Geophysical Research Abstracts
Vol. 18, EGU2016-4106, 2016
EGU General Assembly 2016

Sulfur-accumulating plants convert sulfate salts from soils into environmentally resilient biominerals

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Sulfur-accumulator plants (thiophores), which accumulate atypically high sulfur and calcium concentrations in their aerial biomass, may be suitable for revegetating and phytostabilising reactive sulfur-enriched substrates such as mine tailings, acid-sulfate soils and polluted soils. We present biogeochemical insights on thiophores from the Australian Great Sandy Desert, which accumulate up to 40 times as much sulfur (2-5 %S) versus comparator species. X-ray microanalyses revealed this accumulation relates to peculiar gypsum-like mineralisation throughout their foliage, illustrating a mechanism for sulfate removal from soils and sequestration as sparingly soluble biominerals. However, we did not know whether these species treat the excess Ca/S as a waste to be shed with senescent litter and, if so, how resilient these 'biominerals' are to photo-biodegradation once shed and so to what extent the accumulated elements are recycled back into the reactive/bioavailable sulfate reservoir.

To address these questions, we sampled four foliage (phyllode) fractions from ten individuals of the thiophore, *Acacia bivenosa*: healthy mature phyllodes, senescent phyllodes on the branch, recently shed and older, more degraded ground litter. We selected two thiophores (*A. bivenosa* and *A. robeorum*) and a non-thiophore (*A. ancistrocarpa*) for detailed soil/regolith studies. Samples were collected from trenches bisected by each tree, taken from varying depth (20-500 mm) and distance from the stem (0.1-5 m). Dried foliage was cleaned, sectioned for SEM-EDXS examination and elemental compositions of foliage and soils were determined (microwave-assisted acid digestion + ICP-OES/MS).

Each species generated a 'halo' of elevated S/Ca in the soil immediately beneath their crowns, although that of *A. ancistrocarpa* was of minor magnitude. These anomalies were confined to shallow soil (20-50 mm i.e. influenced by litter), suggesting limited S/Ca re-mobilisation from the litter. Foliar elemental concentration ratios, which indicate relative variations in composition through the litter cycle (healthy > senescent > fresh litter > degraded litter), reveal potentially limiting nutrients were recovered from senescing phyllodes: P (0.38 $\pm$ 0.13), Zn (0.59 $\pm$ 0.24), Mo (0.71 $\pm$ 0.28), Mg (0.86 $\pm$ 0.13). Some non-limiting nutrients or potentially harmful elements were hyper-deposited in senescent tissues: Ba (1.29 $\pm$ 0.22), Ca (1.17 $\pm$ 0.08), Co (1.33 $\pm$ 0.33), Fe (1.49 $\pm$ 0.59) and Mn (1.39 $\pm$ 0.49). Despite this evidence for nutrient recovery and waste removal behaviour (e.g. calcium oxalate production), sulfur remained constant (1.08 $\pm$ 0.12), suggesting thiophores do not regulate sulfur as a limiting nutrient or use biomineralisation to immobilise/detoxify sulfur. Whilst some elements (K, Mg, P) were leached from the litter through photo-biodegradation, sulfur (0.91 $\pm$ 0.12) and calcium (0.99 $\pm$ 0.09) levels remained relatively constant in recent/aged litter, and extensive gypsum-like mineralisation was retained in tissues of even the most degraded litter.

These findings suggest that thiophores, which bioconcentrate sulfur several hundred times from soils into their foliage, return sulfur to the soil as a tissue-encapsulated, sparingly soluble mineral that is recalcitrant to photo-biodegradation under semi-arid climates. These traits show the potential of these plants as part of the toolkit for restoring degraded soils and polluted substrata.