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Foliar habit, tolerance to defoliation and their link to carbon and nitrogen storage

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Summary

1. An innovative hypothesis to explain the higher carbon (C) and nitrogen (N) storage in woody tissues of winter deciduous species as compared to evergreen species is that these storages reflect an adaptation to tolerate herbivory. Support for this hypothesis has been little when manipulative defoliations were partial and/or applied in a single season. Given that repeated defoliations throughout a single season are common in temperate forests and tend to be more severe in deciduous than in evergreen species, we tested this hypothesis considering complete and recurrent defoliation in two sympatric *Nothofagus* species with contrasting foliar habit.

2. In the field, we applied three defoliation intensities for 3 years in naturally coexisting juvenile trees of *Nothofagus betuloides* (evergreen) and *Nothofagus pumilio* (deciduous). Defoliation intensities included complete defoliation (100%) twice during the growing season, partial defoliation (50%) twice during the whole experiment and no defoliation. We evaluated survival, regrowth and C- and N-storage in the leaves, stems and roots of each tree.

3. Complete defoliation caused 100% mortality in *N. betuloides* after the first year and no mortality in *N. pumilio* after 3 years; it induced higher C reductions in *N. pumilio* roots, supported by greater C-storage. Partial defoliation caused no interspecific differences in survival, though it produced a stronger decrease in C-storage in *N. betuloides* than in *N. pumilio*. N concentrations in woody tissues were significantly higher in *N. pumilio* than in *N. betuloides*, and only in the former did they decrease with the defoliation intensity.

4. *Synthesis*. We found a potential functional link between leaf habit, defoliation tolerance and C- and N-storage. The deciduous species tolerated complete and recurrent defoliations better than the evergreen species, which was associated with higher C- and N-storage in stems and roots of the former. This link was not detected under partial defoliation. We suggest that the higher C- and N-storage in the woody tissues of deciduous species as compared to evergreen species is an adaptation to tolerate complete and recurrent defoliations under which temperate winter deciduous species may have evolved.

Key-words: carbon limitation, deciduous, disturbances, ecophysiology, evergreen, herbivory, *Nothofagus betuloides*, *Nothofagus pumilio*, Patagonia, temperate forests

Introduction

Evergreen species differ from winter deciduous species in that they have functional leaves year-round. A less conspicuous but distinctive physiological trait differentiating the two leaf habits relates to carbon (C) and nitrogen (N) storage in perennial, woody tissues, which is higher in deciduous than in evergreen tree species (e.g. Vanderklein & Reich 1999; Millard *et al.* 2001; Hoch, Richter & Körner 2003; Millard & Grelet 2010; Fajardo, Piper & Hoch 2013; Richardson *et al.* 2013). The ecological and evolutionary reasons for the different C- and N-storage in these leaf habits are not clear. The classical and most accepted explanation affirms that winter deciduous species are highly dependent on C- and N-storage in order to meet spring growth demands (Dickson 1989; Kozlowski 1992; Pallardy 2007). This explanation is largely based on species artificially selected for high fruit or wood yield, which is necessarily linked to important seasonal fluctuations in C- (e.g. Boscagli 1982; Mataa & Tominaga 1998; Mataa, Tominaga & Kozaki 1998; Miller *et al.* 1998) and N-storage (Tromp 1983). In wild winter deciduous species, however, the amount of carbohydrates withdrawn from major

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