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

Hans Lambers[1,2], Diego L. Nascimento[3], Rafael S. Oliveira[1,4], and Jianmin Shi[5]

[1]School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley (Perth), Australia

[2]Key Laboratory of Plant-Soil Interactions, Ministry of Education, Beijing Key Laboratory of Biodiversity and Organic Farming, College of Resources and Environmental Sciences, China Agricultural University, 100193, Beijing, PR China

[3]Geosciences Institute, Universidade Estadual de Campinas, Cidade Universitária Zeferino Vaz, Campinas, Brazil

[4]Department of Plant Biology, Biology Institute, Universidade Estadual de Campinas, Cidade Universitária Zeferino Vaz, Campinas, Brazil

[5]College of Forestry, Jiangxi Agricultural University, 1011 Zhimin Road, Nanchang 330045, China

Commentary on Perakis SS & Pett-Ridge JC (2019) Nitrogen-fixing red alder trees tap rock-derived nutrients. Proc. Natl. Acad. Sci. USA 116(11):5009-5014.

Perakis and Pett-Ridge (1) recently reported that N_2-fixing red alder (*Alnus rubra*) trees obtain significantly more rock-derived strontium than five codominant nonfixing trees in a mixed temperate rainforest in Oregon Coast Range, USA. 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* species produce cluster roots (2). In fact, actinorhizal species in different families produce cluster roots, and we are unaware of any actinorhizal species that do *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* species (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* species (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 N_2 fixation and mineral weathering. We do not question their finding that N_2-fixing *Alnus rubra* took up more rock-derived strontium than co-occurring nonfixing trees, but remain unconvinced by their explanation. Symbiotic N_2 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 N_2 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, when this causes nitrification, accounting for export of nitrate from *Alnus rubra stand*s (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, and hence, release of nitric acid does not offer a likely mechanism for enhanced weathering. Rather, we should consider the evidence that *Alnus 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 *Alnus rubra* trees obtain rock-derived strontium and mineral nutrients by the activity of their cluster roots, rather than their actinorhizal N_2-fixing roots.

References

1. Perakis SS & Pett-Ridge JC (2019) Nitrogen-fixing red alder trees tap rock-derived nutrients. *Proc. Natl. Acad. Sci. USA* 116:5009-5014.
2. Hurd T & Schwintzer C (1996) Formation of cluster roots in *Alnus incana* ssp. *rugosa* and other *Alnus* species *Can J Bot* 74:684-1686.
3. Shane MW & Lambers H (2005) Cluster roots: a curiosity in context. *Plant Soil* 274:101-125.
4. Abrahão A, Lambers H, Sawaya ACHF, Mazzafera P, & Oliveira RS (2014) Convergence of a specialized root trait in plants from nutrient-impoverished soils: phosphorus-acquisition strategy in a nonmycorrhizal cactus. *Oecologia* 176:345-355.
5. Shane MW, Cawthray GR, Cramer MD, Kuo J, & Lambers H (2006) Specialized 'dauciform' roots of Cyperaceae are structurally distinct, but functionally analogous with 'cluster' roots. *Plant Cell Environ.* 29:1989-1999.
6. Teodoro GS*, et al.* (2019) Specialized roots of Velloziaceae weather quartzite rock while mobilizing phosphorus using carboxylates. *Funct Ecol* in press:doi.org/10.1111/1365-2435.13324.
7. Shi J, Strack D, Albornoz F, Han Z, & Lambers H (2019) Differences in investment and functioning of cluster roots account for different distributions between *Banksia attenuata* and *B. sessilis,* with contrasting life history. *Plant Soil* in press:10.1007/s11104-11019-03982-11106.
8. Barton L, Tang C, & McLay CDA (1997) Acidification potential of ten grain legume species grown in nutrient solution. *Aust. J. Agric.* 48:1025-1032.
9. Hinsinger P, Plassard C, Tang C, & Jaillard B (2003) Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: a review. *Plant Soil* 248:43-59.
10. Homann PS, van Miegroet H, Cole DW, & Wolfe GV (1992) Cation distribution, cycling, and removal from mineral soil in Douglas-fir and red alder forests. *Biogeochemistry* 16:121-150.

Figure 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. Photo: Jianmin Shi.

Figure 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). Photos: Diego Nascimento and Grazielle Teodoro.