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Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings

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Summary

- Climate models suggest that more frequent drought events of greater severity and length, associated with climate change, can be expected in the coming decades. Although drought-induced tree mortality has been recognized as an important factor modulating forest demography at the global scale, the mechanisms underlying drought-induced tree mortality remain contentious.
- Above- and below-ground growth, gas exchange, water relations and carbon reserve accumulation dynamics at the organ and whole-plant scale were quantified in *Populus tremuloides* and *P. balsamifera* seedlings in response to severe drought. Seedlings were maintained in drought conditions over one growing and one dormant winter season.
- Our experiment presents a detailed description of the effect of severe drought on growth and physiological variables, leading to seedling mortality after an extended period of drought and dormancy. After re-watering following the dormant period, drought-exposed seedlings did not re-flush, showing that the root system had died off.
- The results of this study suggest a complex series of physiological feedbacks between the measured variables in both *Populus* species. Further, they reveal that reduced reserve accumulation in the root system during drought decreases the conversion of starch to soluble sugars in roots, which may contribute to the root death of drought-exposed seedlings during the dormant season by compromising the frost tolerance of the root system.

Introduction

Nonstructural carbohydrates (NSC) reserves play a fundamental role in plant germination, growth, reproduction, defense and survivorship under stress. Although most of these roles have been studied for more than a century (Brown & Escombe, 1898; Halsted, 1902), the interaction between NSC reserves and water transport, especially under hydraulic stress, has not received much attention until recently. Although potentially critical in understanding and projecting drought-induced tree mortality with climate change, the underlying interrelationships between carbon dynamics and water transport at the organ and whole-plant level are far from understood (McDowell *et al.*, 2008; McDowell & Sevanto, 2010; Sala *et al.*, 2010; Ryan, 2011). Furthermore, the notion that, under drought stress, carbon allocation and water transport are probably closely coupled processes has received growing appreciation (Galvez *et al.*, 2011; McDowell, 2011; McDowell *et al.*, 2011; Landhäusser & Lieffers, 2012; Sala *et al.*, 2012). In a recent review, Sala *et al.* (2012) suggested that carbon reserves in trees are sustained at a minimum level, which is needed to maintain metabolic processes and hydraulic integrity, particularly under episodes of severe drought. The authors further speculated that the maintenance of hydraulic integrity is prioritized in order to avoid hydraulic failure, which could make tissue carbon reserves irretrievable (i.e. if xylem suffers catastrophic levels of embolism) after water transport ceases, and the potential remobilization of reserves from sources to sinks would not be possible.

The interaction between carbon dynamics and water transport under drought conditions is probably more complex than is currently understood. With a few exceptions (Galvez *et al.*, 2011; Anderegg, 2012; Anderegg *et al.*, 2012), the interaction between carbon and water has been traditionally assessed using functional proxies of whole-plant carbohydrate and hydraulic status (e.g. mass accumulation, CO_2 assimilation and stomatal conductance) instead of direct measurement (i.e. content and concentration of NSC and percentage loss of hydraulic conductivity (PLC)). An understanding of the possible feedbacks between carbon dynamics and water relations (McDowell & Sevanto, 2010) from a wider, more integrative perspective is crucial to interpret current ecological phenomena, such as drought-induced sudden aspen decline across the western USA and Canada (Michaelian *et al.*, 2010; Worrall *et al.*, 2010; Anderegg *et al.*, 2012).

Xylem vulnerability to hydraulic failure and stomatal behavior (e.g. the timing and cues of stomatal opening and closure) are important drivers of plant responses to drought stress, and can