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Abstract:	With growing interests in decline and die-back events due to increased climate variability, ecophysiological roles and dynamics of non-structural carbohydrates (NSCs) draw wide attention recently. Accordingly, a lot of field data have been collected, but these achievements were not well incorporated in process-based vegetation models yet that handled. In most of vegetation models, NSCs ecophysiology were implicitly or ignored. This review tried to fill the gap between recent developments of empirical and modeling studies on NSCs ecophysiology. We summarized the characteristics and dynamics of NSCs recently found in field studies, and then examined how these findings have been incorporated into vegetation models so far. Furthermore, we proposed five NSCs modeling issues, such as: dual NSCs pools, sink-limited allocation, limitation of NSCs transports, symbiont, large-scale NSCs simulation. Development of process-based vegetation models considering NSCs ecophysiology explicitly will help to enhance our modeling capacity to understand vegetation responses to climate change.

Recent field findings and modeling on non-structural carbohydrates (NSCs): how to synthesize?

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Abstract

24

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1. Introduction

Massive tree mortality has been reported worldwide over the last decades, which seems to be related to more frequent droughts and high temperature (Allen *et al.*, 2010; Sevanto *et al.*, 2014). Droughts and heat waves not only increase tree water stress, but also affect photosynthesis-respiration carbon balances (McDowell, 2011; Yan *et al.*, 2020). Trees store large amounts of assimilated carbon with the form of NSCs and use them for various metabolic activities (Hoch, 2015). The presence of NSCs pools plays an important role in balancing between production (source) and consumption (sink) (Chapin, 1990; Li *et al.*, 2016). Therefore, some studies suggested that the storage and allocation processes of NSCs can be used as a useful indicator for understanding and monitoring tree mortality and recovery from stressed conditions (Klein *et al.*, 2016; Liu *et al.*, 2019).

Despite the growing body of field studies on tree NSCs dynamics, most process-based vegetation models either do not consider NSCs or yet remain very simply reflective (Fang *et al.*, 2020). Although the model capability of simulating photosynthesis and evapotranspiration has improved significantly over the last few decades, physiological processes associated with tree mortality remain not fully understood. In order to better simulate the stresses of forest ecosystems under ongoing changing climate, the NSCs role in tree growth and mortality needs to be properly reflected in vegetation models (Mahmud *et al.*, 2018). The purpose of this study is to explore strategies for improving the NSCs simulations within process-based vegetation models through a comparative review on empirical and modeling studies on NSCs dynamics.

This study consists of three parts. In the first section, we described empirical evidence on types and characteristics of NSCs. We briefly summarized types of NSCs with its respective roles in tree physiology, and then explained organic difference in NSCs concentration and its temporal variability. We also addressed lagging effects of NSCs on tree growth and exploring the relationship between NSCs and tree mortality. In the second section, we reviewed previous efforts to model NSC dynamics and their limitations, based on which we provided alternative algorithms of NSCs dynamics and their relations with carbon allocation within the NSCs models. Finally, in the third section, we

66   discussed five key remaining issues to improve the NSCs simulations to fill the gaps between recent

67   empirical and modeling studies on NSCs ecophysiology.

68

69   **2. Characteristics of NSCs dynamics: empirical evidence**

70   *2.1 Type and function of NSCs*

71   NSCs are transformed forms of photosynthetic carbon assimilated by plants into high

72   molecular carbohydrates that are usable for metabolic activities (Chapin, 1990; Hartmann and

73   Trumbore, 2016; Li *et al.*, 2016). The main function of NSCs include respiration, osmoregulation,

74   defense against pests and disease, substrate migration, as well as various roles within plant body

75   (Klein and Hoch, 2015; Martínez-vilalta *et al.*, 2016). Though NSCs have various type of carbon

76   composite, many studies divided them into two general types: soluble sugar (SS) and starch (St)

77   (Martínez-vilalta *et al.*, 2016; Furze *et al.*, 2019; Liu *et al.*, 2019). SS contains mono- and di-

78   saccharides such as glucose, fructose, and sucrose, while St is a polymer carbohydrate where

79   monosaccharides are linked in long-chained form (Pfister and Zeeman, 2016; Hartmann *et al.*, 2018).

80   SS is a soluble material that can pass through osmosis membrane, and free to move within

81   plants, so it is used to play a main functional role of NSCs in various plant organs (Klein and Hoch,

82   2015). For example, glucose and fructose are involved in respiration and osmoregulation, while

83   disaccharide sucrose and trisaccharide raffinose are main substances used for carbohydrate transfer in

84   plants (Hartmann and Trumbore, 2016; Furze, 2019). Unlike SS, St is an insoluble substance that

85   limits its movement among tree organs. St has a large energy storage than SS and serves as an energy

86   repository for each organ (Chapin, 1990; Pfister and Zeeman, 2016). SS and St are interconvertible, so

87   depending on their conditions, St is converted to SS to obtain metabolic energy or SS to St to store

88   surplus energy (Williams *et al.*, 2013; Dietze *et al.*, 2014; Furze *et al.*, 2019).

89

90   *2.2 NSCs of different plant organs*

4

91   Trees have considerable amount of NSCs, and multiple studies show that NSCs represent up

92   to 10% of total dry biomass (Kozlowski and Pallardy, 1997; Martínez-vilalta *et al.*, 2016; D'Andrea *et*

93   *al.*, 2019). The concentration and temporal dynamics of NSCs vary with types of organ, such as

94   leaves, stem, and roots, because of their different strategies in storing and using the NSCs (Li *et al.*,

95   2018; Furze *et al.*, 2019). Trees allocate leaf-generated carbohydrates to other organs as a form of SS

96   to support their physiological activity (Fang *et al.*, 2020). The allocated SS is used for respiration,

97   tissue generation and/or storage in the form of St (Hartmann and Trumbore, 2016; Piper and Paula,

98   2020). Leaves often have relatively high SS concentrations compared to other organs, but account for

99   a small proportion of total NSCs amount of trees (Kozlowski and Pallardy, 1997). In contrast, though

100   stem has relatively low concentration, it generally accounts for the largest NSCs pool in tree organs

101   because of its large biomass (Zhang *et al*., 2014). Root NSCs show relatively stable concentration

102   compared to leaf and stem in temporal variations (Furze *et al.*, 2019).

103

104   *2.3 Temporal dynamics of NSCs*

105   Trees need a certain level of SS to maintain minimal life activity like osmoregulation and

106   respiration. The need varies depending on species and environment, but if SS drops below a certain

107   level, St is hydrolyzed to supplement SS (Smith *et al.*, 2018; Schiestl-Aalto *et al.*, 2019). In this

108   regard, it was reported that St often decreases sharply under drought conditions but SS remains

109   relatively stable (He *et al*., 2020), or even slightly increases (Li *et al*., 2018). This indicates the

110   temporal NSCs dynamic at the whole-tree scale appears to be driven mostly by changes in St (Hoch *et*

111   *al*., 2003; Martínez-vilalta *et al*., 2016). In contrast, for trees with a high SS-to-St ratio, the increase of

112   SS concentration during cold winter is quite usual to avoid freezing damages, which affects seasonal

113   patterns of tree NSCs (Richardson et al., 2013; Furze, 2019). As well, since seedlings have relatively

114   more SS than St, the temporal variation of NSCs is not always led by St (Hartmann *et al*., 2018). The

115   various field evidence indicates that the relative importance of SS and St in NSCs dynamics varies

116   depending on climate conditions and developmental stage of trees.

117   NSCs concentration also changes seasonally throughout the year. NSCs accumulate when

118   production exceeds consumption in late spring and summer, and stored NSCs are often used in winter

119   to support basic metabolic activity such as maintenance respiration (Dietze *et al.*, 2014). NSCs are

120   also used to make new leaves and fine roots in the beginning of following growing season, and then,

121   decline until new production is sufficiently greater than consumption (Klein *et al.*, 2016). Meanwhile,

122   seasonal patterns of NSCs differ between deciduous and evergreen trees, partly due to their difference

123   in leaf phenology. In evergreen trees, the NSCs increase rapidly in spring and then decreases after

124   reaching its peak around early June (Furze *et al.*, 2019; Schiestl-Aalto *et al.*, 2019). On the other hand,

125   deciduous trees have higher concentration and later peak of leaf NSCs around late summer or early

126   autumn than evergreen trees, which is believed because of relatively short leaf life-span and rapid

127   growth (Li *et al.*, 2016; Martínez-vilalta *et al.*, 2016; Furze *et al.*, 2019).

128

129   *2.4 Relations of NSCs with climate and disturbance regimes*

130   It is considered that the differences in concentration and its temporal variability of tree NSCs

131   are also relevant with climate and disturbance regimes which cause different allocation and growth

132   strategies (Gough *et al.*, 2010; Martínez-vilalta *et al.*, 2016). Under favorable growing conditions,

133   plants tend to invest more in growth than storing NSCs, but plants in barren or disturbed habitats

134   adapt themselves for harsh growing conditions by increasing NSCs storages for mitigating damage

135   reduction and promoting rapid recovery (Kozlowski, 1992; Körner, 2003). Li *et al.* (2016) inspected a

136   total of nine sites from tropical to cold-temperate forests in China and found that leaf NSCs decreased

137   with temperature. Similarly, Liu *et al.* (2019) identified a negative correlation of the starch

138   concentrations of leaf and branch organs with precipitation in a semi-arid forest of Mongolia. These

139   results imply that local limiting factors of tree growth can determine different NSCs concentrations

140   across climatic gradients, in which plants maximize growth rather than storing NSCs under favorable

141   environments (Kobe, 1997; Imaji and Seiwa, 2010).

6

142 NSCs create buffering between source (photosynthesis) and sinks (growth of organs) in plant

143 carbon allocation often leading to time-lagged responses over hours to decades (McDowell, 2011;

144 Hoch, 2015; Tixier *et al.*, 2019). NSCs produced by daytime photosynthesis can be used later for

145 nighttime respiration and seasonal growth, and even stored for future disturbances over decades

146 (Martínez-vilalta *et al.*, 2016; Herrera- Ramirez *et al.*, 2020). For example, Richardson *et al.* (2013)

147 found the NSCs of the hemlock trees in Harvard Forest aged from 1 to 31 years. They also found that

148 there is a one-year time lag between carbon sequestration from the flux tower and woody biomass

149 increments from tree-ring data. As well, field evidence has been reported showing delayed tree

150 mortality after certain drought events (Trugman *et al.*, 2018). Brien *et al.* (2014) also confirmed that

151 seedling have longer survival periods in drought conditions, depending on their NSCs conditions.

152 When disturbances such as high temperature, drought, pathogen, and herbivory occur, trees mitigate

153 fatal damage leading to death and earn a recovery time by using the stored NSCs (Pootrer and

154 Kitajima, 2007; Trugman *et al.*, 2018).

155

156 *2.5 Relations of NSCs with tree mortality*

157 For the last decade, many studies suggested that NSCs play an important role in tree mortality

158 mechanisms (Klein *et al.*, 2014; Schiestl-Aalto *et al.*, 2015; Davi and Cailleret, 2017; D'Andrea *et al.*,

159 2019). Mcdowell *et al.* (2008) suggested hydraulic failure, carbon starvation, and biotic agents

160 (disease and pests) as main causes of tree mortality (Fig. 1), which factors work either independently

161 or together depending on the duration and intensity of stressed conditions (Sala *et al.*, 2012; Sevanto

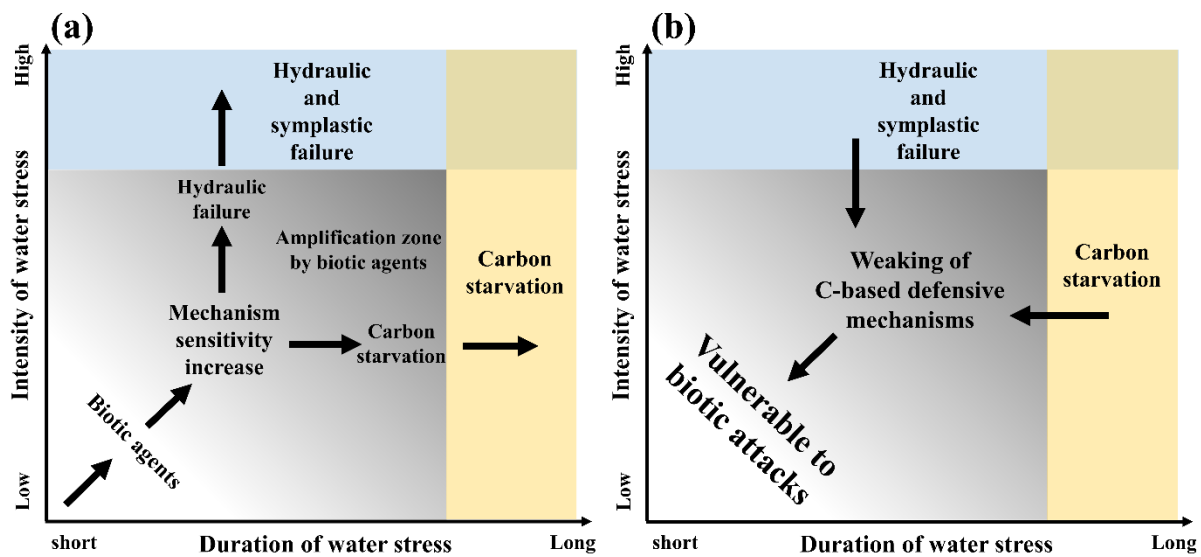162 *et al.*, 2014; Hoch, 2015).

163

Fig. 1. Theoretical relationships based on hydraulic frameworks between duration and intensity of water stress, and three hypothesized mortality mechanisms: carbon starvation, hydraulic failure, and biotic agents. The (a) shows that the likelihoods of occurrence of intrinsic mechanisms (Hydraulic failure, Carbon starvation) increases after experiencing biotic agents, and (b) shows the opposite case in which trees becomes more vulnerable to the biotic attacks after intrinsic mechanisms. Modified from Fig. 3 of McDowell *et al* (2008).

Hydraulic failure is a phenomenon under acute and severe droughts by xylem cavitation, causing surrounding cells desiccated and eventually leading tree mortality (Adams *et al.*, 2017). In contrast, carbon starvation is a mechanism by negative carbon balance in which photosynthesis is below respiration consumption usually under chronic droughts. Though carbon starvation is not destructive like hydraulic failure, it often causes impairment of tree metabolism due to lack of carbon energy (Mcdowell *et al.*, 2008). The damages caused by hydraulic failure and carbon starvation is often amplified when droughts occur with high temperature.

The sensitivity of tree mortality to the above mechanisms also depends on stomatal response strategies of tree species to droughts (i.e., isohydric vs. anisohydric plants) (Mcdowell *et al.*, 2008; Sevanto *et al.*, 2014). Isohydric species reduce embolism risk by closing stomata under drought

181 conditions but at the cost of reduced carbon assimilation, therefore the probability of carbon starvation

182 increases depending on previously stored NSCs. In contrast, anisohydric species frequently sustain

183 high stomatal conductance to maintain photosynthesis even under drought conditions despite the risk

184 of xylem cavitation. On the other hand, external causes, such as diseases and pests, could cause tree

185 die-back independently but the effect becomes more lethal when trees are already weakened by

186 hydraulic failure and/or carbon starvation, and vice versa as illustrated in Fig. 1.

187   NSCs called an attention as a key indicator of tree mortality because of their important roles,

188 such as recovery of cavitation, buffer in carbon imbalances, and production of defense substrates

189 against external causes (Mcdowell *et al.*, 2008; Dietze *et al.*, 2014; Martínez-vilalta *et al.*, 2016).

190 Severe and chronic droughts are expected to occur more frequently in the future (Allen *et al.*, 2010),

191 which emphasizes the importance of monitoring and predicting temporal dynamics and spatial

192 patterns of NSCs to understand tree growth and mortality under changing climate. Because the

193 amount and variation of NSCs differ by climate, vegetation phenology, and tree morphological

194 characteristics, it is necessary to collect long-term NSCs data across the different species and biomes

195 covering enough climatic variability (Martínez-vilalta *et al.*, 2016; Jones *et al.*, 2019). However, there

196 exits practical limitations to obtain such field NSCs data, which requires alternative approaches to

197 develop proxy parameters of the NSCs dynamics (e.g., leaf area; Schönbeck *et al.*, 2018) or to

198 simulate them using process-based NSCs models (Hoch, 2015).

199

200 **3. Modeling NSCs dynamics**

201   Most process-based vegetation models are categorized into a source-limited model

202 emphasizing better estimation of primary productivity and growth through photosynthesis than carbon

203 allocation and storage processes (Merganičová *et al.*, 2019). In those models, gross primary

204 production (GPP) is mainly used for autotrophic respiration (maintenance and growth respiration) and

205 construction of plant organs, therefore growth allocation and respiration are determined primarily by

206 photosynthesis.

207 In general, these productivity-driven source-limited models do not consider the NSCs storage

208 pools (e.g. the Joint UK and Environment Simulator (JULES) model) or implicitly treat NSCs as an

209 intermediate parameter of carbon balance between source (i.e., productivity) and sinks (i.e.,

210 respiration and growth) (e.g. BIOME-BGC). Therefore, most of these models do not take into account

211 for NSCs-mediated buffering or time-lagged responses of tree growth and mortality processes under

212 stressful environments (Mahmud *et al.*, 2018; Fang *et al.*, 2020). Even considered, the source-limited

213 models simplifies NSCs storage pools because the models consider only key eco-physiological

214 processes to compensate model complexity and capability as well, the role of NSCs was little

215 understood yet (Asaadi *et al.*, 2018). For examples, some controlled experiments showed that, in spite

216 of increased respiration consumption, NSCs also increased (Anderegg, 2012) or was maintained

217 (Klein *et al*., 2014) under stressed conditions. These results demonstrate that temporal dynamics of

218 NSCs was not simply explained by carbon balance between GPP and consumptions from respiration

219 and growth, as described in most source-limited models. Since NSCs are important for tree survival

220 and recovery, vegetation traits of NSCs dynamics need to be considered explicitly in modeling carbon

221 balance and allocation process (Ryan, 2011; Hartmann *et al*., 2015).

222 Though details on NSCs storage and transfer processes still remains controversial, NSCs data

223 have been collected more ever over the last decade (Wiley and Helliker, 2012; Friend *et al.*, 2014;

224 Quentin *et al.*, 2015; Schönbeck *et al.*, 2018), which provides new insights for explicit NSC modeling.

225 Accordingly, several NSCs modeling studies suggested to reflect the characteristics of both dynamic

226 process-based and static carbon-balance models (Hartmann *et al.*, 2018; Fang *et al.*, 2020),

227 summarized in Table 1.

Table 1. A list of previous modeling studies with explicit NSCs storage pools

Type	Model	Description	No. of NSCs pools	Spatial simulation scale	Reference
Dynamic process-based model	RHESSys	A NSCs storage pool was added to RHESSys model to estimate the likelihood of tree mortality.	Single	Landscape	Tague *et al*., 2013
	FöBAAR	Performing comparisons between alternative NSCs algorithms: none, single, and dual storage pools	Single and dual	Stand	Richardson *et al*., 2013
	CASSIA	Daily tree growth limited by a NSCs storage pool	Single	Individual	Schiestl-Aalto *et al*., 2015
	CASTANEA	Performing model simulation to determine carbon and hydraulic physiological thresholds for tree mortality	Single	Stand	Davi and Cailleret, 2017
	CASSIA	Understanding of carbon allocation combined wood growth and carbohydrates with short-term vegetation hydraulics	Single	Individual	Fang *et al*., 2020
	CASSIA	Applying dual NSCs pools and allocation to belowground symbionts	Dual	Individual	Schiestl-Aalto *et al*., 2019
	JULES	Response to extreme climate events such as drought, NSCs module of SUGAR (Simple model of labile carbon storage and utilization) was added in model	Single	Stand and above	Jones *et al*., 2019
	BIOME-BGC	Two NSCs pools were added, and the model's prediction performance of temporal variability of starch and sugar were evaluated across the biome	Dual	Stand	Cho *et al*., 2022
Static balance-based model	Carbon balance approach model	Flowchart was created to describe and quantify the tree carbon allocation using tree carbon sinks, source, and pools data	Dual storage pools in each organ (e.g., leaf, stem, root)	Individual	Klein and Hoch, 2015
	Data assimilation model	Test whether adding the storage pool improves the performance of seedling growth modeling	Single storage pool	Individual	Mahmud *et al*., 2018

3.1 Single versus dual NSCs pools

At the early development of NSCs modeling, single-pool approach was more popular than dual NSCs pools. Tague *et al.* (2013) assessed stress-related tree mortality likelihoods in southern Rocky Mountains using modified RHESSys (Regional Hydro Ecological Simulation System) model with a single NSC pool. Davi and Cailleret (2017) emphasized the importance of a carbon reserve pool as a result of exploring the cause of tree mortality using CASTANEA model. Mahmud *et al.* (2018) also confirmed the necessity of carbon storage pools in seedling growth modeling through experimental simulation using carbon balance model. Jones *et al.* (2019) added a NSC storage pool to JULES model to increase carbon flux accuracy on large area and confirmed that the variability of growth and respiration differs significantly from the original model due to buffering effect on the NSC storage.

On the other hand, it has been suggested that use of dual storage pools is more effective in modeling growth stress and mortality of trees (Schiestl-Aalto *et al.*, 2015; Hartmann *et al.*, 2018). Accordingly, some modeling studies divided the NSCs into multiple components. Richardson *et al.* (2013) proposed a model with dual NSCs pools, 'fast' and 'slow', considering different roles and turnover rates of SS immediately available and St better specialized to storage (Liu *et al*., 2019; He *et al*., 2020). In the dual-pool modeling, the St pool was usually interconvertible with the SS pool. Klein and Hoch (2015) proposed a method for simulating both SS and St within their static carbon-balance modeling framework. In process-based modeling approach, Schiestl-Aalto *et al.* (2019) provided an example of simulating dual NSCs pools at an individual level. Cho *et al*. (2022) recently reported a biome-specific approach for the simulation with dual NSCs storage pools. In spite of scientific robustness on the distinction between slow and fast NSC pools, the dual-pool approach is rarely applied yet and needs further investigations with case studies.

3.2 NSCs and growth allocation

254   Since NSCs are linked with GPP and carbon consumption, such as growth and respiration, the

255   NSCs pools are inevitably associated with the carbon allocation process. Various methods have been

256   developed to control growth allocation with NSCs pools at a landscape scale. For example, Tague *et*

257   *al.* (2013) applied a threshold method. A certain fraction of annual NPP is stored in the NSCs storage,

258   while the other remains for tree growth. When the ratio between leaf and above-ground biomass falls

259   below the threshold, NSCs carbon is then reallocated for growing tree organs. Jones *et al.* (2019)

260   modified the growth allocation process by adding a NSCs storage to the JULES model, where it

261   depends on the Michaelis-Menten reaction kinetics affected by total amounts of NSCs storage. Cho *et*

262   *al.* (2022) applied a sink-limited growth allocation strategy to the BIOME-BGC model, where the

263   growth allocation is dynamically controlled by starch pool size.

264   At an individual tree level, more complex rules of growth allocation were suggested based on

265   tree developmental stage, climate condition, and the amount of NSCs. For example, Schiestl-Aalto *et*

266   *al.* (2015) proposed an individual-based vegetation model, CASSIA, where growth of plant organs are

267   dynamically constrained by temperature and NSCs storage size. These modeling studies indicate a

268   recent shift of modeling paradigm on carbon allocation process by emphasizing sink-limited growth

269   strategy regarding NSCs pools.

270

271   *3.3 NSCs transport to organs and symbionts*

272   NSCs models can be classified into stand and above-level and individual-level models (Table

273   1). In general, the stand and above-level models have single or dual NSCs pools at a whole-tree scale,

274   while the individual-based models simulate the NSC pools of each organ (Dick and Dewar, 1992;

275   Klein and Hoch, 2015). The stand and above-level models implicitly assume that NSCs transfer

276   between organs is not limited, which is not true under drought conditions, particularly, for the long-

277   distance transport of SS from leaves to roots (Sevanto, 2014). Trees use xylem water pressure and

278   gradients of solute concentration between organs to move carbohydrate in leaf to stem and root. Dick

279   and Dewar (1992) proposed a mechanistic model where sugar transport rates were driven by

280   concentration gradients to simulate root development. In addition, Fang *et al.* (2020) performed stem-

281   wood growth modeling using both NSCs and hydraulic gradients. In this sense, it is important to add

282   hydraulic control mechanisms for NSCs transport in a future modeling study for simulating NSC

283   dynamics.

284   Below-ground symbionts (e.g., mycorrhizal fungi) are also important consumers of NSCs and

285   it has been known that the allocation to mycorrhizal fungi is more considerable than expected (Nehls,

286   2008; Deckmyn *et al.*, 2014). Hence, the role of below-ground symbionts should be a key subject for

287   enhanced NSC modeling but our understanding regarding the belowground symbionts and its relation

288   with tree NSCs is not yet enough for modeling in the NSC dynamics. So far, we found only one case

289   study to model dynamic allocation of NSCs to mycorrhizal fungi (Schiestl-Aalto *et al.*, 2019).

290

291   **4. Major issues in modeling dynamics and allocations of NSCs**

292   With the above field and modeling studies, we identify several major issues in NSCs

293   modeling as follows, potentially critical to understand NSC dynamics and their spatial patterns: (1)

294   interconvertible processes between SS and St; (2) relations between NSC storages and growth

295   allocation; (3) the conductance of NSCs transport between tree organs; (4) the role of symbionts, such

296   as mycorrhizae, in NSCs dynamics; and (5) model application across different biomes and climate

297   regions. Though some issues have been addressed partly in previous studies, new developments or

298   further refinements still remain to improve model performance on the NSC-related phenomena, such

299   as stress-and-recovery and die-back processes especially under hydroclimate change.

300

301   1) *Interconversion between dual NSCs pools*

302   Several empirical studies classified NSCs into 'slow' and 'fast' components such as SS and

303   St, respectively. These two NSCs pools differ in chemical and physical properties, as well as their

304   ecophysiological roles in tree growth. So far, only a few studies incorporated the dual-pool approach

305   in NSCs modeling (Richardson *et al.*, 2013; Schiestl-Aalto *et al.,* 2019; Cho *et al.*, 2022). In these

14

306 models, SS and St pools are located between the source and sink, and the primary production is stored

307 in St pool or allocated to growth through SS pool. St and growth usually compete for carbon

308 allocation from SS, further addressed in the next modeling section below.

309 St has been widely used as a single indicator of carbohydrate status of trees (Kozlowski and

310 Pallardy, 1997). Carbon stored in St pool can be reconverted to SS when SS is insufficient. Schiestl-

311 Aalto *et al.* (2019) set a conservative value for SS, over which SS is converted to St and under which

312 St is reconverted to SS, leading to more stable SS concentrations than St. This simple approach is

313 useful to mimic the role of St in subsidizing SS to prevent harmful SS reduction under stressed

314 conditions. However, there exists other field evidence to show very dynamic temporal behavior of SS

315 rather than stable (Richardson et al., 2013; Furze, 2019). Though all physiological mechanisms cannot

316 be covered by the model (Asaadi *et al*., 2018), NSCs models need to explain both the conservative

317 and dynamic temporal patterns of SS.

318 Interconversion between SS and St is an enzymatic process driven by temperature, pH and

319 enzyme concentration, such as phosphorylase (Hassid and Putman, 1950). Under high- or low-

320 temperature conditions, the conversion of SS to St would be limited resulting faster SS accumulation

321 than St, which is strategically sound to compensate increased respiration and to prevent cold damage,

322 respectively. The current dual-pool approach, however, usually assume that SS-St interconversion

323 occurs freely without any limitation when a prescribed condition such as the conservative SS

324 threshold meets (Schiestl-Aalto *et al.,* 2019). To capture dynamic temporal variations in SS and St, we

325 propose that a substrate- and temperature-limited enzymatic process, such as Michaelis-Menten

326 equation, need to be incorporated into dual-pool NSCs models. With better understanding on this

327 enzymatic process, it would be possible to develop robust algorithms and parameterization at the

328 species or biome levels. Rather than relying solely on field data, simultaneous attempts using model

329 experiments is necessary to enhance our understanding on the interconversion process between dual

330 NSCs pools.

331

332   2) *Sink-limitation framework of growth allocation*

333   Trees face with many stressful situations over their lifespan, therefore store certain amount of

334   energy (e.g., starch) to reduce damage from stresses and to facilitate recovery (Chapin *et al*, 1990). As

335   an important modulator of tree responses to growth stress and survival, NSCs need to be handled

336   explicitly in vegetation process model to regulate growth allocation as suggested that 'the carbon

337   allocation of trees will work to maximize and optimize growth and survival (Kobe., 1997; Trugman *et*

338   *al*., 2018)'. Carbon balance experiments also confirmed increased allocation to NSC storages despite

339   good growth conditions based on continuous carbon isotope labeling (^{13}C) for a whole-tree young

340   *Picea abies* (L.) H Karst (Hartmann *et al*, 2015).

341   In a source-limited paradigm, the growth allocation is primarily controlled by GPP as

342   described in most traditional vegetation process models (Fatichi *et al.*, 2019). An explicit

343   consideration on NSC pools changes this paradigm to sink-limited framework, where sink storages

344   (i.e., NSCs) primarily regulate growth allocation with secondary role of GPP (e.g. Jones *et al.*, 2019;

345   Schiestl-aalto *et al.*, 2019; Cho *et al*., 2022)). In spite of a more realistic carbon economy of trees, the

346   sink-limited framework was not yet adopted extensively in the process-based vegetation models

347   (Tague *et al*., 2013; Schiestl-Aalto *et al*., 2015; Jones *et al*., 2019).
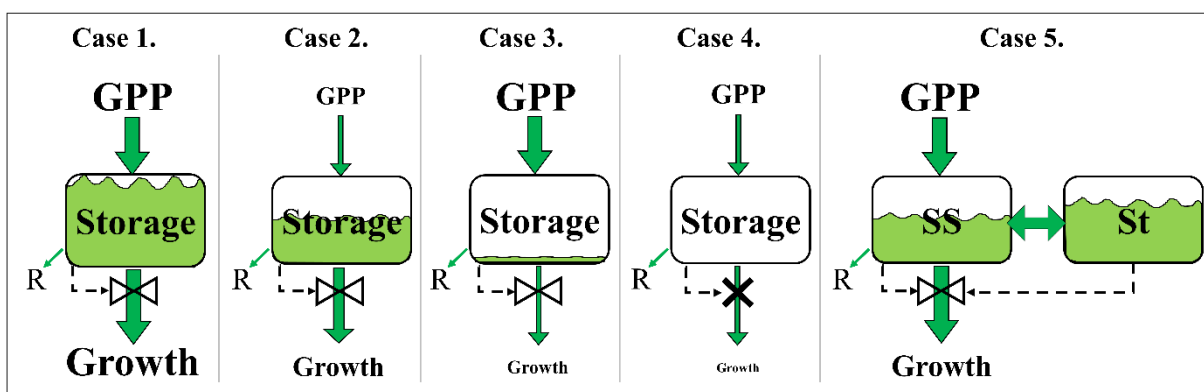
348

349   Fig. 2. Strategical carbon allocation schemes. Storage and SS/St represent single- and dual

350   NSCs storages, respectively. In the dual storages, SS and St are soluble sugar and starch pools,

351   respectively. Background green color in the boxes represents the amount of stored carbon. The size of

352   arrow and letters indicates magnitudes of respective fluxes. Valve and dotted line indicate controls of

353   NSCs pools on growth allocation. R represents autotrophic respiration (maintenance and growth

354   respiration).

355

356   We suggest examples of simple sink-limited frameworks for growth allocation as illustrated

357   in Fig. 2. For the case of single NSCs storage pool (Cases 1-4), storage size explicitly controls growth

358   allocation (e.g. Schiestl-Aalto *et al*., 2015; Jones *et al*., 2019; Fang *et al*., 2020). When both GPP and

359   storage are high (Case 1), growth allocation is limited by other constraints, such as lacks of nutrients

360   for new tissue production. Peak growing season without severe droughts could be an example. When

361   GPP is low, growth flux can be maintained (even reduced) by previously stored NSCs. Growth in

362   early growing season could be this case (Case 2). However, if storage itself is low, growth is

363   substantially reduced (Case 3) or even stops (Case 4). In these cases, GPP is primarily used to refill

364   the storage pool. Late spring could be an example when GPP is greater than respiration after spring

365   onset or when GPP is recovered from severe droughts (Case 3). Meanwhile, growth can stop with

366   empty or under certain levels of storage pool, possibly by long droughts or abnormally high

367   temperature (Case 4).

368   On the other hand, Case 5 in Fig. 2 is an extension of the sink-limited framework from single-

369   to dual-pool NSCs storages. In the dual-pool framework, GPP fills SS storage and then, SS is

370   allocated to St and growth, in which either or both SS and St control the growth allocation (e.g.

371   Schiestl-Aalto *et al.*, 2019; Cho et al., 2022). For example, in Schiestl-Aalto *et al.* (2019), growth

372   allocation was set to be reduced when either SS or St pools are below a certain threshold. Cho *et al*.

373   (2022) designed growth to be controlled by a fraction of St storage to its maximum pool size.

374   Carbon storage and allocation varied by several factors such as species, phenology, and

375   climate conditions (Li *et al*. 2018; Jin *et al*., 2018). Although vegetation models cannot simulate full

376   dynamics of carbon allocation in trees, it is necessary to attain a reasonable capability for simulating

377   tree growth and survival especially under stressed conditions (Hartmann *et al*., 2020). Although recent

378   modeling studies tried to improve carbon allocation dynamics within the source-limited modeling

17

379   frameworks (Guillemot *et al*., 2017), we expect the sink-limited allocation scheme more common in

380   the future process-based vegetation models.

381

382   3) *Hydraulic restriction of NSCs transport between organs*

383   It is well known that the transport of carbohydrates is closely related to solute concentration

384   and xylem water potential (Nikinmaa *et al.*, 2014; Sevanto, 2014). Carbohydrates produced by

385   photosynthesis in leaves are transported to phloem increasing the solute concentration (Ryan *et al.*,

386   2014). Then, increased phloem concentration draws water through osmosis from xylem, which

387   increases the turgor pressure of transport flows and delivers carbohydrates to sink tissues (Hölttä *et*

388   *al.*, 2009; Ryan *et al.*, 2014). However, when there is a problem in the xylem water flow (e.g.,

389   cavitation) during droughts, the phloem flow is also affected. This mechanism limits the allocation of

390   carbohydrates from leaves to stems and roots, which would increases risk of carbon deficiency in

391   spite of certain amount of energy stored in leaves (McDowell and Sevanto, 2010).

392   Regarding carbon transport limitation through phloem, Sevanto (2014) confirmed that the

393   survival of piñon pine (*Pinus edulis*) was closely related to the phloem function affected by hydraulic

394   failure. Dick and Dewar (1992) proposed a model which explicitly considers carbon transport from

395   leaf to stem and root. Most vegetation models, however, assume that NSCs allocation and transport

396   occur freely without any resistance. To apply this carbon transport mechanism into the models, it is

397   necessary to further understand relations of carbon fluxes with NSCs (storage) and water potential

398   gradients between organs (driving force). In particular, it is uncertain when long-distance

399   carbohydrate transports from leaf to root fail leading to organ-level partial carbon starvation

400   (McDowell, 2011; Sevanto, 2014; Gustafson *et al.*, 2015; Piper and Paula, 2020). Nevertheless, there

401   were several studies reporting the rapid changes of root NSCs under droughts compared to other

402   organs (summarized by Li *et al.* (2018)), which suggests an urgent need for consideration of organ-

403   scale NSCs storages and transport mechanisms between them within the model. The application of

404 transport-limited mechanism will improve the model capability to simulate carbon starvation and

405 mortality.

406

407   4) *Feedback mechanism between tree NSCs and root symbionts*

408   A symbiotic relationship with ectomycorrhiza is a widespread phenomenon for terrestrial

409 plants. In particular, the symbionts were found in almost trees living in temperate and boreal zones

410 (ca. 80~90%) (Read, 1992). As for the massive mortality of pine trees (*Pinus densiflora*) in South

411 Korea, it was hypothesized that the pine trees became vulnerable to the high temperature and drought

412 in early spring season when mycorrhizal fungi did not grow yet (Lim, 2016). Deckmyn *et al.* (2014)

413 mentioned the importance and need for the plant-fungi feedback relationship in vegetation process

414 model. Schiestl-Aalto *et al.* (2019) deduced that approximately 10% of daily GPP is allocated to root-

415 associated fungi.

416   Many studies suggested that symbionts in the rhizosphere act as a 'missing sink' of carbon

417 allocation more than expected (Nehls, 2008). However, because the mycorrhizae affect the increase of

418 vegetation production along with the supply of water and nutrients, it is controversial to regard it

419 simply as a carbon sink. For example, Orwin *et al.* (2011) added a mechanism for nutrient absorption

420 through mycorrhizal fungi to MySCaN (Mycorrhizal Status, Carbon and Nutrient cycling; based

421 partly on the CENTURY model). In the MySCaN model, root carbon is allocated to mycorrhizal

422 fungi, and if there is an imbalance in the ratio between carbon and nutrient, fungi help absorption of

423 nutrients from surrounding soil. Though quantifying the give-and-take fluxes between mycorrhizal

424 fungi and trees is yet uncertain (Treseder, 2004; Orwin *et al.*, 2011), modeling the symbiotic

425 relationship suggests some challenging points, such as effect of mycorrhizae phenology and extreme

426 weathers on seasonal carbon starvation (Jolicoeur *et al.*, 2002; Phillips *et al.*, 2008).

427

428   5) *Macro-scale simulation of NSCs dynamics across biomes and climate regimes*

429   Many forests are being affected by climate change, and eventually vegetation will undergo

430   geographical shifts and succession to find suitable habitats for growth and survival (Barros *et al.*,

431   2018; Batllori *et al.*, 2020). Widespread massive tree mortality might be an early symptom of the

432   change in tree acclimation and replacement. Hence, drought- or heat-induced tree mortality need to be

433   properly monitored and predicted with vegetation models at a macro scale across various biomes and

434   climate regions (Sala *et al.*, 2012; Hoch, 2015). We suggest that conventional source-limited

435   vegetation models might be less effective to simulate tree mortality due to lacks of explicit handling

436   of NSCs storages. Since most NSCs models were evaluated at specific stand or tree levels, it raises a

437   question about worldwide applicability and calls a critical attention for a need of universal

438   parameterization and evaluation of those NSCs models. For this, global datasets of NSCs observation

439   is necessary.

440   Tree NSCs varies depending on various factors, such as climate, species, plant organs,

441   vegetation developmental stages, and historical disturbances (Quentin *et al.*, 2015; Liu *et al.*, 2019).

442   Periodic collection of field NSCs data is practically hard because of its physical limitation and

443   uncertainty in sampling design at the landscape scale. Jones *et al.* (2019) mentioned that although

444   NSCs modeling was performed in Amazonian Forest, there were no ways to evaluate the model

445   prediction on NSCs dynamics over the entire region. Recent promising effort by Martínez-vilalta *et*

446   *al.* (2016) complied woldwide field NSCs data from previous studies, which includes seasonal NSC

447   data (including total NSCs, SS, and St) from 123 literatures with metadata information on species,

448   regions, periods, organs, functional types, biomes, and analyzing methods. Growing body of NSCs

449   database will help to parameterize and to evaluate the model performance on NSCs dynamics across

450   different biomes and climate regions.

451   As an alternative approach to overcome the lack of field NSCs data, a new method using

452   spectroscopy and shortwave-infrared (1,300 and 2,500 nm wavelength) showed high sensitivity to leaf

453   NSCs determination (Asner and Martin, 2015; Ramirez *et al.*, 2015). Although this method rendered a

454   high explanatory power about 80% of the laboratory experiments, stand-level measurements using

455   airborne imageries produced only 49% explanatory power (Asner and Martin, 2015). These results

456   suggest that remote sensing would be a promising tool to monitor leaf-NSCs at large scales but still, it

457   has limitation for practical applications for forest management and decision-making.

458

459   Lastly, other remaining issues, such as NSCs relations with defense materials and

460   reproduction, remain further challenges. It is worthwhile to note that recent studies using isotope

461   tracking methods are drawing attention to identify between-organ carbon transports and allocation

462   processes in trees (e.g. Richardson et al., 2013; Hartmann et al., 2015; Trumbore et al., 2015;

463   Ceballos-Núñez et al., 2018). These studies would enhance our understanding on carbon balance from

464   production to allocation, storage, and consumption across the whole-tree, and therefore help to

465   separate for net effects of drought and heatwave on NSCs dynamics for tree growth and mortality

466   processes (Dietze *et al.*, 2014). Next generation models need to have mechanistic capability and

467   understanding for carbon storage and allocation dynamics while maintaining model performance on

468   production estimation by conventional models (Trumbore, 2006).

469

470   **5. Conclusion**

471   In this study, a literature review was provided to link empirical findings so far on the

472   characteristics and dynamics of tree NSCs storages with recent developments of process-based NSCs

473   modeling. Empirical studies confirmed temporal and spatial variations of NSCs relevant with various

474   abiotic and biotic factors. Even latest models do not capture the NSCs variability well since the

475   models are yet limited to simulate site-specific NSCs dynamics or not enough sophisticated to capture

476   major processes regarding NSCs dynamics. Accordingly, we derived five major modeling issues in

477   simulating spatial and temporal patterns of NSCs dynamics as follows: (1) interconversion between

478   dual NSCs pools (i.e., rapid soluble sugar and slow starch pools), (2) incorporation of sink-limited

479   growth allocation strategy, (3) hydraulic limitation of NSCs transports between organs, (4) feedback

480   mechanisms between tree NSCs and root symbionts, and (5) large-scale simulations of NSCs

481 dynamics. In particular, this review emphasizes limitation of traditional source-limited models to

482 simulate die-backs and recovery of various tree biomes driven by ongoing climate change. We

483 suggest that it is important to further improve process-based vegetation models to explicitly consider

484 NSCs dynamics and their role in growth allocation, which will enhance our modeling capacity to cope

485 with vegetation response to climate change.

486

487

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492

7. Author Contribution

494 **Nanghyun Cho**: Conceptualization, Writing - Original Draft. **Sinkyu Kang**: Supervision, Writing -

495 Review & Editing. **Casimir Agossou, Taehee Hwang**: Visualization, Writing - Review & Editing.

496 **Eunsook Kim, Jong-Hwan Lim**: Project administration, Writing - Review & Editing. All authors

497 read and approved the final manuscript.

498

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