

Variation of mobile carbon reserves in trees at the alpine treeline ecotone is under environmental control

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Summary

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- In low temperature-adapted plants, including treeline trees, light-saturated photosynthesis is considerably less sensitive to temperature than growth. As a consequence, all plants tested so far show increased nonstructural carbohydrate (NSC) tissue concentrations when exposed to low temperatures. Reduced carbon supply is thus an unlikely cause for low temperature range limits of plants. For altitudinal treeline trees there is, however, a possibility that high NSC genotypes have been selected.
- Here, we explored this possibility using afforestations with single-provenance conifers along elevational gradients in the Southern Chilean Andes and the Swiss Alps.
- Tree growth was measured at each of four approximately equidistant elevations at and below the treeline. Additionally, at the same elevations, needle, branch and stem sapwood tissues were collected to determine NSC concentrations.
- Overall, growth decreased and NSC concentrations increased with elevation. Along with previous empirical and experimental studies, the findings of this study provide no indication of NSC reduction at the treeline; NSC increased in most species (each represented by one common population) towards their upper climatic limit. The disparity between carbon acquisition and structural carbon investment at low temperature (accumulation of NSC) thus does occur even among genotypes not adapted to treeline environments.

Introduction

During the last few decades there has been increasing evidence that low temperature during the growing season is responsible for the formation of high-elevation treelines (Tranquillini, 1979; Körner, 1998; Jobbágy & Jackson, 2000; Grace *et al.*, 2002). In low temperature-adapted plants, including altitudinal treeline trees, light-saturated photosynthesis reaches *c.* 50% of full capacity at +5°C, whereas no tree has ever been shown to exhibit significant growth below 5°C (James *et al.*, 1994; Körner, 2006; Solfeld & Johnsen, 2006; Alvarez-Uria & Körner, 2007). As a consequence, all plants tested so far show an increment in non-structural carbohydrate (NSC = soluble sugars + starch) tissue concentrations when exposed to low temperatures. Thus, a carbon supply limitation – as proposed by, for example, Stevens & Fox (1991) and Wardle (1993) – is an unlikely cause for low temperature range limits of plants. Rather, the growth-limitation hypothesis (GLH), which claims that cell and tissue formation are the processes that are first limited by the altitudinal decrease in temperature (Körner, 1998; Grace *et al.*, 2002), seems to work given that a growing number of empirical studies have found no decrease, and most often an increase in NSC concentrations with elevation (e.g. Piper *et al.*, 2006; Shi *et al.*, 2008; Fajardo *et al.*,

2011; Hoch & Körner, 2012). It remains, however, unresolved whether this phenotypic pattern reflects a short-term physiological response driven by stronger limitations on growth relative to carbon gain or, rather, an adaptive response of treeline populations to better cope with the harsh conditions at treeline (Sveinbjörnsson, 2000; Smith *et al.*, 2003). Consequently, NSC accumulation with elevation could be an evolutionary response to resist harsh conditions (Monson *et al.*, 2006), a consequence of genetically limited growth (Premoli *et al.*, 2007), with trees under low-temperature conditions allocating more carbon into storage, or the phenotypic result of a direct reduction in growth in cold environments (Körner, 1998). It is the purpose of this study to determine if the increase in carbon reserves with elevation is an immediate physiological response of trees to lower temperatures or not.

Field surveys assessing the GLH have the inherent disadvantage of being unable to measure and account for probable intra-specific, genetic adaptation (i.e. natural selection) differences along elevation. So far, several studies have demonstrated that variation in many morphological and physiological traits along the altitudinal gradient is under genetic control (Oleksyn *et al.*, 1998; Premoli, 2003; Li *et al.*, 2004; Piper *et al.*, 2006; Premoli *et al.*, 2007; Vitasse *et al.*, 2009). For example, Premoli *et al.*