

Drought induces opposite changes in the concentration of non-structural carbohydrates of two evergreen *Nothofagus* species of differential drought resistance

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Abstract

• **Introduction** One current explanation for worldwide drought-induced tree mortality states that reduced photosynthesis and continued respiration lead to carbon depletion and eventually to carbon starvation.

• **Methods** To determine if variations in gas exchange are consistent with variations in carbon storage, and if such consistency may depend on the drought resistance of a species, I examined the non-structural carbohydrates (NSC) concentration and gas exchange in seedlings of two *Nothofagus* species of differential drought resistance under severe drought—just before death—and under well-watered conditions.

• **Results and discussion** Drought provoked decreased photosynthesis and had no effect on leaf respiration in both species, whereas NSC concentrations varied oppositely: it decreased in the relatively more drought-susceptible species (*Nothofagus nitida*) whilst it increased in the relatively more drought-resistant species (*Nothofagus dombeyi*). Thus, if carbon balance would have been inferred from gas exchange alone, I would have wrongly concluded that carbon depletion occurred in both species. In stressed seedlings of *N. nitida*, photosynthesis and NSC concentrations were negatively correlated in roots ($r_2 = -0.57$, $p = 0.03$) and not correlated in stems ($r_2 = -0.05$, $p = 0.58$), indicating that carbon depletion due to reduced photosynthesis was not occurring at harvest time, but it took place earlier when water stress was milder.

• **Conclusions** Results demonstrate that carbon depletion cannot be predicted from measurements of gas exchange. Drought-induced mobilization of carbon storage appeared influenced by the drought resistance of the species and by drought intensity.

Keywords Carbon starvation hypothesis · Carbon storage · Climate change · Drought · Photosynthesis

1 Introduction

Worldwide massive tree mortality is one of the most evident and concerning effects of drought associated with climate change (Adams et al. 2009; Allen et al. 2010; Bréda et al. 2006; Liang et al. 2003; van Mantgem et al. 2009). The mechanisms involved in drought-induced tree death, however, remain unclear (McDowell et al. 2008; Sala et al. 2010). One appealing explanation that was suggested earlier (Parker and Patton 1975) and that emerged again later (Adams et al. 2009; Bréda et al. 2006; McDowell et al. 2008) is that drought produces a decrease in the reserves of carbohydrates (i.e., carbon depletion, Sala et al. 2010) of plants and eventually mortality. The reasoning behind this explanation is basically as follows: (1) drought produces stomatal limitations on photosynthesis, (2) the level of photoassimilates (carbohydrates) decreases, (3) metabolic demand for carbohydrates is no longer met by photosynthesis, (4) carbohydrates are mobilized from storage to satisfy a continued metabolic demand, and (5) concentrations of carbohydrates in storage sites decrease leading to carbon depletion (McDowell et al. 2008). Accordingly, it is proposed that if drought persists the whole-plant carbon demand for growth and maintenance becomes progressively greater than the whole-plant carbon availability (i.e., current

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