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Ectomycorrhizae in a soil-weathered granitic bedrock regolith: Linking matrix resources to plants

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Abstract

The spatial distribution of mycorrhizae and hyphae in a regolith of thin soils overlying deeply weathered granitic bedrock was investigated at Santa Margarita Ecological Reserve in southern California. The regolith supports mature *Quercus agrifolia* trees and consists of thin soils (24–100 cm) overlying four varieties of granitic parent materials, and a fault gouge. Evergreen plants with deep, extensive root systems are favored during inherent seasonal droughts of Mediterranean climate. However, sub-soil roots are confined to the fractures and are physically restricted from the matrix micropores of the weathered granitic bedrock where the bulk of the regolith plant available water exists. Ectomycorrhizal (EM) root tips were found throughout the regolith to depths of ~4 m. Some EM infection frequencies of fracture-confined roots (range 1–63%) were similar to those found in the upper 30 cm of soil (range 33–94%). Hyphae were recovered from all depths and material types: soil (averaged 75.0–127.8 m cm^{-3}), fracture (2.5–30.2 m cm^{-3}), and matrix material (1.2–10.0 m cm^{-3}). Hyphae in the form of rhizomorphs were also recovered from deep, matrix materials. Total N was extremely low in the fractures and negligible in the matrix materials; therefore we postulate that N deficits are not driving the formation of ectomycorrhizal infection within the bedrock. Hyphae have been shown to act as water conduits and can transport matrix water, otherwise unavailable to plants, from micropores to fracture-confined, mycorrhizal roots. The formation of mycorrhizae in weathered bedrock fractures, and hyphal extension into the matrix, may be crucial to the water balance of evergreen trees in Mediterranean climates by providing a link between matrix resources and the plant.

Keywords: *Quercus agrifolia* (coast live oak); Ectomycorrhizae; Hyphae; Deep regolith; Weathered granitic bedrock; Mediterranean climate

1. Introduction

The ability to access deep water reserves is an important factor governing the establishment and growth of native, perennial plant communities in Mediterranean climatic regimes. In California, this is the case with *Quercus agrifolia* (coast live oak).

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Because *Q. agrifolia* is evergreen, it has a water demand throughout the entire year and must have adaptive mechanisms that allow survival through seasonal droughts. Distribution of *Q. agrifolia* is governed in part by physical environmental factors that buffer against the low annual rainfall, seasonal droughts, and high evaporative demands inherent in the habitat range. Coast live oaks commonly occur on north-facing slopes, in drainages, in alluvium where deep roots can access stored water, and within rugged terrain where rock cover can concentrate runoff (Pavlik et al., 1991; Sawyer and Keeler-Wolfe, 1995; Zedler et al., 1997). In southern California, where 20% of the state's coast live oak woodlands occur, granitic bedrock underlies most of the *Q. agrifolia* habitat range (Fig. 1). This granitic bedrock is commonly weathered to depths of several meters, while overlying soils are relatively thin (Graham et al., 1994; Sternberg et al., 1996).

In the semi-arid region of southern California, the mean annual precipitation ranges from 355 to 457 mm, and over 90% of the rainfall occurs from October through April (NOAA, 1996). However, the actual amount of precipitation can vary considerably year to year, from 97 to 720 mm. In years of high precipitation, water reserves are recharged within the porous, deeply weathered granitic bedrock (Sternberg et al., 1996). In years of low precipitation, evergreen tree species, such as *Q. agrifolia*, must have the ability to access these water reserves in the weathered bedrock. Even in normal years, plant available water is commonly depleted from the upper meter of the regolith by mid-growing season, and access to deeper reserves may be essential.

It is common for root systems of woody plants to extend from shallow soils into bedrock substrates (Hellmers et al., 1955; Arkley, 1981; Zwieniecki and Newton, 1994; Canadell and Zedler, 1995; Wang et al., 1995; Sternberg et al., 1996). These rock substrates can provide essential resources, such as water and nutrients, and it has been demonstrated that plants actually exploit these resources (Wang et al., 1995; Sternberg et al., 1996; Hubbert et al., 2001b; Rose et al., 2003). However, in weathered granitic rock the structural fabric of the matrix material remains relatively unaltered and, due to physical restrictions, root extension remains confined to the fracture spaces. Therefore, roots are unable to directly access matrix resources, such as water, much beyond the fractures. The water-holding capacity of weathered granitic rock approaches that of overlying soils (Jones and Graham, 1993; Hubbert et al., 2001a). Most of the water is held within micropores of the weathered matrix. It is still not clear, however, how water held within the matrix reaches fracture-confined roots. Hubbert et al. (2001b) report that, during the dry season, plant-available water was completely depleted from the matrix material at distances greater than 25 cm from the fractures. Unsaturated flow for this coarse-material was estimated to be on the order of

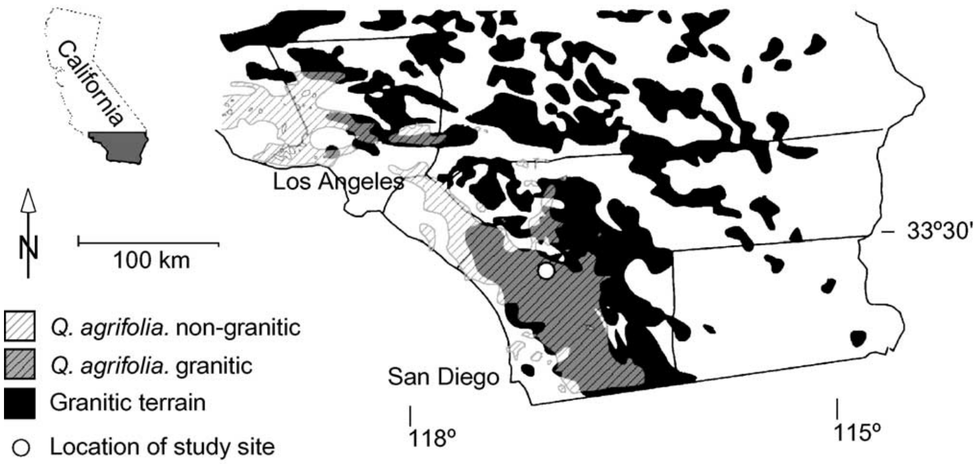

Fig. 1. Map of southern California showing *Q. agrifolia* habitat range, distribution of granitic terrain, and the study site location northeast of San Diego. *Q. agrifolia* distribution modified from Griffin and Critchfield (1972), granitic terrain map from Frazier (1997).