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An experimental approach to explain the southern Andes elevational treeline[1]

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- *Premise of the study:* The growth limitation hypothesis (GLH) is the most accepted mechanistic explanation for treeline formation, although it is still uncertain whether it applies across taxa. The successful establishment of *Pinus contorta*—an exotic conifer species in the southern hemisphere—above the *Nothofagus* treeline in New Zealand may suggest a different mechanism. We tested the GLH in *Nothofagus pumilio* and *Pinus contorta* by comparing seedling performance and carbon (C) balance in response to low temperatures.
- *Methods:* At a southern Chilean treeline, we grew seedlings of both species 2 m above ground level, to simulate coupling between temperatures at the meristem and in the air (colder), and at ground level, i.e., decoupling air temperature (relatively milder). We recorded soil and air temperatures as well. After 3 yr, we measured seedling survival and biomass (as a surrogate of growth) and determined nonstructural carbohydrates (NSC).
- *Key results: Nothofagus* and *Pinus* did not differ in survival, which, as a whole, was higher at ground level than at the 2-m height. The root-zone temperature for the growing season was 6.6°C. While biomass and NSC decreased significantly for *Nothofagus* at the 2-m height compared with ground level (C limitation), these trends were not significant for *Pinus*.
- *Conclusions:* The treeline for *Nothofagus pumilio* is located at an isotherm that fully matches global patterns; however, its physiological responses to low temperatures differed from those of other treeline species. Support for C limitation in *N. pumilio* but not in *P. contorta* indicates that the physiological mechanism explaining their survival and growth at treeline may be taxon-dependent.

Key words: carbon source–sink balance; leaf habit; missing taxon; nonstructural carbohydrates; *Nothofagus pumilio*; Patagonia; *Pinus contorta*; plant–climate interactions; timberline.

Alpine treelines are conspicuous vegetation boundaries that characterize most mountain landscapes around the world. On a global scale, alpine treelines have been claimed to be physiologically controlled by low temperature and are hence considered one of the most responsive to global warming (Tranquillini, 1979; Körner, 1998; Jobbágy and Jackson, 2000; Grace et al., 2002; Körner 2012a). In a search for general trends, Körner and Paulsen (2004) found that most alpine treelines (particularly in the northern hemisphere) are located at an isotherm of 6.7°C (±0.8 SD) of mean root–zone temperature for the growing season. This striking result cemented the notion that low temperatures during the growing season control the treeline elevation. The most plausible explanation for this so far has been that low temperatures affect trees' carbon (C) balance (Körner, 1998). A recent worldwide study in 13 alpine treeline regions confirmed the existence of this narrow isotherm for treelines (rectified to 6.4°C ± 0.7 SD) and concluded that the mechanism explaining this pattern is C sink limitations in trees (Hoch and Körner, 2012).

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The temperature limit of tree growth represents a threshold that markedly separates trees from other life forms that are able to grow above the treeline elevation, e.g., alpine vegetation. The discussion about the physiological mechanism for treeline formation has been focused on how low temperatures affect C acquisition or C usage. It has been affirmed that in low temperature-adapted plants, including treeline trees, light-saturated photosynthesis reaches approximately 50% its full capacity at +5°C, whereas no tree has ever been shown to exhibit significant growth (e.g., cell division) below 5°C (James et al., 1994; Solfjeld and Johnsen, 2006; Alvarez-Uria and Körner, 2007; Rossi et al., 2007). As a consequence, all low temperature-adapted plants tested thus far have shown an increase in their C reserves (i.e., nonstructural carbohydrate [NSC] concentrations) when exposed to colder temperatures (e.g., Hoch and Körner, 2009), suggesting that plant growth and development are not limited by carbon supply. These observations contradict the carbon-limitation hypothesis (as proposed by Stevens and Fox (1991) and Wardle (1993)), which suggests that tree growth at cold temperatures is limited by carbon supply. The growth limitation hypothesis (GLH), on the other hand, proposes that cell and tissue formation—and not C acquisition—are the processes that are first limited by the elevational decrease in temperature (Körner, 1998). A growing number of empirical studies support the GLH, i.e., these 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., 2012; Hoch and Körner, 2012). Further support for this hypothesis is found in the duration of mitosis and cell multiplication, which exponentially increases with decreasing temperatures, tending to reach infinite levels below approximately 6°C (Körner, 2003); there is