HIGH FOLIAR NUTRIENT CONCENTRATIONS AND RESORPTION EFFICIENCY IN *EMBOTHRIUM COCCINEUM* (PROTEACEAE) IN SOUTHERN CHILE[1]

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- *Premise of the study:* Southern South American (SA) Proteaceae species growing in volcanic soils have been proposed as potential ecosystem engineers by tapping phosphorus (P) from soil through their cluster roots and shedding nutrient-rich litter to the soil, making it available for other species. We tested whether *Embothrium coccineum* (Proteaceae) has effectively lower P nutrient resorption efficiency and higher litter P concentrations than co-occurring, non-Proteaceae species.
- *Methods:* In southern Chile, we assessed the P and nitrogen (N) resorption efficiency of senescent leaves and fresh litter of *E. coccineum* and co-occurring tree species in a soil fertility and moisture gradient (600–3000 mm of annual precipitation) in Patagonia, Chile. We determined P and N concentrations, leaf mass per area (LMA), and ratios of N/P and C/N in mature and senescent leaf cohorts and fresh litter.
- *Key results: Embothrium coccineum* showed significantly higher P and N resorption efficiency than co-occurring species; in fact, *E. coccineum* fresh litter had the lowest P-content. While *E. coccineum* showed significantly lower fresh litter P concentrations than the rest of the species, it showed significantly higher N concentrations. *Embothrium coccineum* also had lower LMA and similar N/P and C/N ratios when compared with co-occurring tree species.
- *Conclusions:* We found that *E. coccineum* efficiently mobilized P and, to a lesser extent, N before leaf shedding. We did not find support for the ecosystem engineering hypothesis via shedding P-rich litter. We suggest that southern South American Proteaceae may be taking up other nutrients besides P, probably N, from the young, volcanic soils of this region.

Key words: cluster roots; *Drimys winteri*; facilitation; *Nothofagus betuloides*; nutrient-rich litter; Patagonia; precipitation gradient; Proteaceae; *Raphithamnus spinosus*; *Schinus patagonicus*.

Positive plant–plant interaction, i.e., facilitation, is the process by which some plant species ameliorate stressful conditions that would otherwise impede other species to colonize such environments (Bertness and Callaway, 1994). The amelioration of stressful conditions can result from the creation of novel habitats that lead to an increased number of species within a community (McIntire and Fajardo, 2014). In this particular case, facilitator species have been given several names, such as ecosystem engineers, ecosystem constructors, or foundation species (Jones et al., 1994). Ecosystem engineers can alter the habitat conditions of a given community directly through the action of their own morphological structures (autogenic engineers, e.g., coral reefs, cushion plants, trees) or indirectly through the conversion of inorganic or organic matter to forms more accessible for other plants (allogenic engineers) (Jones et al., 1994).

One plant group that may act as ecosystem engineers in southern South America are the species in the Proteaceae family (Lambers et al., 2012). Species of this family are typically nonmycorrhizal (Brundrett, 2002) and form cluster roots, which are functionally important for plant nutrition by enhancing phosphorus (P) acquisition (Neumann and Martinoia, 2002; Lambers et al., 2006; Delgado et al., 2013). Some evidence has also indicated that Proteaceae cluster roots may facilitate nitrogen (N) acquisition (e.g., Lamont, 1972; Schmidt et al., 2003; Paungfoo-Lonhienne et al., 2009; Piper et al., 2013). In southwestern (SW) Australia and in South Africa—where Proteaceae mostly prevail—soil P availability is low because total P is low, and Proteaceae tend to conserve P through high P remobilization (i.e., resorption efficiency) from senescent leaves (Lambers et al., 2006, 2012; Denton et al., 2007). Consistent with a conservative strategy under low soil P content, foliar P concentrations in Proteaceae are also very low (<0.05%, Read et al., 2005; Denton et al., 2007). The ecological role of cluster roots

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