



Sulfur accumulation in gypsum-forming thiophores has its roots firmly in calcium



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ABSTRACT

Recent studies suggest sulfur-accumulators (thiophores and gypsophiles) produce foliar gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) as a novel biomineralogical tolerance mechanism against sulfate salinity and excess soluble calcium (e.g. gypsic soil). However, little is known of the geochemical and ecophysiological aspects of foliar gypsum. The compositional, developmental (biomass, root development) and functional responses (photosystem performance and water relations), to soils with contrasting relative SO_4^{2-} and Ca^{2+} pore-water concentrations (incl. a gypsum treatment), were examined in two gypsum-forming desert thiophores (*Acacia bivenosa* L. and *A. ligulata* A.Cunn. ex Benth.) and a sympatric non-thiophore comparator (*A. ancistrocarpa* Maiden & Blakely). Sulfur and calcium were accreted broadly as a function of the relative abundance of Ca^{2+} and SO_4^{2-} ions in soil solution, and interspecific responses revealed thiophores are preferentially Ca accumulators, tending to maximise Ca uptake for the given conditions and scaling sulfate accumulation in relation to Ca, a co-regulation behaviour absent in the comparator. The thiophores were also sensitive to sulfur limitation, and these observations are consistent with cytosolic Ca^{2+} and SO_4^{2-} regulation through gypsum precipitation. However, the gypsum-forming species were not comparatively tolerant to the gypsum treatment, most likely due to a lack of tolerance to limited P bioavailability resulting from the formation of sparingly-soluble calcium-phosphate soil minerals. The outcomes indicate that the capacity for gypsum biomineralisation does not, by itself, confer tolerance to the full suite of geochemical stress factors presented by gypsic soils (e.g. constrained P bioavailability). The findings steer future research towards testing alternative hypothesis pertaining to the ecophysiological basis of gypsum formation (e.g. osmoregulation) as well as examining whether obligate gypsophiles, which are also challenged by constrained P bioavailability, benefit by forming gypsum biominerals.

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1. Introduction

Sulfur-accumulating plants, also known as thiophores (Duvigneaud and De Smet, 1968), are capable of accumulating excessive (order of magnitude) sulfur (S) concentrations in their foliage and are frequently also calcium (Ca) accumulators (Moore et al., 2014). These accumulators are often gypsophiles (grow exclusively in gypsic soil) or gypsovags (tolerant to gypsic soil)

occupying semi-arid or desert habitats (Al-Ani et al., 1971; Boukhris and Lossaint, 1970; Duvigneaud and De Smet, 1968; Ruiz et al., 2003), although a group of recently identified thiophores (*Acacia* subg. *Phyllodinae*) also inhabit coastal and riparian habitats where gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) is less common (He et al., 2012; Reid et al., 2016).

Plants growing in soils with high pore-water concentrations of Ca (e.g. calcareous soils), sulfate (e.g. acid-sulfate soils) or both (e.g. gypsic soils) are vulnerable to accumulating toxic cytosolic Ca^{2+} and SO_4^{2-} levels (Curtin et al., 1993; Hawkesford, 2007; Ruiz et al., 2003; White, 2003) and must employ regulatory mechanisms at the cellular level to tolerate these conditions. For example, free cytosolic Ca^{2+} ($\text{Ca}_{\text{[cyt]}}$) concentrations must be tightly controlled to prevent Ca phosphate precipitation, interference with enzymatic function and to support the messaging and regulatory roles played

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by Ca (Hawkesford et al., 2012; Lecourieux et al., 2006; McAinsh and Pittman, 2009; White, 2003). Many species regulate $\text{Ca}_{[\text{cyt}]}$ by co-precipitating Ca with oxalate ($\text{C}_2\text{O}_4^{2-}$) to form sparingly-soluble Ca oxalate biominerals (Fink, 1991; Franceschi and Nakata, 2005), including thiophores and gypsosvags (Borer et al., 2012; He et al., 2012; Reid et al., 2016). When considering high foliar S levels, amounts in excess of requirements for organic compound synthesis are usually present as sulfate (Boukhris and Lossaint, 1970; Thomas et al., 1959) and some of the mechanisms previously proposed for protection against toxic $\text{SO}_4^{2-}_{[\text{cyt}]}$ include vacuolar compartmentalisation (Hawkesford, 2007), enhanced protein assimilation (Ruiz et al., 2003) and salt gland excretion (Storey, 1994). More recent studies reported a novel gypsum biomineralisation in the foliage of thiophores, which may be involved in both Ca and sulfate regulation (He et al., 2012; Palacio et al., 2014; Reid et al., 2016) and Palacio et al. (2014) evidenced foliar gypsum in numerous widely-distributed Mediterranean gypsophiles conforming to the so-called 'element accumulator' edaphic ecotype (Moore et al., 2014). This indication that foliar gypsum may be relatively common in gypsophiles is supported by an analysis of 44 species from gypsic soils (Moore et al., 2014), which shows non-dominant species accumulate 0.4% S and 2.5% Ca, compared with 3.0% S and 4.7% Ca in the dominant gypsophiles. This suggests that the 'accumulator' (thiophore) trait constitutes an ecophysiological strategy for success in gypsic soils and those of similarly challenging geochemical characteristics.

To date, most investigations of relationships between plant traits and adaptation to soils containing gypsum soil have focused on the gypsic soils' adverse physical characteristics, e.g. ability of seedlings to penetrate surface crusts (Romão and Escudero, 2005) and of root development in low-porosity soils (Poch et al., 1998; Poch and Verplancke, 2008) when the gypsum content is substantial (>25%). Little is known about the geochemical factors that influence gypsum mineralisation in thiophores, and how this mineralisation affects the plants nutritionally and ecophysiological. Improved knowledge of foliar gypsum mineralisation will not only enhance our understanding of how plants adapt to and tolerate environments with high sulfate salinity and how these species could be used for ecological restoration of S-enriched substrates, e.g. acid-sulfate soils and mine tailings (Ernst, 1998), but may also provide some insight to the possible links between mineral nutrition and gypsophile ecology.

In this study, we set out to test the following hypotheses: 1) gypsum-forming thiophores co-regulate S and Ca uptake and foliar accretion to facilitate foliar gypsum precipitation; 2) consequently, they express increased tolerance to the geochemical stress factors imposed by soil gypsum vs. non-thiophores; and 3) gypsum mineralisation necessitates atypical sulfur demand to support adequate growth and function. We cultivated two gypsum-forming thiophores (*Acacia bivenosa* L. and *A. ligulata* A.Cunn. ex Benth.) and

a sympatric non-thiophore comparator (*A. ancistrocarpa* Maiden & Blakely (Fabaceae)), as part of two controlled experiments designed to elucidate linkages between contrasting SO_4^{2-} and Ca^{2+} availability and foliar composition, plant development, function and also stress responses to soil containing gypsum. To the authors' knowledge, this is the first study to systematically examine links between soil geochemistry and plant gypsum biomineralisation, and to evaluate the influence of the gypsum-forming phenotype upon tolerance to soils high in soluble sulfate and Ca.

2. Methods and materials

This study consisted of two glasshouse experiments (December 2014–July 2015), in which two thiophores (*A. bivenosa* and *A. ligulata*) and a non-thiophore comparator (*A. ancistrocarpa*) were grown (5 replicates) in eight soil treatments devised to understand interspecific (i.e. thiophore vs. non-thiophore) variations in response to a wide range of Ca and sulfate concentrations in soil pore-water. To minimise unwanted treatment effects, all treatments were prepared from the same base soil (described subsequently). Natural lime and gypsum sands (Aglime, Western Australia) were rotary-mixed with the base soil to produce calcareous (5% mass lime sand) and gypsum (3% mass gypsum) treatment mixtures. The added proportions of gypsum and lime sands were minimised to produce soil pore-water geochemical conditions characteristic of naturally occurring calcareous and gypsic soils, whilst minimising the influence of physical effects (e.g. crusting and consolidation), which were not the focus of this study. The two soil mixtures, together with nutrient-amended base soil, comprised eight treatments described in Table 1.

2.1. Soil and mineral amendments characterisation

Particle size distribution (sand, silt, clay) was determined using standard gravimetric methods (Gee and Bauder, 1986), carbonate was determined by titration, and eCEC was determined from exchangeable cations (1 M NH_4Cl) (Rayment and Lyons, 2011, p. 294). Elemental composition was determined using either Leco-type analyses (organic carbon (C) and N) or microwave-assisted acid (3:2 HNO_3 :HCl vol) digestion (170°C, 40 min, 1.8 MPa, MW3000, Anton Paar GmbH), followed by elemental analysis (Al, B, Ca, Co, Cu, Fe, K, Mg, Mn, Mo, Na, P, S & Zn) using Inductively Coupled Plasma Optical Emission Spectrometry (Optima 7300DV ICP-OES, Perkin Elmer Inc). Values obtained for certified reference materials (NCS ZC73003) fell within a satisfactory range ($\geq 90\%$) for the digestion method.

The base growth media was a fine sand (USDA) with relatively low values for cation exchange capacity (1.6 meq 100 g^{-1}), soluble ion content (electrical conductivity = $23 \pm 3\ \mu\text{S cm}^{-1}$), organic

Table 1

Summary of soil treatments used for plant growth media and associated soil pore-water geochemical parameters, including sulfate and Ca concentrations, their relative concentration ratio ($\sim\text{SO}_4^{2-}:\text{Ca}^{2+}$), pH and EC ($\pm\text{SD}$).

Treatment	SO_4^{2-} (μM)	Ca^{2+} (μM)	$\sim\text{SO}_4^{2-}:\text{Ca}^{2+}$	pH	EC ($\mu\text{S cm}^{-1}$)
Calcareous:Low sulfate	120 \pm 38 (max) 19 \pm 4 (min)	2300 \pm 500	0.009–0.05 (0.03)	8.02 \pm 0.06	Up to 500
Calcareous:Moderate sulfate	500	2300 \pm 500	0.2		
Calcareous:High sulfate	2500	2300 \pm 500	1		
Gypsum	20000 \pm 500	14900 \pm 700	1.3	6.70 \pm 0.06	2900 \pm 260
Sulfate-enriched:Low Ca	5000	20 \pm 9	250	7.52 \pm 0.29 (6.6 at beginning of experiment).	120 \pm 70
Sulfate-enriched:Moderate Ca	5000	800	6		
Sulfate-enriched:High Ca	5000	1600	3		
Control:no Ca or SO_4^{2-} addition	50 \pm 34 (max) 16 \pm 1 (min)	20–50	0.3–2.5		

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