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REVIEW

Accumulation *versus* storage of total non-structural carbohydrates in woody plants

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Abstract

Key message **A contribution to understand the eco-physiological significance of the total non-structural carbohydrate reserves through making a distinction between accumulated and stored pools along with their respective roles played in woody plants.**

Abstract Plant assimilates are partitioned to growth, defense, maintenance and reserves. Reserves of total non-structural carbohydrates (TNC) are accumulated when the demand for carbon (C) is lower than C supply. Accumulated TNC are stored if not used for growth and metabolism during the growing period. The assessment of the physiological significance of TNC reserves in trees should distinguish between accumulated and stored pools. Accumulated fraction of TNC is characterized by a rapid turnover rate that buffers temporary negative C balance of trees in an annual cycle, whereas stored fraction is characterized by a slow turnover rate that could buffer demand for TNC throughout all tree life during stressful conditions. The increased need for TNC during acute adverse environmental conditions associated with the slow turnover of stored TNC reserves induces the remobilization of the fraction of TNC initially destined for growth and defense which could be a cause of tree mortality. The observed C "sequestration" could be due to the slow turnover dynamic of stored TNC that could be in turn, an adaptive strategy to survive adverse conditions at long term, especially in areas characterized by poor nutrient availability, repeated disturbance and prolonged drought periods. The storage-growth tradeoff is discussed.

Keywords Accumulation · Storage · Remobilization · Total non-structural carbohydrates · Growth

Abbreviations

TNC	Total non-structural carbohydrates
C	Carbon

Introduction

Total Non-structural Carbohydrates (TNC) reserves represent an available source of carbon (C) and energy that can be used by plant whenever the demand for C overweigh the amount of the new assimilates. Reserves of TNC enable metabolism in the dormant season (Carbone et al. 2014), dormancy release, bud burst, rapid recovery after defoliation and drought (Eyles et al. 2009; Launay et al. 2009) and early wood growth (El Zein et al. 2011). Many studies reported the role of TNC reserves in mediating the effects of stress (Kozlowski 1992) through enhancing the tolerance to environmental stress, especially when C gain is limited (O'Brien et al. 2014).

Although the role of the TNC in plant growth and performance is well documented, controversy still exists about storage function and regulation and about how TNC pools build-up over time. One cause of controversy could be related to what we consider storage in plants. TNC reserves are often treated physiologically together in studies aiming to answer the pending questions about C budget in trees (Kobe 1997; Schaefer et al. 2008; Ogee et al. 2009; Sala et al. 2012) and considered thus one TNC pool. Some authors, however, have already determined two pools of TNC (Ogle and Pacala 2009; Kuptz et al. 2011; Richardson et al. 2013) with different traits and behaviors. The different behaviors of the different TNC pools may result from different roles played within the tree. Therefore, it is necessary to consider each pool of TNC separately when studying stress

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effects on plant reserves or when debating some important issues like storage regulation.

The aim of the present paper is to reevaluate the ecological and physiological significance of TNC reserves in plants, making a distinction between accumulated (new C) and stored (old C) pools. The main points to discuss will be: i) The characterization of the two pools of TNC in the light of available studies; ii) The remobilization of TNC during growing period, moderate stress and acute adverse conditions and iii) The storage-growth tradeoff. Discussing these topics will help to understand better the process of TNC storage in trees and the role of TNC reserves in response to climate change, stress and disturbance.

Accumulation *versus* storage

During photosynthesis, newly assimilated C in the chloroplast is exported to the cytosol to synthetize sucrose. A fraction of the sucrose will be immediately used for growth, whereas another fraction is converted to starch to provide C for continued growth and metabolism at night (Gordon et al. 1980). All remaining sucrose will be loaded into the phloem to be translocated to other organs of the plant to ensure many roles (respiration, growth, defense, symbiosis, storage, etc.). The translocation of TNC from leaves to roots and soil was observed to be remarkably a quick process (Högberg et al. 2008; Epron et al. 2011) even under C limiting conditions (Lacointe et al. 2004; Warren et al. 2012).

Sucrose -which is metabolically active- is the transport form of sugars within the plant that will be converted to starch -which is immobile and metabolically inert- when accumulated in the different organs of the plant. Accumulation occurs in all organs successively downward from the leaves and branches to the trunk and roots. TNC are accumulated throughout the year (whenever the demand for TNC is low) to be used during growing season (when the demand for TNC is high). The "accumulation" starts during spring, increases during summer and becomes maximal early in the winter in deciduous species (Davidson et al. 2021; Tromp 1983). In evergreen species, the maximal accumulation of TNC is reported to be at the end of spring (Schaberg et al. 2000; Furze et al. 2019). Evergreen species that store less TNC per unit plant biomass than deciduous species- do not need a large fraction of the TNC pool to enable metabolism during the dormant season and to support early growth in spring (old leaves are supposed to contribute TNC to initiation of spring growth (Wyka et al. 2016)), so the fulfillment of TNC is achieved fast in comparison to deciduous species that will deplete TNC reserves during dormant season and early spring.

Photosynthetic inputs seem to exceed tree demand in an annual cycle (Hoch et al. 2003; Poorter et al. 2006) and trees accumulate continuously new TNC (Trumbore et al. 2015). A positive correlation was obtained between individual tree biomass and whole-tree total TNC pool size (Furze et al. 2019). Accumulated fraction of TNC is thus unlikely to be wholly depleted during the growing period in normal conditions (Adams et al., 2013; O'Brien et al., 2014). Thus, if accumulated C is not totally used during the current year, the excess of TNC of the following year will be accumulated on. The previous accumulated pool of TNC becomes an old pool stored in deeper structures that will contain increasingly the oldest C (Trumbore et al. 2015). Consequently, the stored pool becomes more important in C budget as the tree ages according to DeJong (2016), who suggested that "the capacity of a tree to store TNC depends largely on the function of xylem and phloem anatomy and is created as trees grow". In this perspective, we could consider storage as a result of an excess of the accumulated fraction of TNC not used within a determined timescale (a year in general). Some storage organs "lignotubers" are reported to not be discerned macroscopically till the age of 2 and 4 years old in the case of *Phillyrea angustifolia* and *Arbutus unedo* respectively (Paula et al. 2016).

The vegetative growth stage that starts from seed germination through the development of the primary supporting structure, relies firstly on the remobilization of TNC available on the seeds. Upon the increase of the photosynthetic capacity, TNC are accumulated and remobilized seasonally to meet the demand for C and energy of the plant. We suggest, therefore no storage of TNC in this stage. However, during the reproductive growth stage characterized by the maturation of tissues manufactured during vegetative phase and the development of flower buds, flowers, fruits and seeds, most of the TNC are accumulated and subsequently stored in all organs of the tree during usual environmental conditions.

The distinction between stored and accumulated pools of TNC could be based on two aspects: carbon age and TNC localization in tree structures. Accumulated and stored TNC pools are physically distinct because they are stored in younger versus older rings, respectively. It has been found a positive correlation between TNC age and radial depth in stems and roots (Richardson et al. 2015; Futze et al. 2020).

The exact localization of the two TNC pools could depend on tree species. Richardson et al. (2015) for example, showed that two third of TNC that correspond to the new TNC (less than one year) are localized in the upper five rings of stemwood in the case of *Pinus strobus* and *Quercus rubra* whereas one third of TNC (old pool) is localized in the following deeper rings.

Characterization of the accumulated *versus* stored TNC pools

Residence time—Turnover rate

The C assimilated is always accumulated before its subsequent use. Assimilation of C and growth process were already suggested by many authors to be unsynchronized (Arneth et al., 1998; Navarro et al., 2008; Rocha and Goulden, 2009). For instance, a strong correlation was obtained between net ecosystem exchange of CO_2 in one year and biomass increment in the following year (Kuptz et al. 2011). Even in herbaceous species, newly assimilated C is not used directly for growth (Gibon et al. 2004).

As mentioned before, a fraction of new TNC is used for current growth and metabolism. The remaining fraction of TNC is accumulated and subsequently used depending on C age: Accumulated fraction of TNC could be used within the first year after C assimilation, mainly during the growing period, whereas stored fraction could be used at the long term (Carbone and Trumbore 2007; Högberg et al. 2008; Warren et al. 2012) depending on environmental conditions that affect the magnitude of tree demand. Richardson et al. (2013) already differentiated between a TNC pool that changes in size seasonally and a TNC pool which buffers tree demand on multi-annual time scales. They suggested furthermore, a physical separation between the two pools of TNC in trunks and roots.

Some authors have also identified two fractions of TNC considering “transient” *versus* “stored” (Ogle and Pacala 2009; Chantuma et al. 2009; Kuptz et al. 2011) or “fast” *versus* “slow” reserves (Richardson et al. 2013) distinguishing thus two physical pools of TNC: “new” *versus* “old” that should correspond to accumulated *versus* stored pools respectively. Recent assimilates are a “ready to use” fraction of TNC that could be remobilized quickly to satisfy plant demand.

The accumulated pool could follow an annual pattern of depletion and replenishment whereas stored pool could be increasing slowly over the entire life of the tree in normal conditions (Fig. 1A). While the turnover rate of accumulated pool is fast, that of stored pool is low due likely to being localized in old deep structures. The remobilization of old fraction of TNC could happen just in case of total depletion of accumulated pool (Richardson et al. 2013).

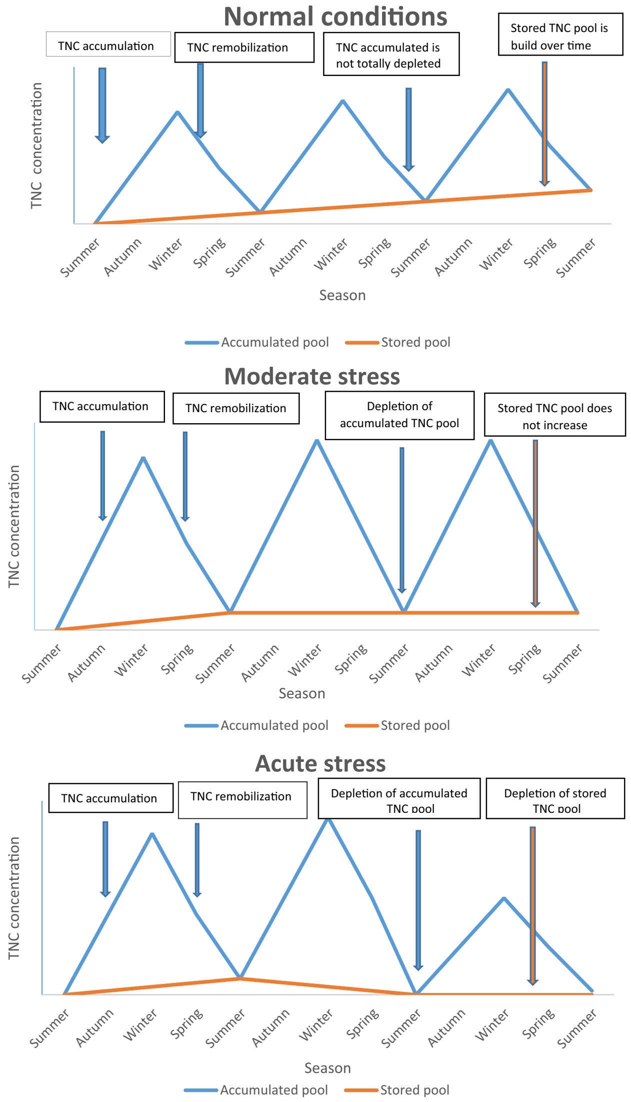

Fig. 1 The behavior over time of the accumulated and stored pools of Total Non-structural Carbohydrates (TNC) in trees during: Normal conditions: Accumulated pool is fluctuating over the seasons, stored pool is build slowly over time. Moderate stress: Accumulated pool decreases and could be depleted, stored pool does not increase over time. Acute stress: Accumulated pool is depleted and stored pool is remobilized and could be depleted

Behavior during stress

Considering reserves of TNC as a single pool, this could increase, decrease or even stay constant during a drought for example (e.g., Galiano et al., 2011; Galvez et al., 2011; 2013; Anderegg and Anderegg, 2013) (Table 1) and this response can even differ between organs of individual trees (Hartmann et al., 2013). By contrast, if we consider two pools of TNC reserves, we could suggest that the accumulated fraction of assimilates should increase immediately during the first stage of stressful conditions. During drought, for example, growth declines earlier than photosynthesis resulting in an increase of TNC accumulated (Muller et al. 2011). The same result was observed when the limiting factor is nitrogen (El Omari et al. 2003). However, such increase is transient and will be followed by a

Table 1 Growth and Total Non-structural Carbohydrates (TNC) responses during stressful conditions in some species

Species	Tree organs	TNC response	Growth response	Growing conditions	Reference
Hevea brasiliensis	Trunk	Increase	Decrease of radial growth	Tapping (latex production)	Silpi et al. (2007)
Pinus pinaster	Branches, stems and roots	Maintained	No effect	Single branch defoliation	Puri et al. (2015)
Prosopis denudans	Shoots, and roots	Maintained	No effect on growth and inflo-resence production	Slight defoliation 33%	Vilela et al. (2016)
Fagus sylvatica	Trunk,and roots	Maintained	No effect	Slight water stress	Scartazza et al. (2013)
-*Eucalyptus globulus* -*Eucalyptus Smithii* High growth rate	Roots, stems and leaves	Maintained	Increase growth followed by hydraulic dysfunction	Drought	Mitchell et al. (2013)
Quercus petraea (deciduous)	Stems and roots	Maintained	Decrease (independently of CO2 supply)	Defoliation with different levels of CO_2	Schmid et al. (2017)
Juglans regia	Branches	Maintained	Moderate growth deficit (app 30%)	Shade 67%	Lacointe et al. (2004)
Quercus velutina	Roots, stems and leaves	Maintained	Decrease	Half Defoliation	Wiley et al. (2013)
Quercus velutina	Roots, stems and leaves	Decrease at short term (3 weeks) and replenishment after 4 months	Decrease	Total defoliation	Wiley et al. (2013)
Pinus pinaster	Branches, stems and roots	Decrease (replenishment by the end of summer)	Reduced stem basal area (−37%)	Defoliation 50%	Puri et al. (2015)
Prosopis denudans	Shoots and roots	Decrease (replenishment in the second year)	Decrease or prevention of blooming in the following season	Heavy defoliation 66%	Vilela et al. (2016)
Pinus pinaster	Branches, stems and roots	Decrease (replenishment by the end of summer)	Reduced stem basal area (−84%) Reduced shoot length (−45%)	Defoliation 100%	Puri et al. (2015)
Quercus ilex (evergreen)	Stems and roots	Decrease but increase at the end of growing season	Decrease (independently of CO_2supply)	Defoliation with different levels of CO_2	Schmid et al. (2017)
-*Acer rubrum* -*Betula papyrifera* -*Fraxinus americana* -*Quercus rubra* -*Quercus velutina*	Shoots and roots	Maintained	Decrease	Defoliation 50%	Maguire and Kobe (2015)
	Shoots and roots	Decrease In all species	Decrease	Shade X Drought	Maguire and Kobe (2015)
	Shoots and roots	Decrease in intolerant species to shade	Decrease	Shade	Maguire and Kobe (2015)
	Shoots and roots	Maintained in tolerant species to drought	Decrease	Drought	Maguire and Kobe (2015)
	Shoots and roots	Decrease in intolerant species to drought	Decrease	Drought	Maguire and Kobe (2015)
Pinus halepensis	Branches and roots	Decrease	Decrease	Strong drought	Klein et al. (2014)
Acacia karroo	Roots	Decrease (replenished and matched that of unburnt plants within 1 year)	The leaf area of resprouters match that of unburnt plants within 4 to 5 months	Fire	Schutz et al. (2009)
Pinus sylvestris	Stems	Decrease	Decrease of radial growth	Extreme drought	Galiano et al. (2011)
Populus tremuloides	Roots	No TNC depletion	Decrease	Severe drought (3 months)	Galvez et al. (2011)

Table 1 (continued)

Species	Tree organs	TNC response	Growth response	Growing conditions	Reference
-Pinus edulis *-Juniperus osteosperma*	Roots, branches and needles	No TNC depletion	Death	Severe drought	Anderegg and Anderegg (2013)
-Populus tremuloides -P. balsamifera	Leaves, stems and roots	Reduced	Death	Severe drought (1 year)	Galvez et al. (2013)
Pinus radiata	Roots, stems and leaves	Reduced	Decrease	Drought	Mitchell et al. (2013)
Conservative growth					

decrease of accumulated TNC to ensure plant metabolism. The depletion of the accumulated pool will be followed by a decrease of stored TNC if stressful conditions persist. So, depending on the timescale of observation/experimentation, the accumulated fraction of TNC could increase, decrease or stay constant, whereas the fraction of stored TNC should decrease when the accumulated fraction is depleted.

Localization of the accumulated versus stored TNC reserves

Some authors subdivided TNC reserves into above- and belowground fractions (Berninger 2000; Allen et al. 2005) with a higher concentration of TNC in the belowground than in the aboveground parts of the tree (Da Silva et al., 2014). As mentioned before, mature trees could contain—in normal conditions- high amounts of stored pool of TNC in roots due to a higher proportion of radial and axial parenchyma cells (Pratt et al., 2007). However, accumulated fraction occurs in all organs, but is periodically depleted and replenished to ensure growth and metabolism. It could be considered a seasonal "transient" storage within trees. Richardson et al. (2015) reported less seasonal interconversion of sugars and starch occurring in belowground organs in comparison to aboveground ones suggesting thus a high cycling of accumulated pool in branches and stems and a low cycling of a stored pool of TNC in roots. Furze et al. (2019) obtained the same result, i.e., a seasonal depletion of TNC in branches and a constant TNC content in roots throughout the year, which accounted for 25–35% of whole-tree TNC reserves in deciduous species. We suggest, therefore, that aboveground reserves could be dominated by accumulated fraction, whereas belowground reserves are dominated by the stored fraction of TNC.

On the other hand, new structures (small branches, fine roots, new leaves) were observed to contain the recent C (Gaudinski et al. 2009; Warren et al. 2012) while old structures (large branches, coarse roots and stems) contain old C (Hartmann and Trumbore 2016). This could lead to suggest that old C is -in general- not used to build-up new biomass. Root reserves were not used to support springtime growth nor a biomass regeneration after defoliation or shoot excision. Avice et al. (1996) reported that a 95% of TNC -that was remobilized from organs remaining after shoot excision within 30 days- was lost by root and shoot respiration whereas just 5% of this C was recovered in the new leaves. Morvan-bertrand et al. (1999) also demonstrated that after a regrowing period of 28 days, 54% of the C fixed before defoliation in the case of *Lolium perenne* was remobilized to ensure plant metabolism and only 1% was incorporated into entirely new tissues. Thus, we can conclude that storage occurs in old structures (roots and trunk) whereas accumulation occurs in all organs and is mainly used for new growth. Therefore, when we speak about underground TNC reserves, there is more probability that it concerns the stored fraction rather than the accumulated fraction of TNC.

Taking into account all the characteristics of the stored and accumulated fractions of TNC, we assume that if we consider TNC reserves as a whole, we will not be able to evaluate accurately the eco-physiological significance of TNC reserves in tree growth and performance. The size of the accumulated fraction -especially at the end of the growing season- could be high in the aboveground part of the tree, whereas the stored pool of TNC of mature trees could dominate in roots. Furze et al. (2019) for instance, -considering TNC reserves as a whole- observed that the roots were not the major storage organ as branches stored comparable amounts of starch throughout the year. Therefore, depending on season, tree age and stress history, the relative contribution of the two pools of TNC to tree performance in normal and stressful conditions will be different.

Remobilization process

Remobilization is a process of redistribution of TNC that occurs usually when the demand for C overweigh the amount of the new assimilates. This could occur at the beginning of the growing period or during stressful conditions. The remobilization is driven by the intrinsic sink strengths created by the different plant tissues (Millard and Grelet 2010).

Remobilization during growing period

A fraction of assimilates produced daily by photosynthesis accumulates throughout the year to support the demand for C during the growing period. Accumulated fraction of TNC in the previous year was suggested to be of primary importance for spring growth in trees (Tromp 1983; Vilela et al. 2016). Some deciduous species, for instance, exhibit blooming before any leaf emergence (Grainger 1939; Gougherty and Gougherty 2018).

The process of accumulation occurs in all organs of the plant, enabling thus a fast use of TNC to satisfy the demand of plant organs. A TNC translocation between leaves and roots could last several days depending on the height of the trees (Kuptz et al. 2011). Even old leaves of evergreen species could be a source of C remobilized during spring growth as reported in some studies (e.g., Cerasoli et al. 2004).

On the other hand, accumulated TNC was characterized to be a fast pool in comparison to stored fraction (slow pool). The high turnover rate could explain the use of new assimilates (accumulated) firstly rather than old ones (stored) as suggested to be the case in most forest ecosystems under normal circumstances. Gaudinski et al. (2009) for instance, estimated that the mean age of TNC used to grow both leaf buds and new roots is less than one year. Then and during the growing season, trees become rapidly autonomous (Hoch et al. 2003; Keel et al. 2007) due to the compensatory effect of photosynthesis. Fruit set, for instance, was shown to depend on new assimilates rather than on TNC remobilized (Breen et al 2020). The compensatory effect of photosynthesis, along with the high turnover of the accumulated pool between the different organs of the tree could explain the maintenance of TNC concentration over the growing season obtained in several studies (Hoch et al. 2003). So, in normal conditions and even under maximum demand for TNC, those could never be depleted, especially if they are quantified at the whole-tree level (Bustan et al. 2011). The depletion could be observed transiently at the organ level (Furze et al. 2019) but the plant organs became autonomous during the growing period and the accumulated fraction of TNC is quickly replenished indicating no C limitation in normal conditions. The magnitude of C remobilization was demonstrated to be independent of growth rate and leaf habit (Piper 2020).

Remobilization during stressful conditions

Many results provide evidence that plants remobilize TNC reserves during stressful conditions (Maguire and Kobe 2015). Considering the two pools of TNC reserves, the accumulated fraction during the previous year will be remobilized firstly during stressful conditions (Fig. 1B) and when totally depleted, the stored fraction of TNC could also be remobilized to meet tree demand (Richardson et al. 2013). We could suggest that the stressful condition resulting in C limitation to growth process could be “experienced” by trees, only if the accumulated fraction of TNC is exhausted (because stored fraction is not a “ready to use” pool). The depletion of the accumulated TNC pool could lead therefore to stop growth process that was observed in many studies. Moderate stress (slight defoliation, slight water stress) was reported to not affect growth rate (Vilela et al. 2016; Scartazza et al. 2013), whereas high stress conditions such as heavy defoliation or a severe drought was observed to cause a reduction of growth rate (Puri et al. 2015; Vilela et al. 2016) (Table 1). The reduction of growth during stressful conditions could be also due to other factors other than C limitation, such as hormonal signals that affect cambial activity (Puri et al. 2015).

The slow turnover rate of stored TNC pool could be useful for a progressive use during long term stress, enabling -whenever C assimilated is lower than the compensation point- tree metabolism. As evidenced by some studies, the demand for C for respiration process and osmotic adjustment could decrease TNC pools during longer periods of stress (drought for example) until the plant dies (McDowell, 2011). O'Brien et al. (2014) obtained a positive relationship between TNC and drought survival by manipulating TNC concentrations within seedlings of ten tropical tree species. Trees with reduced levels of TNC reserves are more likely to die (Margolis and Waring 1986), whereas after defoliation for example, saplings with larger initial TNC reserves were more likely to survive (Canham et al. 1999). Kobe (1997) demonstrated also a relationship between interspecific variation in the storage of TNC and tree species differences in sapling survival and growth.

Remobilization during sudden and acute adverse conditions

Both accumulated and stored fractions of TNC could be remobilized consecutively during acute disturbance to provide plants with C needed for maintenance (Fig. 1C). If the accumulated fraction of TNC is totally exhausted, the fraction of TNC initially destined for growth and defense might also be remobilized from neighboring tissues to buffer as soon as possible C demand of the plant (Chapin et al. 1990) given the fact that the rate of remobilization of the stored TNC is not sufficient for being a slow pool. Also, the urgent need for C could result in the break-down of structural C (hemicellulose) (Hoch 2007; Schädel et al. 2009). Furthermore, the shift from carbohydrates to other reserve compounds such as lipids and the recycling of existing metabolites like proteins to meet plant demand was also reported (Fischer et al., 2015). So, trees could remobilize and broke down other molecules (structural carbohydrates, lipids and proteins) to enable maintenance and survival of the plant due to the slow turnover rate of the stored pool of TNC.

Tree mortality observed in some cases could be due to the depletion of some metabolites (e.g., compounds destined to defense) and the inability to use quickly stored TNC (for being a slow pool) rather than to the depletion of all stored TNC. Reserves of TNC in trees are demonstrated to be almost never completely depleted, although they could exhibit some seasonal variation (Würth et al. 2005; Spann et al. 2008). Maguire and kobe (2015) observed during a combined treatment of drought and shade a minimum of 0.25% of TNC remaining in the roots. Also, Canadell and López-Soria (1998) reported 4% of starch remaining within roots of dead plants after multiple clipping.

The fact that reserves of TNC are almost never fully depleted was explained by some authors (Millard and Grelet 2010) by "sequestration". We suggest, however, that the inability to use all stored reserves immediately in severe stress conditions is due to the slow turnover of the stored fraction of TNC that could have the main role of enabling plant metabolism during extended time period of stress. Many studies have shown that stored C dating back to decades could be remobilized to ensure root (Schuur and Trumbore, 2006; Carbone et al., 2011) and stem (Muhr et al., 2013) respiration especially when forest stands ages (Czimczik et al. 2006). Furthermore, trees could deplete totally stored C leading to plant death after a period of several years of extreme stress (Galiano et al. 2011; Galvez et al. 2013; Hartmann et al. 2013).

All this show evidence that stored TNC fraction could be reused in a prolonged period of stress. Therefore, the fraction of TNC identified as "sequestered" should belong to stored but, not to the accumulated pool of TNC. The continuous use of accumulated TNC (new C) firstly results in a fraction of stored TNC that could date back to a several decades, which is not due to a "sequestration" but: i) to a C demand satisfied just by accumulated pool and ii) to the slow behavior of the stored fraction of TNC. McCarroll et al. (2017) demonstrated that early wood formation is preferentially build-up using young reserves accumulated in the previous summer, whereas during poor growing conditions, trees use older TNC reserves.

The tendency to maintain some amount of stored pool of TNC (threshold) -enabled by its slow turnover rate- makes evidence of some specific physiological roles played during stress to enable proper tree functions (Adams et al., 2013). It could enable new root growth mainly as a metabolic substrate and as regulatory signals (Willaume and Pagès 2011) ensuring safety margins in stressful conditions through maintaining hydraulic transport and metabolism, root respiration (Druege et al. 2000; 2004), C for partners in a symbiosis relationship (Smith and Smith 2012); cold tolerance, osmoregulation (Dietze et al. 2014), vascular integrity during drought (Sala et al. 2012) and absorption of nutrients (carbohydrates provide energy for symplastic absorption of elements from the soil), etc.

We conclude that the fraction of stored pool of TNC could provide the energy necessary for whole-tree maintenance, enabling thus survival during prolonged periods of stress, as an adaptation strategy during adverse conditions such as extended shading (Kobe 1997), severe herbivory (Wiley and Helliker, 2012) and in particular to overcome the consequences of climate change. This is especially true for old trees that accumulate a large fraction of stored C throughout their whole life. The ability of trees to store a large fraction of TNC—that should be due among other factors, to genetic traits- could have an effect on the resilience capacity to a sudden and acute disturbance.

The recovery from an acute stress or a disturbance (fire, for example) was reported to depend on TNC reserves (Piper and Paula 2020). The period time of TNC replenishment in the organs till levels prior to stress or disturbance was observed in many studies to range between a few months and one year (Table 1), indicating that the accumulated fraction of TNC plays a primordial role in maintaining C balance in trees. We suggest that if the recovery time after stress occurs after the growing period, this could mean that the TNC fraction remobilized is the accumulated pool. However, if the recovery process lasts more than a year and the TNC reserves were not replenished after the growing season, this could signify that the stored fraction of TNC was remobilized during the stress period. Canadell and López-Soria (1998) for instance, reported that two years after multiple clipping, TNC reserves were less than unclipped plants.

Growth and storage tradeoff

Allocation of carbohydrates to build-up reserves is considered by some authors to be a purely passive consequence of the balance between C supply via photosynthesis and C demand for growth and metabolism. The main argument is that TNC cannot accumulate when growth is C limited (Bansal and Germino, 2008; Millard and Grelet 2010). Some studies by contrast, reported the possibility that the storage process in plants is regulated and therefore could be considered an active process (Le Roux et al. 2001; Chantuma et al. 2009; Genet et al. 2010) given the fact that it occurs at a time when TNC could otherwise be used for growth.

The debate about the tradeoff between growth and storage process should differentiate between accumulated and stored pools given their different behavior and respective roles in tree growth and survival. The main point to take into account in this discussion is the fact that the growth of trees is reported to depend –as mentioned previously- on the C assimilated and accumulated during the previous year (Kagawa et al., 2006; Helle and Schleser, 2004). Growth does not depend exclusively on current assimilates and the reduction of growth in some stressful conditions does not mean necessarily that it results from a C limitation. Schmid et al. (2017) for instance, demonstrated that the reduction of growth rate after defoliation does not depend on environmental CO_2.

The suggested passive process of accumulation of TNC does not mean that it is a process of low priority. It could result from the excessive production of assimilates that is too much higher than the tree demand for C and energy in a yearly basis. Poorter et al. (2006) reported that leaves may produce three to four times their own C cost per year, which could explain the increase of the concentration of TNC in trees with age (Ryan et al. 1997). Furthermore, Hoch et al. (2003) reported an observed amount of TNC in deciduous species sufficient to replace the leaf canopy four times. Trumbore et al. (2015) on the other hand, demonstrated that the flux of C inward into stems is higher than the flux of C outward indicating a continuous accumulation of TNC within stems. So, it is unlikely that carbon supply could limit mature tree growth in normal conditions (Fatichi et al. 2014; Körner, 2015). A high TNC reserves were observed in many studies, regardless of season, climate or habitat (Würth et al. 2005). Even in stressful conditions (drought, for example), is has been shown that growth is not limited by C supply (Piper et al. 2017).

The main argument in favor of growth-storage tradeoff and storage regulation is the maintenance or the increase of TNC reserves in periods of high C demand (Silpi et al. 2007; Bustan et al. 2011). We suggest that this could result from the remobilization of the accumulated pool of TNC from other tree organs to support the high demand for C. Measurements are often done using stem or branch samples, but almost never using root samples for the difficulty of sampling. The maintenance or the increase of TNC could also result from the reduction of growth during the shift from vegetative to reproductive stage increasing thus the amount of current assimilates.

The maintenance of TNC concentration when growth is reduced during some stressful conditions (Table 1) does not necessarily mean that storage is actively regulated. This could also result from a remobilization of the accumulated TNC from other organs. The reduction of growth could be due to environmental conditions (cold, drought, etc.) or to a critical loss of reserves other than a C during defoliation for example (Puri et al. 2015). Silpi et al. (2007) on the other hand, reported an increase of TNC in trunks following tapping process. We suggest that the increase observed is due to a remobilized TNC from other organs of the tree to support latex regeneration stimulated by tapping and to enable defensive processes. Tapping is a stressful process that could lead to stimulate defense mechanisms rather than enabling growth process.

Another issue of storage-growth tradeoff is that related to the differences observed between resprouters and obligate seeders. It has been reported that resprouters allocate more assimilates to storage and exhibit low growth rates in comparison to obligate seeders that store less carbohydrate reserves and achieve higher growth rates, especially in the first few years from germination (Pate et al. 1990; Verdaguer and Ojeda 2002). Some studies, however, have demonstrated that resprouters do not exhibit a low growth rate (Schwilk and Ackerly 2005) nor a preferential allocation to root reserves after clipping (Palacio et al. 2020).

We suggest that the ability to store more carbohydrate reserves could be an adaptive trait that enables resprouters to regenerate after a disturbance. Resprouters exhibit more storage parenchyma (Bowen and Pate 2017) than seedlings that have a reduced storage capacity (Hartmann et al. 2018; Ryan 2011). Furthermore, resprouters are individuals with a great root mass that requires a higher TNC amount for both maintenance and recovery process, whereas seedlings allocate carbohydrate reserves to vegetative growth and early reproduction (Fitter and Hay 2002).

We emphasized previously about the importance of previous TNC reserves for the current growth both in normal and stressful conditions. The ability of trees to regenerate after a disturbance relies on the amount of carbohydrates stored previously, although it is not the determinant factor for the growth rate the tree could achieve. The ability to store more carbohydrate reserves and/or to achieve a determined growth rate is related to genetic traits and evolutionary behaviors. In a work done by Chew and Bonser (2009), they observed that resprouters were not slower growing and that they did not allocate more resources for storage in comparison to seeders. They suggested that the differences in growth rate are not due to differences in carbohydrate allocation to storage and that growth process is related to some characteristics of tree life history like the size at maturity and life-span. Some physiological traits are reported to be independent of C budget of trees. For instance, the shift from reproductive to vegetative phase is reported to be independent of TNC reserves in olive trees (Bustan et al. 2011) contradicting thus the growth-storage trade-off theory.

For all these reasons, we suggest that TNC accumulation is not actively regulated. The accumulated fraction of TNC within the different organs of the tree will be allocated to ensure many other physiological functions besides storage (Fig. 2). We conclude that studies of C budget in trees should make a distinction between accumulated and stored pool along with the consideration of their respective roles played in tree growth and survival.

Conclusions

TNC reserves in trees could determine their vigor and ability to survive adverse conditions and to achieve high growth rates. However, the assessment of the role and significance of TNC reserves in trees should make a distinction between accumulated and stored pools. Based on many works, we demonstrated throughout the present study different behaviors of the two pools that could be attributed to the distinct roles played within plants: the role of accumulated fraction -characterized by a fast turnover rate- is to ensure annual plant metabolism and growth, whereas stored reserves -characterized by a slow turnover rate- have a substantial role in adaptive responses to C limitation allowing plant survival under a wide range of adverse environmental conditions. During acute adverse conditions, tree mortality could be due to the break-down of assimilates initially destined to defense rather than being a result of C starvation. Accumulated fraction of TNC is seasonally depleted and replenished whereas the stored fraction of TNC could be increasing throughout the whole life of the tree in normal conditions. The different dynamics of the two pools make necessary to associate the measurement of TNC concentration/content along with C age determination in studies of C budget in trees.

The high turnover rate of the accumulated pool makes it distinguishable from the process of storing (in the strict sense): it could be considered a transient pool depleted and replenished periodically that is allocated to all organs to ensure spring growth, symbiosis with soil microorganisms, defense, regeneration from a disturbance, etc. The remaining part of the accumulated pool not used for growth and metabolism will be stored to be used gradually during prolonged

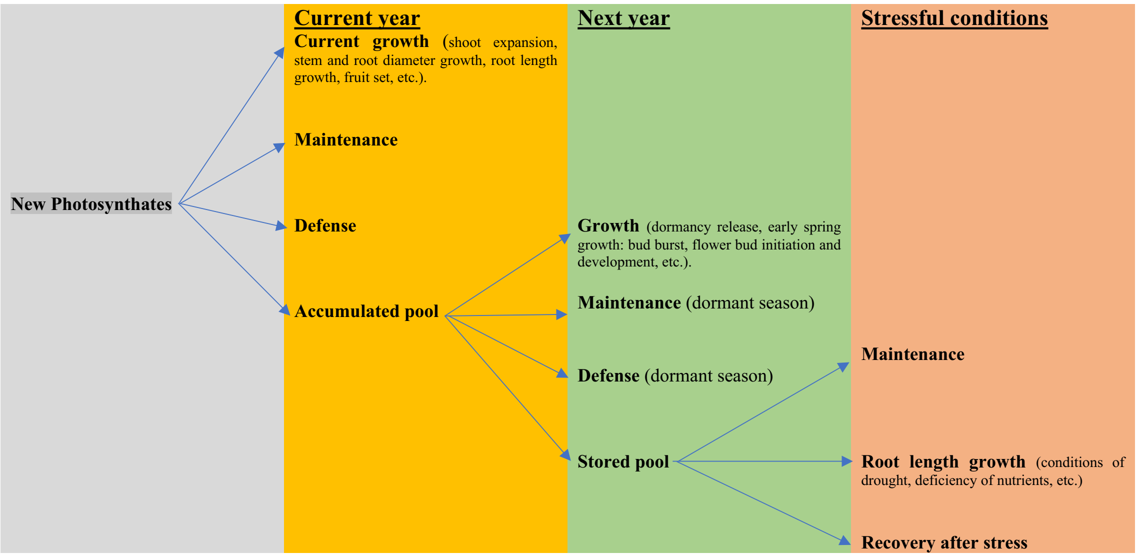

Fig. 2 Determination of the roles of accumulated and stored Total Non-structural Carbohydrates pools in woody plants

periods of stress. The amount of stored pool of TNC in mature trees could be higher, especially if the tree didn’t experience stressful conditions, so assessing TNC reserves as a whole could make some ambiguity in studies of carbon storage and allocation in woody plants.

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Declarations

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