Commentary

The importance of storage and redistribution in vascular plants

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The resilience of plants to changes in their environment is crucial for survival. For vascular plants, storage and redistribution of resources are important components conferring resilience under the effects of changing environmental conditions. This process has additional significance for woody shrubs and trees due to their size, longevity and tight coupling to the environment in many natural systems (e.g., Körner 2000).

The health and survival of long-lived vegetation has a direct influence over broader scale cycling of carbon, water and nutrients in forest systems (e.g., Thorley et al. 2015). Social, economic and environmental outcomes rely heavily on the health of the global forest (Wardle et al. 2003, Easterling and Apps 2005, Hanewinkel et al. 2013, Katila et al. 2014). Evidence suggests that in the coming decades, the world's forest ecosystems will face unprecedented challenges through the rate of environmental change (McDowell and Levanic 2014, Frank et al. 2015, Gauthier et al. 2015, Lewis et al. 2015, McDowell and Allen 2015, Millar and Stephenson 2015, Teskey et al. 2015, Trumbore et al. 2015). Never before has such emphasis been placed on our need to understand the resilience of the global forest system.

Among species of trees and woody shrubs, a wide diversity of physical, chemical and physiological mechanisms are employed to cope with environmental change. A unifying goal among vascular plants is the optimization of resource distribution to ensure sustainable growth and survival. Two interconnected conduits for resource transport exist in trees—the phloem and the xylem—that enable storage and transport of assimilates throughout daily and seasonal cycles. This capacity gives rise to two significant properties that are especially important to the longevity of vascular plants—that of storage to buffer against short- to medium-term resource deficiencies, and the ability to modify resource distribution to cope with prevailing environmental conditions.

A wide range of literature has been published dealing with the processes of carbon, water and nutrient acquisition by woody plants (for reviews, see Körner 2003, 2006, Kreuzwieser and Gessler 2010, Lukac et al. 2010). Less characterized are the processes of storage and recycling of resources in response to environmental change (e.g., Hartmann et al. 2015, Wyka et al. 2016). Buffering of the system, through the acquisition and storage of resources in excess of that required for growth and metabolism, has the potential to provide insurance against deleterious effects (e.g., Hoch and Körner 2003) or provide readily available substrate to mobilize in response to the formation of canopy gaps, neighbour mortality or periodic rainfall events (e.g., Würth et al. 2005). Considerable scope exists for the study of how trees balance resource investment, storage and remobilization in an effort to achieve optimal investment in growth.

In this issue of *Tree Physiology*, Wyka et al. investigate these fundamental processes to determine how three related pairs of woody shrubs of contrasting deciduousness cope with adverse conditions. With a focus on these contrasting growth strategies, the authors illustrate that deciduous species accumulate larger concentrations of labile carbon among tissues than do evergreen species. These results indicate the important role that storage and remobilization likely play in the re-establishment of photosynthetic capacity during canopy re-emergence. Interestingly, while Wyka et al. demonstrate that this pattern holds true for carbohydrates, they also show that such patterns are less clear for nitrogen-containing metabolites. Warren and Adams (2004) argue that for evergreen tree species, accumulation of RuBisCO in excess of that required for photosynthesis may act as a leaf-based storage of nitrogen, perhaps explaining these observations. Previous investigations in deciduous species offer somewhat conflicting results; however, the tendency of deciduous species to store labile nitrogen in woody tissues most likely varies among tree genera in both

capacity and chemical form (see [Piper and Fajardo 2014](#), [Pfautsch et al. 2015](#), [Piper et al. 2015](#)).

While a range of studies have investigated fluctuations in labile carbon and nitrogen pools in woody plants (e.g., [Wiley and Helliker 2012](#), [Dickman et al. 2015](#), [Hartmann et al. 2015](#), [Woodruff et al. 2015](#)), one of the most detailed spatio-temporal studies to date is that of [Hoch et al. \(2003\)](#), detailing both within-tree spatial variation in metabolite concentrations and seasonal variation among metabolite pools in both evergreen and deciduous species. Of the most important conclusions from this study, [Hoch et al. \(2003\)](#) illustrated that in the deciduous species under investigation, one to three canopies' worth of carbon was stored over winter. This gives unprecedented insight into the magnitude of buffering these trees adopt in order to cope with damaging temperatures experienced during the winter months. Assuming that all of this resource is available for remobilization, it appears that some deciduous trees are equipped to cope with 'false springs' and the subsequent risk of damage to an emergent canopy. This capacity, and its influence over the occupation of space in a re-developing canopy, highlights the importance of overwinter storage to facilitate the rapid and extensive re-emergence of photosynthetic tissues.

The complexity of remobilization and storage among plant tissues has necessitated a range of approaches to investigate patterns of carbon and nitrogen allocation in woody plants. An important caveat must be placed upon the terminology used to describe the storage and remobilization of non-structural pools within plant tissues. While the concentration of metabolites in stem, branch and root tissues offers insight into storage capacity and remobilization, it is important to consider the delineation between concentration and measures of flux. Although concentration may offer comparative measures of resource storage among plants adopting similar growth strategies, this may offer little interpretation of flux, which underpins the principle of partitioning and remobilization. In addition, labile metabolites may be removed from the plant, with metabolism and exudation undoubtedly having significant influence over tissue concentrations. Finally, storage of metabolites often requires careful packaging of photoassimilates in highly reduced forms; hence, the diversity of storage metabolites is often restricted to a relatively small set of chemical groups. Despite this phenomenon, few studies concurrently quantify the full scope of metabolomic and proteomic complexity. Interpretation of such data should acknowledge the scope of chemical analysis employed and its implications for understanding the processes contributing to storage and remobilization of resources.

While extensive evidence exists for the importance of remobilization of resources in vascular plants, several processes of carbon and nitrogen movement are yet to be fully characterized. For example, the fundamental basis of how phloem transport operates is still under contention ([Fu et al. 2011](#), [Knoblauch and Oparka 2012](#), [Liu et al. 2012](#)). In addition, carbohydrate

concentration in xylem water may be influenced by leakage from the phloem stream ([Gessler et al. 2007](#)); therefore, at times of low phloem and xylem flow such as those experienced under water deficit, the influence of this leakage may be exacerbated, leading to higher concentrations of photoassimilates in xylem water. Similarly, extensive evidence for the role of carbon and nitrogen storage and remobilization has been shown across a range of tree species (e.g., [Körner 2003](#), [Millard and Grelet 2010](#)); however, the question of limitation remains among species occupying fire-prone and resource-limited environments ([Giertych et al. 2015](#), [Pellegrini et al. 2015](#), [Zeppel et al. 2015](#)).

Allocation of resources to defence from pathogen attack is another important consideration for trees. From the leaf to the forest scale, predicted future climates may exacerbate pressures from forest pathogens ([Chakraborty 2013](#)); thus, combined with longevity, investment in chemical and structural defences has particular significance. [Wyka et al. \(2016\)](#) suggest that the absence of a detected allocation of resources to defence compounds implies investment in structural defences for evergreen species. More broadly, a range of studies illustrate investment in chemical defences across a range of plant genera (e.g., [Eichenberg et al. 2015](#)) and that allocation of carbon and nitrogen resources to chemical defences play an important role in resistance against pathogen attack (e.g., [Schultz et al. 2013](#)). Undoubtedly, patterns in tree defences vary with genera and the prevailing selection pressures (e.g., [Frost and Hunter 2008](#)).

Investigations of resource storage and partitioning in woody species focus on one of the most significant yet understudied strategies that species employ to occupy diverse and varying environmental conditions. Characterizing the quantity, identity and flux of resources throughout woody tissues will provide valuable insight into physiological responses as well as elucidate candidate tools for use in diagnostic assessments of health. Investigations such as those detailed in [Wyka et al. \(2016\)](#) will provide a fundamental understanding of the properties that determine the resilience of woody species and lead to more informed management for the benefit of global forest health.

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