmental or phenological stages and under
193 environmental conditions leading to true C limitation (e.g. sustained severe defoliation,
194 deep shade) a tradeoff between storage and growth could be possible. The issue is now
195 identifying these situations in different organs and their relevance for the C balance and
196 survival of trees (Hartmann *et al.*, 2013; Galvez *et al.*, 2013).

197 The fact that genes which control basal functions in all plants are sensitive to
198 sugar and starch (Gibon *et al.*, 2009), suggests that such ‘sensing’ is likely universal in
199 plants. The consequences of this for trees and their C balance are, however, completely
200 unknown. Although we currently know a lot about the molecular regulation of C-
201 storage at the cellular level, there is still a large gap of knowledge at the level of the
202 whole plant, especially for large plants like trees. System-level approaches integrating
203 data from transcriptomic, enzymatic, metabolomic and growth analysis similar to those
204 already implemented in *Arabidopsis* (Smith & Stitt, 2007) or agricultural crops (Muller
205 *et al.*, 2011) but applied to woody plants, could offer promising tools to unravel the
206 timing of events leading to the coordination of C allocation and growth in trees (Stitt &
207 Zeeman, 2012).

208 A pressing need is to identify the fraction of NSC that is available (potentially
209 mobilized) in trees (Millard & Grelet, 2010; Rocha, 2013). This implies estimating the
210 dynamics of NSC pools and their lifetime plus the fraction of NSC that is sequestered
211 (i.e. never recovered). Time-integrated tracing techniques, such as using bomb ¹⁴C-
212 tracers, offer promising tools to unravel the turnover of NSC pools and their potential
213 sequestration. Richardson *et al.* (2013) used bomb ¹⁴C to model NSC dynamics in trees
214 and found that the inclusion of two NSC pools, one with a slow turnover (up to 31
215 years) and one with a more dynamic nature gave the best prediction of radial growth
216 and the amount and mean residence time of storage C. Also Carbone *et al.* (2013) used
217 the radiocarbon (¹⁴C) ‘bomb spike’ to estimate the age of C used by red maple trees for
218 stem respiration, tree ring growth, and stump production after harvest. They concluded
219 that younger NSC is preferentially used for growth and current metabolic demands,
220 while more recently stored NSC (ca. 1-2 year-old), contribute to annual ring growth and
221 metabolism during the dormant season. Bomb ¹⁴C can also be used to determine the age
222 of NSC remobilized after disturbance before tree survival is impaired. For instance,
223 Vargas *et al.* (2009) found that new root production of tropical trees after hurricane
224 damage relied on C assimilated up to 11 years earlier, while that of unaffected trees

225 used newly assimilated C. Similarly, Carbone et al. (2013) estimated that stump sprouts
226 of harvested red maple trees relied on C up to 17-year-old. From stable carbon isotope
227 labeling it is known that NSC pools are turned over rapidly (e.g. Würth *et al.*, 1998),
228 and new C is mixed with old C before becoming invested in structural growth (Keel *et*
229 *al.*, 2007).

230 We also need to determine if trees have a critical threshold for NSC, below
231 which survival is at risk. There is evidence that species and genotypes of drought-
232 sensitive and resistant trees exhibit differential mobilization of NSC in response to
233 water shortage (Regier *et al.*, 2009; Piper, 2011). In these studies, drought caused a
234 decrease of NSC concentrations in drought-sensitive plants, but an increase in resistant
235 plants. This could indicate a differential ability to regulate baseline NSC as well as
236 growth thresholds in genotypes differently adapted to stress. We need experimental
237 studies that quantify minimum C pools in plants, and evaluate whether these thresholds
238 vary depending on the organ, the species, and the environment. For example, Sevanto *et*
239 *al.* (2013) estimated the theoretical threshold of soluble sugar concentrations in bark and
240 phloem tissues required to produce osmotic pressure equal to the pre-dawn leaf water
241 potential. They subsequently compared such theoretical thresholds with the solute
242 contents of drought-stressed pine seedlings and concluded that hydraulic failure could
243 be associated with loss of adequate tissue carbohydrate content required for
244 osmoregulation.

245 We should move beyond correlative approaches and determine if observed
246 decreases in the growth of trees under long-term C-imbalances are due to a C allocation
247 to storage. Experiments with CO₂ fertilization as an additional treatment should be
248 carried out (e.g. Handa *et al.*, 2005; Duan *et al.*, 2013). Such experiments should be
249 performed at the whole plant level and recording temporal changes in C allocation to
250 growth and NSC pools after the imposed treatment (e.g. defoliation, drought) at
251 different levels of CO₂ availability. For example, Duan *et al.* (2013) recently analyzed
252 the effect of drought and increased temperature on the growth, NSC concentrations and
253 C-balance of *Eucalyptus globulus* seedlings grown at different CO₂ concentrations.
254 Their results show that under moderate drought increased CO₂ availability promotes
255 *both* C allocation to growth and NSC storage. However, such beneficial effects of CO₂
256 fertilization disappear when drought becomes severe.

257 Finally, we need to evaluate if a potential tradeoff between NSC storage and
258 growth actually matters for the C balance and survival of a tree in the long-term, and

259 whether and to what extent this effect depends on tree age, habitat and growth
260 conditions. Without filling these important knowledge gaps it seems difficult to
261 critically evaluate if and to what extent C storage can compete with growth and
262 particularly, whether it matters under stress. To date we are left with the empirical
263 evidence that drought and temperatures below 5 °C prevent growth, irrespective of C
264 supply.

265

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272

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