Do cluster roots of red alder play a role in nutrient acquisition from bedrock?

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Perakis and Pett-Ridge (1) recently reported in PNAS that N₂-fixing red alder (*Alnus rubra*) trees obtain significantly more rock-derived strontium than 5 codominant nonfixing trees in a mixed temperate rainforest in the Oregon Coast Range. The authors ascribe this to the fact that excess fixed N generates acidity, accelerating leaching of rock-derived nutrients. However, what the authors do not point out is that *Alnus* spp. produce cluster roots (2). In fact, actinorhizal species in different families produce cluster roots, and we are unaware of any actinorhizal species that does not produce cluster roots (3).

Cluster roots mobilize poorly available phosphorus and other elements because they release large amounts of carboxylates (3). Functionally equivalent but morphologically very different specialized roots occur in, for example, Cactaceae (4), Cyperaceae (5), and Velloziaceae (6). Carboxylate-releasing cluster roots in *Banksia* spp. (Proteaceae) are capable of mobilizing phosphorus from the surface of limestone and laterite by releasing carboxylates (7). The root hairs of individual rootlets interact very closely with lateritic gravel (Fig. 1). Vellozioid roots of *Barbacenia* spp. (Velloziaceae) grow inside quartzite rock (Fig. 2) and dissolve minerals from these rocks (6).

Perakis and Pett-Ridge (1) claim that excess fixed N generates acidity, accelerating leaching of rock-derived nutrients. They suggest a link between N₂ fixation and mineral weathering. We do not question their finding that N₂-fixing *A. rubra* took up more rock-derived strontium than co-occurring nonfixing trees but remain unconvinced by their explanation. Symbiotic

N₂ fixation is associated with rhizosphere acidification (8). Proton release compensates for an unbalanced cation–anion uptake at the soil–root interface. The question is whether differences in proton release account for differences in strontium accumulation among forest trees. Do actinorhizal plants really enhance the release of nitric acid, as suggested as the mechanism for increased mineral weathering in the rooting zone (1)? Rhizosphere acidification is primarily the result of an imbalance of the uptake of cations and anions associated with symbiotic N₂ fixation, leading to a net release of protons into the rhizosphere (9), balanced by carboxylate accumulation in the plant. Further acidification may occur if N that has been fixed enters the soil as litter or exudates, causing nitrification and accounting for export of nitrate from *A. rubra* stands (10). Therefore, the production of nitrate occurs following entry of organic N in the soil and is not restricted to the immediate environment of the roots of actinorhizal plants that mobilize strontium. Neighboring nonfixing plants would be equally affected; hence, release of nitric acid does not offer a likely mechanism for enhanced weathering. Rather, we should consider the evidence that *A. rubra* produces cluster roots. There is overwhelming evidence that cluster roots and their functional equivalent mobilize sparingly available phosphorus (3) or phosphorus that is locked up in rock (4, 6, 7). We surmise that *A. rubra* trees obtain rock-derived strontium and mineral nutrients by the activity of their cluster roots, rather than their actinorhizal N₂-fixing roots.

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Fig. 1. Cluster roots of *Banksia attenuata* (Proteaceae, slender banksia) intimately interacting with lateritic gravel, from which they mobilize sparingly available phosphorus by releasing carboxylates, mainly citrate, malate, and *trans*-aconitate (7). New cluster roots can be seen growing in the gap of stone particles and on the surface of stones, indicated by green arrows.

Fig. 2. Roots of *Barbacenia tomentosa* (Velloziaceae) growing inside quartzite rocks from the Brazilian campos rupestres. (A) Section showing a cross-section of a root. (B) Section showing a longitudinal section of a root. These roots release carboxylates, mainly malate and citrate, which mobilize mineral nutrients and weather the rock (6). Note the weathered aspect of the rock near the roots and the mobilized material (arrow). Image credits: Image courtesy of D.L.N. and Grazielle S. Teodoro (photographer).

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