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Commentary

Dynamical systems for plant carbon storage: describing complex reserve dynamics from simple fluctuations in photosynthesis and carbon allocation

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This scientific commentary refers to ‘Modeling starch dynamics from seasonal variations of photosynthesis, growth and respiration’ by Oswald and Aubrey (doi: 10.1093/treephys/tpad007).

The assimilation of carbon through photosynthesis can vary considerably throughout the year (Dietze et al. 2014). To survive, trees must form an energetic buffer in the form of non-structural carbohydrates (NSCs, i.e., soluble sugars, starch, lipids, hemicellulose and sugar alcohols; Gibon et al. 2009, Signori-müller et al. 2021). While the size and seasonal amplitude of this buffer are known to vary considerably among climates and species, most models of tree NSC dynamics still use simple allometric scaling ratios (Franklin et al. 2012, Furze et al. 2019, Fermaniuk et al. 2021). This static treatment of carbon allocation may explain why most vegetation models likely underestimate allocation to NSCs (Würth et al. 2005, Franklin et al. 2012). In this special issue of *Tree Physiology*, Oswald and Aubrey (2023) emphasize the role of non-structural carbohydrates (NSCs) as a central axis of a tree’s carbon balance, pointing the way forward for future vegetation models to incorporate allocation between NSC reserves and growth as a dynamic process rather than a fixed fraction of photosynthesis.

Understanding the complex dynamics that drive variation in NSCs has been a key challenge for plant physiologists for many years (Körner 2011). The NSCs are known to play a variety of roles in plant physiological function Chapin et al. 1990, Dietze et al. 2014, Hartmann and Trumbore 2016), yet a long-standing issue in NSC dynamics is whether the environment constrains growth directly (sink limitation) or indirectly by constraining photosynthesis, thus limiting growth (source limitation; Körner 2003, Muller et al. 2011). Both scenarios have clear implications for how NSCs accumulate and contract and have often been presented as independent processes. Oswald and Aubrey (2023) suggest that NSC dynamics are really the product of both sink and source limitations. The framework for understanding NSC dynamics also includes the relative importance of passive and active reserve formations of NSC in plants (Chapin et al. 1990, Kozlowski 1992, Wiley and Helliker 2012). That is, whether carbon allocated to storage is primarily the surplus from photosynthetic gain minus the costs of growth and respiration (passive storage), or whether the allocation of photosynthesis to storage is prioritized at the expense of growth (active reserve formation; Wiley and Helliker 2012). More recent research suggests that the non-metabolic functions of NSCs, particularly for osmoregulation, may be more important than previously thought (Blumstein et al. 2023). The interplay among these competing mechanisms is thought to result in the complex carbon dynamics that are observed in woody and herbaceous plants (Martínez-Vilalta et al. 2016).

Oswald and Aubrey (2023) cut through these debates by using a theoretical approach to demonstrate that complex NSC dynamics can result from a lagged response to the internal feedbacks caused by relatively simple fluctuations in photosynthesis and carbon demand for allocation. In their model, NSCs are the result of a balance between carbon supply (photosynthesis) and carbon use (allocation). Mathematically, this tug of war is a fixed point, or a steady-state solution, that trees may achieve whenever supply is equal to demand. Yet, the location of this fixed point is a moving target precisely because the conditions that drive photosynthesis and allocation change with time (e.g., seasonality; see Box 1). Essentially, the attractor represents the observed difference between photosynthesis and growth (i.e., NSC), while the nullcline is the result when photosynthesis equals growth. The fact that the attractor and the nullcline are out of sync is what drives NSC accumulation, Oswald and Aubrey (2023) argue with their model (Box 1). Of course, in natural environments, a perfect balance between supply and demand seldom occurs. The result is that NSC storage orbits the nullcline, generating an attractor that reveals the true path of steady solutions (Box 1). As Oswald and Aubrey (2023) show, the dynamics of tree NSC concentrations can be well approximated using an attractor that lags the nullcline, reflecting some physiological realism in the ways that plants respond to their environment. With their model, Oswald and Aubrey (2023) use these drivers to re-create patterns as well as minima and maxima observed in global assessments (Martínez-Vilalta et al. 2016) and show how these can vary with growing season length across latitudes. Their model also provides insights into how the plant size affects the differences in NSC dynamics among seedlings, saplings and trees (e.g., Hartmann et al. 2018). As the ratio of photosynthetic and respiration rate per plant mass declines with increasing plant size, this reduces what they define as the response rate, effectively increasing the time lag in the NSC reserve variation in larger trees. For stressed trees in environments where photosynthesis and growth rates are lower, the response of NSC to the attractor increases the lag, reducing the variation over time.

Most Dynamic Vegetation Models (DVMs) are static, deterministic representations of tree dynamics (Fatichi et al. 2014, Berzaghi et al. 2020). This may contribute to why most models fail to simulate carbon sink–source feedbacks. Variation in these feedbacks in time and space can signify physiological acclimation, a missing component in DVMs (Berzaghi et al. 2020). Even in the absence of acclimation, such feedbacks may represent early warning signals before tree mortality events (Scheffer et al. 2009, Boettiger et al. 2013). Several previous studies have shown that delayed tree mortality following disturbance is often related to declines in growth (Ogle et al. 2000, Anderegg et al. 2015, Cailleret et al. 2017, Trugman et al. 2018). The main result from Oswald and Aubrey (2023) echoes this: if NSCs cannot accumulate at a rate high enough to support a positive carbon balance, then tree growth will suffer. This reflects what is known about the role of NSC in tree growth following winter dormancy (Furze et al. 2019, Amico Roxas et al. 2021) and disturbance (Trugman et al. 2018). The NSC plays a clear role in maintaining the metabolic status of trees when photosynthesis cannot do so. In the language of Oswald and Aubrey (2023), such a scenario would result in a dampening of the attractor further away from the nullcline and toward mortality. While the lack of growth is not in itself a cause of mortality (although tree radial or fine root growth may be necessary for hydraulic recovery from xylem embolism, e.g., Hammond et al. 2019, Hikino et al. 2022), it is likely an indicator of a carbon balance that is out of sync with a tree's environment. Asynchronies between a tree's physiological state and its environment may also underlie the multi-year lags in the growth recovery of *Pinus ponderosa* populations following drought cessation (Peltier et al. 2019).

The model presented by Oswald and Aubrey (2023) couples NSC dynamics to variation in photosynthesis and growth (Figure 1), suggesting a novel way to incorporate trait flexibility into predictive models. For instance, Xia et al. (2017) showed that by allowing an increase in the ratio of aboveground to belowground allocation, land surface models predict a 16% increase in carbon sequestration over 35 years. Similarly, Montané et al. (2017) compared observations of tree structural growth with predictions of a land surface model, CLM-4.5, using dynamic allometric parameters that allow allocation fractions between organs to vary in time. While they explicitly account for the attractor dynamics revealed by Oswald and Aubrey's (2023) model, they ignore the underlying driver (i.e., the nullcline). Still, Montané et al. (2017) reported large disparities between model predictions and observations of aboveground biomass that exceeded 7000 g C m^{-2}. On the other hand, Martínez Cano et al. (2020) modeled NSC accumulation as the difference between growth and photosynthesis, which are themselves functions of the total NSC pool. Unfortunately, this approach suggests that a tree's carbon balance is always in steady state (i.e., there is no time lag). What ties these modeling approaches together is their reliability on fixed relationships between carbon use, carbon storage and carbon supply. Oswald and Aubrey (2023) suggest that the attractor controls the scale of this relationship and thereby provides a bridge between the approaches of Montané et al. (2017) and Martinez Cano (2020).

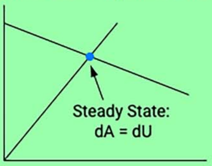
On the surface, it may appear that Oswald and Aubrey (2023) simply argue that growth is driven by NSC, but their results also tell a more complex story. As the NSC usage rate increases, starch concentrations begin to decline sending usage rate into a downward spiral until it reaches a minimum. Simultaneously, ongoing photosynthesis refills starch stores inversely to the usage rate, again feeding back onto the usage rate, driving starch stores up again. Such feedbacks are important to consider in models of tree physiological processes but are not reflected by current DVMs (Quillet et al. 2010, Franklin et al. 2020).

The dynamical model presented by Oswald and Aubrey (2023) may be a valuable starting point for representing tree carbon dynamics in DVMs; however, it is not without its own limitations. First, the authors only consider starch and do not specify which sinks are demanding carbon, leaving open the

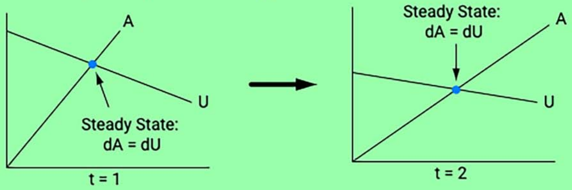
Box 1: What are nullclines and attractors?

Nullcline

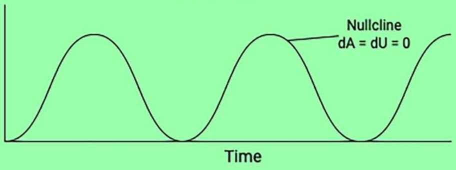
The nullcline represents a steady state, a point where the supply of non-structural carbon (NSC) from photosynthesis (A) is equal to the demand of NSC needed for metabolism (U), the usage rate of NSC. Therefore, the nullcline represents a condition where a plant's supply of NSC (A) is perfectly balanced to meet its demands for NSC. Given the set of equations, dA/dt and dU/dt, a steady state occurs where both equations are equal to 0.



However in plants, both the photosynthetic rate (A) and rate of metabolic demand for NSC of a plant (U) are continuously changing through time in response to changes in the environment and the condition of the plant. As each of these rates for supply and demand change, there is still a mathematical solution with points at dA=dU where they will meet. In other words, for any photosynthetic rate there is a potential match of a metabolic rate (demand) where all newly produced NSC is consumed.

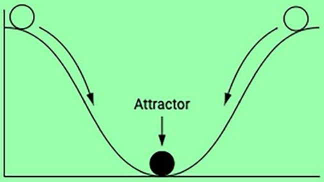


One can follow the movement of this steady state at dA=dU through time as environmental conditions change, tracing it to reveal a curve. This curve of derived steady state points is called the nullcline. The nullcline curve results from the temporal variation in the position of the steady state, driven by changes in environmental conditions that affect photosynthesis and NSC demand, where dA/dt − dU/dt = 0.

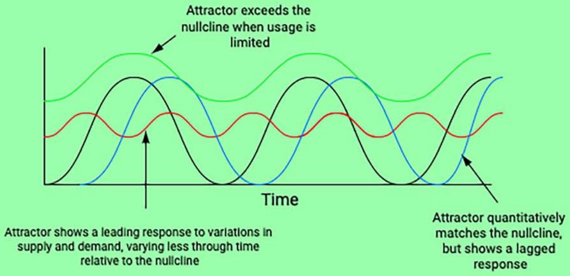


Attractor

While the nullcline curve indicates the qualitative shape that NSC concentrations will follow, as a function of supply and demand, plants seldom exist in this steady state; a perfect balance between NSC supply and demand almost never occurs. With an ideal steady state unreachable, the attractor represents a plants best attempt to approach the steady state nullcline. The attractor represents the discrepancy between NSC supply (A) and demand (U), and acts as a feedback on photosynthetic and metabolic rates that affects NSC. As a result, plants either decrease or increase NSC depending on the direction of their current state relative to the attractor.



As environmental conditions shift, the location of the attractor will oscillate with imbalances between supply and demand. As with the nullcline, one can trace the location(position?) of the attractor through time. Oswald & Aubrey (2023) argue that the attractor (observed NSC over time) will lag the nullcline to varying degrees, depending on the scale of imbalance between NSC supply and demand. Essentially, this reflects a system that is trying to catch up to an equilibrium state while never actually reaching it - the nullcline is a moving target and the attractor is the tree's best approximation to an ideal steady state.



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question of how other NSC fractions might influence and interact in this system. For example, plants may use soluble sugars for a variety of purposes, including as energetic substrate, transport and signal molecules, and osmotic adjustment (Galvez et al. 2011, Sanders and Arndt 2012, Sapes et al. 2021, Blumstein et al. 2023). Less is known about how compounds like lipids or hemicellulose might feedback into these dynamics, but prior work clearly implicates their importance in plant carbon use strategies (Hoch 2007, Fischer et al. 2015, Schoonmaker et al. 2021). Oswald and Aubrey (2023) also acknowledge that their approach is simplified by modeling carbon dynamics with one whole-plant carbon pool rather than considering NSC dynamics in different tissues and organs. Although the whole-tree perspective is important, there is considerable evidence that during periods of drought, NSC is not easily nor equally shared among organs, further complicating Oswald and Aubrey's model (Landhäusser and Lieffers 2012, Wiley et al. 2017, Hart et al. 2021). Moreover, NSC is comprised of multiple pools, which are often described as fast and slow (Vargas et al. 2009, Richardson et al. 2013, Trumbore et al. 2015). During periods of drought, for instance, trees may rely on slow pools of old NSC for survival and/or recovery (Vargas et al. 2009), although the precise role of fast and slow pools in tree recovery from drought is still a subject of debate. It is currently unclear how the dynamics outlined in Oswald and Aubrey (2023) might change when these pools are considered. However, they do point out that expansion of their model to consider multiple pools would be possible. Finally, environments

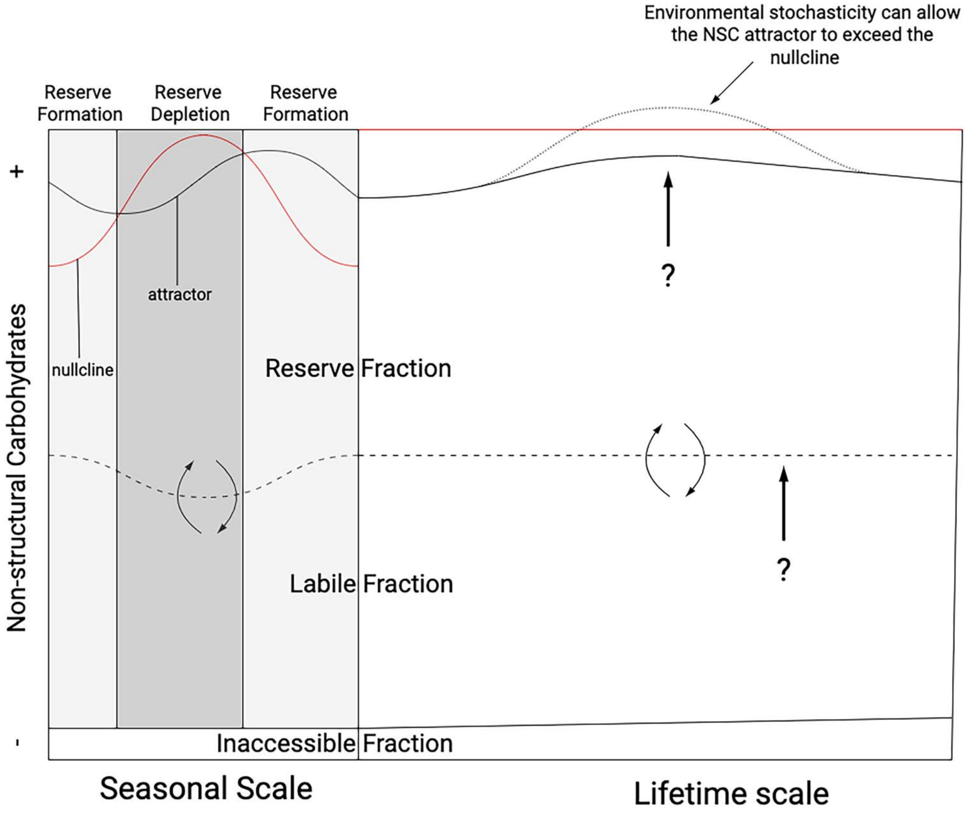

Figure 1. Non-structural carbohydrate dynamics at seasonal and lifetime scales. The model by Oswald and Aubrey (2023) describes an attractor that lags the nullcline at seasonal scales. Some fraction of NSC remains sequestered in older sapwood at seasonal scales and is considered inaccessible to the tree; this fraction might increase with tree age. Not described by Oswald and Aubrey's model (2023), the nullcline may remain either flat or with negative slope at the scale of a tree's entire lifetime, suggesting a perfect balance between NSC supply and demand. Yet, nothing is known about tree NSC dynamics across decadal scales, and thus the amplitude between the nullcline and attractor and the shape of their lines are open questions.

are stochastic and difficult to predict (Lorenz 1963, Saravanan and McWilliams 1997). Our ability to understand dynamics at finer timescales (important for estimates of mortality) necessitates the incorporation of stochastic processes into these dynamical models (Melbourne and Hastings 2008, Sharma et al. 2015).

Although the model presented by Oswald and Aubrey (2023) is not without its limitations, it uses simple mechanistic relationships to provide clear and reliable predictions of complex dynamics. Moreover, their model bypasses the often semantic debate of whether NSC accumulates passively or actively, and whether sink or source limitation inhibits tree growth, that typically treats these influences as dichotomous. The relationships between carbon demand, carbon supply and carbon storage tackled by Oswald and Aubrey (2023) as a dynamical system should be a priority for integration into contemporary DVMs to improve our estimates of vegetation carbon fluxes. Although there is more progress to be made toward improving this model, Oswald and Aubrey (2023) provide an important first step that can guide future modeling efforts using truly mechanistic relationships instead of simple allometric ratios.

Data and materials accessibility

No data were used in this commentary.

Conflicts of interest

No conflicts of interest.

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