REPLY TO LAMBERS ET AL.:

How does nitrogen-fixing red alder eat rocks?

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The symbiotic nitrogen (N)-fixing tree red alder (*Alnus rubra*) is an ecologically and economically important species that has been studied for over 50 y (1, 2). Our recent finding that red alder can preferentially access rock-derived nutrients provides additional insight into the ecology of this N-fixing tree. Our manuscript evaluates several explanations for how red alder eats rocks and suggests that the main driver is nitric acid (3). Lambers et al. (4) agree that red alder preferentially accesses rock-derived nutrients, but instead hypothesize that red alder produces cluster roots, which mobilize rock-derived nutrients by releasing carboxylates.

Our analysis builds on widespread observations that excess fixed N stimulates microbial nitrification to produce nitric acid in soil under red alder (1, 2). Nitric acid can explain both rock-nutrient supply to red alder and broader N-related patterns of rock nutrient depletion across the landscape (5). Lambers et al. (4) dismiss nitric acid, arguing it would supply rock-derived nutrients equally to fixers and nonfixing neighbors. This assumption overstates the homogeneity and scale at which trees shape soil properties. Nitrogen-fixing red alder most strongly acidifies soil immediately below its canopy, with the effect disappearing 5 m laterally (6). This is consistent with widespread evidence that trees alter soils and access nutrients primarily below their canopies, where their litterfall and root turnover are concentrated (7).

The mechanism Lambers et al. (4) propose has 2 parts: carboxylates and cluster roots. We acknowledge that organic acid root exudates could mobilize rock-derived nutrients (3). Many of these organic acids occur as carboxylate anions at typical soil pH (8). Our broad consideration of organic acids thus encompasses the chemical role of carboxylates, although

carboxylates may be exuded with or without protons, as Lambers et al. note. The lack of research on these root exudates in *Alnus* may reflect the high frequency of mycorrhizal colonization, which dominates alder root morphology and function in the field (1, 2). Root exudates are also degraded rapidly in soil (8) and thus cannot explain persistent N-related changes in rock-nutrient biogeochemistry across the landscape (5).

Organic exudates may increase access to rock-derived nutrients, but we disagree that cluster roots are important to red alder in nature. Cluster roots have never been reported on field-grown red alder, despite 50 y of belowground research on this species (1, 2). The study Lambers et al. (4) cite as evidence for cluster roots used hydroponics to eliminate phosphorus completely, whereas added phosphorus suppressed cluster roots (9). Soils of our study region contain ample primary mineral phosphorus (5) and available phosphorus (10). This available phosphorus likely explains why cluster roots have never been observed on field-collected red alder.

We agree that the exact location and mechanism of enhanced mineral weathering by symbiotic N-fixing red alder warrants further study, as do the potential ecosystem benefits to neighboring nonfixing trees. Indeed, the degree to which N-fixers access rock-derived nutrients via nitric acid versus non-N-related mechanisms has bearing on the elusive question of how N-fixers coexist with nonfixers in many ecosystems worldwide (11).

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