

COMMENTARY

The osmotic balancing act: When sugars matter for more than metabolism in woody plants

Randall W. Long¹  | Henry D. Adams²¹Biology Department, Lewis and Clark College, Portland, Oregon, USA²School of the Environment, Washington State University, Pullman, Washington, USA

Correspondence

Randall W. Long, Biology Department, Lewis and Clark College, Portland, OR 97219, USA.

Email: randywloug@gmail.com

Plant economic theory is a useful analogy to understand the allocation of limited carbon resources to competing demands to maximize fitness (Bloom et al., 1985). In this analogy plants are like a business that must acquire resources from the environment to create products for immediate use in carbon sinks such as reproduction, vegetative growth, or defensive compounds. There are also other competing demands for the “currency” of carbon acquired from the environment as carbohydrates stored as solutes to regulate cellular processes or as long-term storage compounds. Together this pool of labile carbon is referred to as non-structural carbohydrates (NSCs) and is composed of soluble sugars (e.g., glucose and sucrose) and more complex carbohydrates. Soluble sugars are the products of photosynthesis and are used as the fuel for respiration and the carbon skeletons to build other organic molecules to meet various carbon sinks. Starch's most basic functions are that it prevents negative feedbacks of photosynthesis from the accumulation of sugars and depletion of inorganic phosphate within the chloroplast (Lambers et al., 2008). Although starch may have evolved to serve these functions, it also can act as a “bank account” to buffer imbalances between carbon supply and demand due to fluctuations in photosynthetic activity and can occur over diel, seasonal, and decadal periods (Chapin et al., 1990).

Following the economic model, storage should only occur when carbon acquisition exceeds the demands of metabolism. This can occur as growth and respiration decline faster than the photosynthetic rate near the conclusion of the growing season (Chapin et al., 1990; Martinez-Vilalta et al., 2016), or under stressful conditions from drought or cold (Korner, 2003; Muller et al., 2011; Peltier et al., 2022). Such a buildup of NSC, often as starch, in response to carbon supply exceeding demand has been termed passive storage (Wiley & Helliker, 2012). However, evidence suggests that NSC storage may be highly regulated and is often a competing sink with growth for recently acquired carbon throughout the growing season (Sala et al., 2012; Wiley & Helliker, 2012). Experiments depriving

saplings of light needed for photosynthesis, then removing this limitation demonstrated that growth was limited until NSC storage was refilled (Weber et al., 2018; Wiley et al., 2013). These experiments suggest that the allocation of resources to storage may be actively regulated but fail to provide an alternative mechanism to the economic model as to why plants allocate carbon to NSCs at the expense of other metabolic demands.

In the economic model, reactive and water-soluble sugar is considered cash on hand, and stored starch can be thought of as savings in a bank account. But what if simply carrying a lot of cash in your pocket (without spending it) could keep you from freezing or getting too thirsty? The economic model of plant carbon allocation can break down when non-metabolic functions of soluble sugars are considered. These include osmoregulation, whereby dissolved sugars lower osmotic water potential in cells, enabling the maintenance of cell turgor (Hartmann & Trumbore, 2016). The same mechanism also reduces the freezing point of the fluid in plant tissues, such that dissolved sugars act as cryoprotectants, essentially antifreeze, that reduce the risk of damage from cold temperatures. These roles are secondary in the economic model where NSCs are primarily thought to serve as storage and buffer environmental conditions by preventing carbon starvation under drought conditions or providing energy for the regrowth of any lost aboveground tissue due to extreme cold events (Clarke et al., 2013). The multiple roles of NSCs in the response to environmental conditions, for either metabolic or non-metabolic functions, have made it difficult for individual studies to make broad conclusions about which function has a greater influence on NSC concentrations (Peltier et al., 2021).

The meta-analysis by Blumstein et al. in this issue strongly suggests that osmoregulatory and cryoprotective functions provided by NSC accumulation may be more important than previously thought. Their research provides a unique insight into the interaction of climate and NSC concentrations by using data from studies across a range of climates and tree species (over 4600 measurements from 90 species in 6 biomes). They compared the concentrations of soluble sugars and starches in both above and belowground tissues to

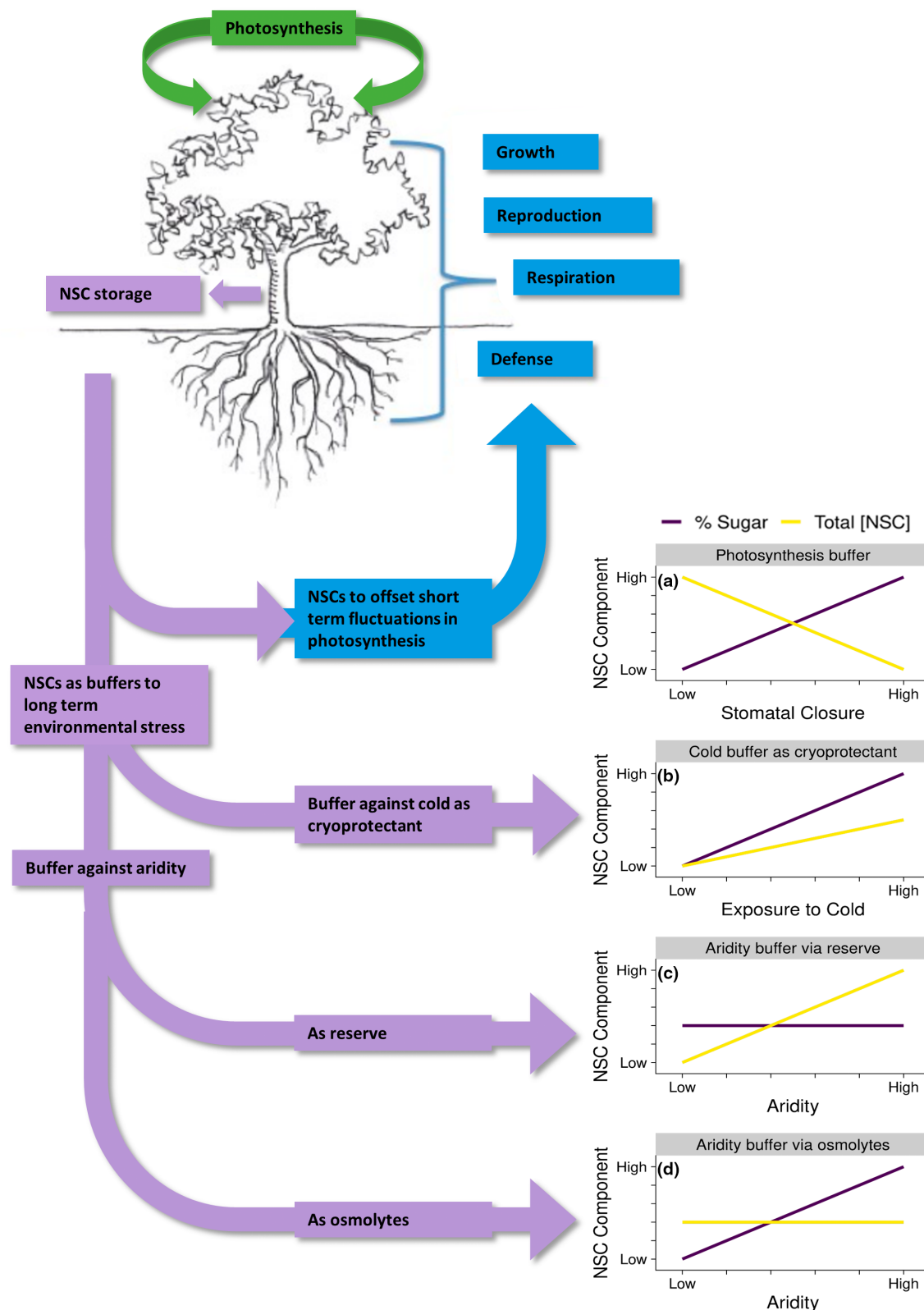


FIGURE 1 A conceptualized diagram of the various roles of non-structural carbohydrates (NSCs) in woody plants (modified from Long et al., 2017). The conceptual diagram highlights non-structural carbohydrate storage (NSC; purple) as a competing sink with all other sinks (blue) for carbon assimilated via photosynthesis as well as its ability to serve as storage to buffer fluctuations in the environment and photosynthetic activity. When NSCs are serving only as storage during short-term, diel or seasonal, limitations in photosynthesis (a), we expect that total NSC concentrations (total [NSC]) will decrease, but that the percentage of total NSC in the form of soluble sugars (% sugar) should increase. When plants are exposed long-term to cold temperatures (b) both total (NSC) and % sugar are expected to increase as soluble sugars serve as important cryoprotectants. Plants from environments exposed to greater aridity could either show increased total (NSC), with no change in % sugar, if a reserve provides a buffer for survival during droughts when photosynthesis is limited (c), or no change in total (NSC), but increased conversion to soluble sugars that act as osmolytes to prevent desiccation and hydraulic failure (d)

evaluate if there were trends related to aridity or low temperatures. If NSCs are primarily buffering environmental stress by acting as osmolytes then we would expect to see an increase in the total NSCs and/or the percentage of soluble sugars as cold or dryness increases to serve as osmolytes (Figure 1). If instead NSCs provide a reservoir of carbon to offset temporary (drought) or permanent (loss of tissue from cold) disruptions of photosynthesis, then we should see increases in total NSCs, but without a corresponding increase in the fraction of NSC as soluble sugars. Using annual climate means, they found that the percentage of soluble sugars increased with increasing aridity and/or cold temperatures, but that total NSCs decreased or were unchanged with aridity or cold. These findings support their hypothesis that NSCs are serving an important role as osmolytes in both arid and cold environments. They also explored how seasonal temperature changes affected NSC dynamics using the climate data from the month the samples were taken rather than the climate means. When the data were analyzed this way they found even stronger relationships with percent soluble sugars in all tissues and higher total NSCs in roots and main stems. This increase could be due to either active (or quasi-active—caused by active downregulation of growth) accumulation of NSCs for cryoprotection or passive accumulation as metabolic demand decreases with cooler temperatures (Dietze et al., 2014).

There has been increased attention as to whether the accumulation of NSCs is passively or actively regulated and to the role NSC storage plays in the overall capacity of plants to withstand stress (McDowell et al., 2022; Wiley & Helliker, 2012). The work done by Blumstein et al. highlights that non-metabolic functions of NSCs, specifically as cryoprotective and osmotically active soluble sugars, appear critical for resilience to both cold temperatures and aridity. This alternative role of NSCs forces us to rethink the economic model in terms of NSCs serving more than just fuel stored for metabolic demands or as an intermediate stage for conversion into other molecules. This is especially true for systems where cold temperatures may limit photosynthesis and NSC accumulation has been thought passive instead of actively regulated (Hoch & Körner, 2012; Piper et al., 2006; Shi et al., 2008). Experiments that manipulate the temperature in common garden settings (e.g., growth chambers), rather than observational studies, could elicit whether populations from colder environments accumulate greater concentrations of NSCs. Evidence of population variation in allocation to NSCs for cryoprotection would support the hypothesis that plants undergo environmental selection for non-metabolic NSC functions (Long et al., 2021). Non-metabolic roles of NSCs are not limited to serving for osmotic regulation or as cryoprotectants. They also serve in other roles important to plant function such as signaling molecules for growth and reproduction and are intermediates for secondary compounds used in defense (Bolouri Moghaddam & Van den Ende, 2012; Monson et al., 2021), yet the amount of NSC needed for these functions, compared to other non-metabolic and metabolic functions is poorly understood.

Some fundamental questions remain to be resolved regarding the allocation of NSCs to metabolic and non-metabolic functions. Notably,

it remains unknown how much NSC is required by plants to satisfy metabolic and non-metabolic needs, which is likely dynamic as environmental conditions shift on diel and seasonal scales. Furthermore, it is not well-known how easily stored starch is converted to sugar under severe environmental stress. It is assumed that there is some metabolic cost associated with starch metabolism, which also requires water, and that there are also direct costs of translocation of NSCs to and from storage sites (Lambers et al., 2008), but it is unclear if these costs are negligible or ecologically relevant. There also may be a lag between the onset of environmental stress and the conversion of starch to soluble sugars to serve as a buffer, which presents an opportunity cost of not investing in growth or reproduction (Dietze et al., 2014). The role of specific sugars also provides an opportunity for exploration as the concentration of specific sugars (i.e., trehalose), has been shown to increase in both *Arabidopsis* and rice under temperature and drought stress (Bhandari & Nayyar, 2014). Understanding differences in performance among different sugars in non-metabolic functions, and the efficiency of their synthesis, would provide further support for understanding the active allocation of NSCs to a non-metabolic pool.

The results of Blumstein et al. highlight the importance of osmoregulatory and cryoprotective functions of NSCs in woody plants. Their findings will hopefully inspire more research on the non-metabolic functions of NSCs, especially their role as buffers to environmental stress. These types of studies will further the field in understanding the degree to which plants actively, quasi-actively, or passively allocate carbon to NSCs to better understand the competing metabolic and non-metabolic demands for plant survival.

DATA AVAILABILITY STATEMENT

No data associated with this commentary.

ORCID

Randall W. Long  <https://orcid.org/0000-0001-9308-9996>

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