Geophysical Research Abstracts
Vol. 21, EGU2019-7651-5, 2019
EGU General Assembly 2019


# Biogeochemical pathways in intracellular $CaCO_3$ mineralisation of plant roots from Mediterranean calcareous soils

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Intracellular calcium carbonate biomineralisation in plant roots has been well known for more than 30 years. Although this process is one of the most impressive cases of immense biologically induced mineral formation in terrestrial ecosystems, intracellular Ca carbonate in roots has received less attention than the well-documented Ca oxalate biomineralisation in roots and plant tissues in general.

Extensive accumulations of intracellularly calcified roots reported here were studied in calcareous soils from Mediterranean environments of the Alicante region, SE Spain. The area is dominated by shrubby xerophyte vegetation and is characterized by a seasonal moisture regime. Soils, developed over marl and limestone bedrock, are typically associated with accumulations of secondary soil carbonate. In the studied profiles, aggregates of calcified fine roots may locally represent more than a half of the soil mass.

Calcifying plants have been identified using DNA barcoding. The technique uses a standard short genomic region, universally present in target biological material and has sufficient sequence variation to discriminate among taxa. DNA has been extracted from very small amounts of plant tissue (mostly vascular cylinders) preserved in dehydrated fragments of calcified roots collected in calcareous soils. We used PCR amplification and tested sequencing using nuclear ITS and plastid (rbcL and matK) loci. Sequences have shown the best match with the data for genera *Hedysarum*, *Onobrychis* and *Astragalus*, all members of shrubs of the Leguminosae family.

Accumulation of $CaCO_3$ in the vacuoles of root cortical parenchyma might reflect rhizosphere buffering and protection of the plant from excessive calcium concentrations in the soil solutions. However, exploratory root growth patterns and morphologically transformed calcified roots indicate plant-controlled $CaCO_3$ mineralisation processes which, coupled with extrusion of protons to the rhizosphere, represent an effective nutrient acquisition adaptation to nutrient-poor calcareous soils, such as the present-day soils of the Mediterranean. Importantly, calcification does not correspond to legume nodules (with nitrogen-fixing symbiotic bacteria) but is limited to terminal (higher-order) fine roots, apparently specialised in precipitation of $CaCO_3$ in their cortical cells, indicating a mechanism such as enhanced uptake of Fe and/or P.

In addition to the study of natural occurrences of calcified roots we performed preliminary experimental laboratory growth of *Hedysarum coronarium*, a legume native to the Mediterranean basin, known for its tolerance to various environmental stresses and for intracellular $CaCO_3$ precipitation. *H. coronarium*, typically adapted to carbonate-rich soils, has been shown to produce substantial amounts of intracellular $CaCO_3$ in artificial calcareous substrate, while plants growing in experimental non-carbonate Ca-rich substrates (wollastonite, gypsum-rich and portlandite mixtures) have produced minor amounts of calcified roots, so far suggesting only limited C sequestration potential of root biomineralisation.