

Organic acid behaviour in a calcareous soil implications for rhizosphere nutrient cycling

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Abstract

Calcareous soils are frequently characterized by the low bioavailability of plant nutrients. Consequently, many vascular plant species are unable to successfully colonize calcareous sites and the floristic composition of calcareous and acid silicate soils has been shown to differ markedly. The root exudation of oxalate and citrate has been suggested to play a pivotal role in same nutrient acquisition mechanisms operating in calcareous soils. The aim of this study was therefore to investigate the nutrient extraction efficiency of three individual organic acids commonly identified in root exudates, i.e. citric, malic and oxalic acid. Our results clearly demonstrate the context dependent nature of nutrient release by organic acids. The degree of P extraction was highly dependent on which organic acid was added, their concentration and pH, and their contact time with the soil. P is generally more efficiently extracted by organic acids at a high pH and follows the series oxalate > citrate > malate. The opposite relationship between pH and extraction efficiency was apparent for most other cations examined (e.g. Zn, Fe), which are more efficiently extracted by organic acids at low pH. A serious constraint to the ecological importance of organic acid exudation in response to P deficiency is, however, their very low P mobilization efficiency. For every mol of soil P mobilized, 1000 mol of organic acid has to be added. It can, however, be speculated that in a calcareous soil with extremely low P concentrations it is still beneficial to the plants to exude organic acids in spite of the seemingly high costs in terms of carbon.

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1. Introduction

Calcareous soils are frequently characterized by the low bioavailability of plant nutrients and by a high base status and pH between 7.5 and 8.5 depending on the quality and quantity of carbonate minerals present (Chen and Barak, 1982; Marschner, 1995). Consequently, many vascular plant species are unable to successfully colonize calcareous sites and the floristic composition of calcareous and acid silicate soils has been shown to differ markedly (Mabey, 1996; Conti et al., 1999; Lee, 1999).

In calcareous soils, P is largely unavailable to plants due to the formation of metal complexes (e.g. Ca–P and Mg–P), rendering P only sparingly soluble. Furthermore, many micronutrients (e.g. Fe, Mn, Cu and Zn) that are freely

available in acid soils are only sparingly available in calcareous soils, due to their poor solubility at high pH (Brady and Weil, 1999). Experiments have shown calcifuge plants (those which cannot establish well on calcareous soils) to be primarily excluded from growth in calcareous soils due to poor P use efficiency, and in a small proportion of species their Fe use efficiency (Tyler, 1992, 1994; Kerley et al., 2001).

In order for plants to establish and grow successfully on calcareous soils requires adaptations to overcome the nutrient deficient conditions prevailing on these soils. A number of mechanisms by which plants can adapt to nutrient deficient soils have been suggested; (1) luxury uptake of nutrients during periods of abundance, storage in roots, and release to shoots in times of deficiency (Gupta and Rorison, 1975; Veresoglou and Fitter, 1984); (2) developmental regulation of plant C partitioning to maintain a high root-to-shoot ratio (Fitter, 1997); (3) colonization of roots by effective mycorrhiza to promote greater soil volume exploitation and enhanced nutrient uptake (Goh et al., 1997); (4) exudation of compounds from the root which promote mineral

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Table 1
Characteristics of the calcareous soil

EC _{1:1} , dS m ⁻¹	1.0
pH (1:1 H ₂ O)	7.58
Carbonates as CaCO ₃ , g kg ⁻¹	204
Moisture, g kg ⁻¹	392
Organic C, g kg ⁻¹	82
Total N, g kg ⁻¹	8.2
C:N ratio	10
Exchangeable cations, mmol _c kg ⁻¹	
Na	2.8
K	4.9
Ca	68
Mg	0.54
Extractable P, mmol kg ⁻¹	0.009

All values are the mean of two determinations.

dissolution, organic matter mineralization, and root uptake of barely soluble nutrient pools from the rhizosphere (Lipton et al., 1987).

Root exudation has been suggested to play a central role in some nutrient acquisition mechanisms operating in calcareous soils (Ström, 1997; Jones, 1998). Calcicole plants (i.e. those that can establish on calcareous soils) generally have enhanced rates of root organic acid exudation, particularly oxalate and citrate, in comparison to calcifuge plants (Ström et al., 1994; Tyler and Ström, 1995; Ström, 1997).

After entering the soil, cations can react with the organic acids to form organo-metallic complexes. If these complexes are soluble they increase the availability of the cation, protect it from precipitation and also provide a direct route for cation uptake (e.g. Fe; Jones, 1998). If, on the other hand, the organic acid-metal complex is insoluble this could decrease the availability of the micronutrient (Brady and Weil, 1999). Once exuded, organic acids may undergo complexation reactions with target metals (e.g. Fe, Mn, Zn and Cu or Ca, which enhances Ca–P mineral dissolution) or non-target metals (e.g. Al, which does not mobilize much P; Cline et al., 1982; Jones and Darrah, 1994). To fully evaluate the importance of the proposed nutrient mobilization mechanism requires a more detailed understanding of the fate of exuded organic acids in calcareous soils.

The aim of this study was therefore to investigate the nutrient extraction efficiency of three individual organic acids commonly identified in root exudates of calcicole plants, i.e. citric, malic and oxalic acid (Ström et al., 1994; Tyler and Ström, 1995; Ström, 1997).

Table 2

Calcareous soil pH after extraction with three organic acid solutions at an initial pH of either 7.5 or <3.5 and at concentrations varying from 1 to 100 mM

Addition (mM)	Oxalate pH=7.5	Oxalate pH<3.5	Malate pH=7.5	Malate pH<3.5	Citrate pH=7.5	Citrate pH<3.5
1.00	7.81±0.02	6.16±0.01	7.83±0.02	5.86±0.11	7.83±0.03	5.81±0.08
10.00	9.02±0.00	6.33±0.08	7.83±0.01	6.12±0.03	8.83±0.02	5.96±0.02
20.00	9.46±0.07	6.60±0.02	7.90±0.01	6.55±0.00	8.63±0.03	6.35±0.05
50.00	9.98±0.01	6.80±0.04	8.10±0.00	6.91±0.21	8.92±0.06	6.70±0.05
100.00	10.23±0.02	7.16±0.21	8.19±0.03	6.99±0.29	9.02±0.01	7.14±0.06

The initial soil pH was 7.58. Values represent mean±SEM.

2. Materials and methods

2.1. Soil

The soil represents a calcareous Typic Rendoll (Rendzic leptosol), derived from Ordovician limestone and is located on the 'alvar' of Öland in Sweden (56° 40'N, 16° 30'E). The site has a mean annual rainfall of 388 mm, mean annual temperature of 7.1 °C, slope of 2.4°, elevation of 30 m and is dominated by calcicole vegetation (e.g. *Artemisia campestris*, *Melica ciliata*, *Sedum album* etc.).

The soil was collected from the Ah horizon (0–10 cm) using a spade, sieved to pass 6 mm and kept field moist at 10 °C until required. Properties of the soil are provided in Table 1.

2.2. Extraction efficiency of organic acids

To determine the concentration-dependent extraction efficiency of the organic acids on P, Fe and Ca and several other cations from the calcareous soil, 12.5 ml of organic acid solution was added to 5.0 g of field moist soil contained in 25 ml polypropylene tubes. Three individual organic acids, citric, malic and oxalic acid were added to soil at concentrations ranging from 1 to 100 mM to determine the soil extraction efficiency (% release as mol ion per mol organic acid added) of P, Fe and Ca. In addition, a single concentration of 10 mM was used to determine the efficiency of the acids in extracting P and cations. The samples were orbitally shaken for 30 min, centrifuged (16 000g, 10 min) and the supernatant examined for pH, P and cations (Fe, Mn, Mg, Ca, Na, K, Cu and Zn; Jobin Yvon Ultracé ICP-OES, Jobin Yvon SA, Longjumeau, France).

To determine the pH effect on the organic acid extraction efficiency the experiments described above was performed both at an initial organic acid pH of 7.5 (adjusted by KOH) and without pH adjustment, resulting in an initial pH of the extractant solutions of between 2.5 and 3.5 (hereafter denoted as pH<3.5).

To determine the time-dependence of organic acid mediated P, Fe and Ca extraction, experiments were performed as described above except that a single concentration of organic acids was employed (10 mM) at high (7.5) pH and shaking times varied between 2 min and 24 h.

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