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Similar variation in carbon storage between deciduous and evergreen treeline species across elevational gradients

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• *Background and Aims* The most plausible explanation for treeline formation so far is provided by the growth limitation hypothesis (GLH), which proposes that carbon sinks are more restricted by low temperatures than by carbon sources. Evidence supporting the GLH has been strong in evergreen, but less and weaker in deciduous treeline species. Here a test is made of the GLH in deciduous–evergreen mixed species forests across elevational gradients, with the hypothesis that deciduous treeline species show a different carbon storage trend from that shown by evergreen species across elevations.
• *Methods* Tree growth and concentrations of non-structural carbohydrates (NSCs) in foliage, branch sapwood and stem sapwood tissues were measured at four elevations in six deciduous–evergreen treeline ecotones (including treeline) in the southern Andes of Chile (40°S, *Nothofagus pumilio* and *Nothofagus betuloides*; 46°S, *Nothofagus pumilio* and *Pinus sylvestris*) and in the Swiss Alps (46°N, *Larix decidua* and *Pinus cembra*).
• *Key Results* Tree growth (basal area increment) decreased with elevation for all species. Regardless of foliar habit, NSCs did not deplete across elevations, indicating no shortage of carbon storage in any of the investigated tissues. Rather, NSCs increased significantly with elevation in leaves ($P < 0{\cdot}001$) and branch sapwood ($P = 0{\cdot}012$) tissues. Deciduous species showed significantly higher NSCs than evergreens for all tissues; on average, the former had 11 % (leaves), 158 % (branch) and 103 % (sapwood) significantly ($P < 0{\cdot}001$) higher NSCs than the latter. Finally, deciduous species had higher NSC (particularly starch) increases with elevation than evergreens for stem sapwood, but the opposite was true for leaves and branch sapwood.
• *Conclusions* Considering the observed decrease in tree growth and increase in NSCs with elevation, it is concluded that both deciduous and evergreen treeline species are sink limited when faced with decreasing temperatures. Despite the overall higher requirements of deciduous tree species for carbon storage, no indication was found of carbon limitation in deciduous species in the alpine treeline ecotone.

Key words: Carbon supply, elevational gradient, *Larix decidua*, *Nothofagus betuloides*, *Nothofagus pumilio*, Patagonia, *Pinus cembra*, *Pinus sylvestris*, Swiss Alps, Alpine treeline.

INTRODUCTION

Alpine treeline ecotones constitute relatively narrow and well-delineated landscape boundaries, whose maximum elevation is thought to be controlled by temperature (Tranquillini, 1979; Grace *et al.*, 2002; Körner, 2012). Globally, high elevation treelines are associated with a mean growing season isotherm of around 6·7 °C (Körner and Paulsen, 2004). Two mutually exclusive hypotheses have been proposed to explain the upper elevation limit of treelines worldwide; these are the carbon limitation hypothesis (CLH) and the growth limitation hypothesis (GLH; Fig. 1). The CLH predicts that the universal elevational reduction in tree growth at or close to the alpine treeline is a consequence of the decline in photosynthetic rates provoked by the altitudinal decrease in temperature (Stevens and Fox, 1991; Wardle, 1993). The treeline thus occurs at the elevation where annual carbon (C) gains can no longer compensate for the requirements of all the C sinks (i.e. respiration, growth and all C losses). Alternatively, the GLH claims that the processes limited by altitudinal decreases in temperature are cell and tissue formation (Körner, 1998), indicating a low temperature threshold for growth itself rather than a limitation on C gain. The change in C storage of trees in relation to elevation has been the most accepted and used proxy to test both hypotheses (Fajardo *et al.*, 2012; Hoch and Körner, 2012). The C storage pool of trees consists of a broad variety of different C-based organic compounds (with species-specific differences in composition and relative proportion), but throughout all tree genera, non-structural carbohydrates (NSC = low molecular weight sugars + starch) are quantitatively the most important C stores, accumulating whenever C sinks (e.g. growth) are more limited than C sources (photosynthesis) (Chapin *et al.*, 1990). Thus, an elevational increase in NSCs provides support for the GLH, while an altitudinal decrease in NSCs supports the CLH.

A large body of empirical studies has found support for the GLH in a variety of treelines (e.g. Hoch and Körner, 2003, 2012; Piper *et al.*, 2006; Shi *et al.*, 2008; Fajardo *et al.*, 2011). Yet, the most important piece of evidence against the GLH was observed in a treeline *in situ* free-air CO_2-enrichment