Decay-induced biomineralization of the saguaro cactus (*Carnegiea gigantea*)

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**ABSTRACT**

The saguaro, *Carnegiea gigantea* (Englemann), is a columnar cactus that grows to 15 m tall and weighs up to several tons, of which 85 to 90% of the mass is water. Roughly 18% of the dry mass consists of the biomineral weddellite (CaC₂O₄·2H₂O). The C in the weddellite derives from atmospheric CO₂ via photosynthesis. A mature saguaro can contain on the order of 1 × 10⁵ g of weddellite. The weddellite crystals occur as aggregates up to 1 mm wide. After the death of the saguaro, a series of minerals crystallize in the rotting flesh. These minerals form from elements released from the decay of the cactus by microorganisms and thus is a type of biologically induced mineralization. During the initial stages of decay, authigenic Mg- and Ca-bearing minerals crystallize from elements released by the putrefying flesh and include lansfordite (MgCO₃·5H₂O), nesquehonite (MgCO₃·3H₂O), several polymorphs of MgC₂O₄·2H₂O including glushinskite, monohydrocalcite (CaCO₃·H₂O), calcite, vaterite, and several unidentified Mg-bearing phases. As the saguaro decays, the soft, water-rich pith shrinks, but the ribs and skin remain intact, producing warm, moist pockets within the dead saguaro. Abundant, glassy lansfordite crystals to 1 mm in diameter grow in these pockets during the cooler winter months. Further decay leaves a dried hollow shell covered by the saguaro skin, inside of which nesquehonite and monohydrocalcite crystallize. Lansfordite and nesquehonite are unstable in the desert and rapidly amorphize after exposure to the atmosphere. Magnesium oxalates are locally abundant in the decayed flesh and occur as crystals up to 1.5 mm in length. The common occurrence of fungal hyphae on the glushinskite suggests that it forms as a result of the reaction between oxalic acid released by fungi and the Mg-rich solutions of the rotting saguaro. During the final stages of decay, the pith consists of a pale-brown to tan-colored sand of weddellite and its transformation product monohydrocalcite. This sand lithifies to porous sponge-like masses during the final stages of saguaro decay. This monohydrocalcite further alters to calcite. The δ¹³CVPDB of the monohydrocalcite and calcite after weddellite range from –1.65 to +0.76‰. The calcite is subsequently solubilized and remobilized, precipitating as calcite in the desert soil, or redistributed by wind. In arid environments, the desert fauna metabolize the atmospheric C bound in the organic matter to CO₂. In contrast, decay of the saguaro adds atmospheric C to the soil as inorganic C via the transformation of the biomineral weddellite to calcite. In areas with high saguaro density, it is estimated that up to 2.4 g/m²/yr of calcite can be added to the desert from the decayed cacti. This inorganic C has geologically long soil residence times, thus effectively sequestering the atmospheric C.

**INTRODUCTION**

Decay affords an environment for authigenic minerals to crystallize. Under favorable conditions, these minerals, such as Ca phosphates and carbonates, can form in a matter of days or weeks and preserve labile tissues such as muscles (Briggs and Kear 1993; Sagemann et al. 1999). Microbial activity is both the driving force behind the decay and concomitant mineralization of soft tissues, and hence is a form of biologically induced mineralization (Lowenstam 1981).

Plant decay under aerobic conditions is a transformation process, with the aid of soil flora and fauna, into the compounds from which the plant was originally composed, predominantly CO₂ and water. In addition to C, H, and O, plants also contain significant quantities of essential macro-elements, such as Ca, Mg, K, and P (Ramirez et al. 2001). After death, these elements do not normally accumulate and crystallize within the decaying plants, although under certain circumstances, these elements can be concentrated. For example, fungi actively concentrate Ca, Mg, and Fe in decaying wood and frequently produce insoluble Ca oxalates (Jellison et al. 1997 and references therein). In arid environments there is a lack of significant organic matter accumulation in soils, which reflects the efficiency of the combined abiotic and biotic decomposition processes (Whitford 1996; Murphy et al. 1998; Núñez et al. 2001).

The most common biominerals in plants are the oxalates weddellite (CaC₂O₄·2H₂O) and whewellite (CaC₂O₄·H₂O) (Franceschi and Horner 1980; Horner and Wagner 1995; Prychid and Rudall 1999). Their presence has been attributed to one or more of the following: detoxification, protection, structural strength, Ca storage, and light gathering and reflection (Horner and Wagner 1995; Volk et al. 2002). The C source for the oxalate in the Ca oxalates is atmospheric CO₂ (Kostman et al. 2001; Franceschi pers com). Calcium oxalates also occur in surficial, diagenetic, and hydrothermal deposits (Russ et al. 1996; Hofmann and Bernasconi 1998), and in meteorites (Fuchs et al. 1973). In addition, Ca oxalate is widely recognized be-