Topsoil depth substantially influences the responses to drought of the foliar metabolomes of Mediterranean forests

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1. Introduction

Soil provides a physical support system and a reservoir of water for terrestrial primary producers (Monteith, 1981). A scarcity of soil resources, particularly water, is often associated with restricted development of plant-soil systems and reduced biomass (Huxman et al., 2004; Knapp and Smith, 2001; Orwig and Abrams, 1997). Soil biological activity and tree growth can be limited by several factors such as nutrients (Bowman et al., 1993; Sardans and Peñuelas, 2015; Sardans et al., 2012a, b), light (Poorter, 1999), temperature (Epstein et al., 1997), or water (Huxman et al., 2004; Rosenzweig, 1968; Sala et al., 1988). Topographic factors such as slope variation and/or soil texture also play important roles in the retention and storage of soil water (Farahani et al., 1998; Fernandez-Illanes et al., 2001) and can influence soil enzymatic activity (Bastida et al., 2008) and erosion (Kinnell and Cummings, 1993). Soil depth is tightly linked with the physiology and respiration rates of tree roots (Pregitzer et al., 1998), the composition of microbial communities (Fierer et al., 2003), and even plant biodiversity (Fuhlendorf and Smeins, 1998). Most of the biological activity and nutrient recycling in soil occurs in the upper topsoil layers, so water availability in these layers is crucial to forests (Jobbagy and Jackson, 2000; Wardle et al., 2004). Hydraulic lift, mainly the transport of water from deep to shallower soil layers through roots to maintain physiological activity (Canadell et al., 1996; Nepstad et al., 1994; Schulze

http://dx.doi.org/10.1016/j.ppees.2016.06.001
1433-8319/Published by Elsevier GmbH.
The metabolome, the chemical phenotype of an organism, is the total set of low molecular weight metabolites (typically <1200 Da) present in an organism at a particular moment (Fiehn, 2002). The metabolome, includes thus amino acids, sugars, and nucleotides from primary plant metabolism and many secondary metabolites such as phenolics and terpenes representing the diverse physiological processes in an organism for maintaining internal homeostasis and function. The first functional responses of an organism facing abiotic and biotic stresses are typically at the metabolomic level (Peñuelas and Sardans, 2009). Metabolomics represents thus a powerful tool for ecological studies (ecometabolomics) to identify the main changes in organisms directly associated with metabolism and performance (Sardans et al., 2011). Metabolomics allows us to understand the metabolic variation of organisms under stressful environmental conditions, including the complete set of metabolites and not just single compounds or families of metabolites (Fiehn, 2002; Bundy et al., 2008; Sardans et al., 2011). The study of the metabolomic changes of wild plant species helps to comprehend the mechanisms behind plant physiological responses to natural or experimental stressors. Metabolomic techniques can also assess the plasticity of specific metabolomes and detect and quantify the metabolic biomarkers linked with specific environmental stressors (Bundy et al., 2008; Sardans et al., 2011; Rivas-Ubach et al., 2016a). Ecometabolomics has advanced our understanding of the natural variability and flexibility of the metabolomes of wild organisms under climatic stressors (Gargallo-Garriga et al., 2014; Rivas-Ubach et al., 2014), amongst seasons (Rivas-Ubach et al., 2012), and under attack from folivorous insects (Rivas-Ubach et al., 2016b). Ecometabolomics is thus valuable for exploring the organism-environment interaction by detecting and quantifying the final phenotypic response of an organism to environmental changes.

The physiological response to drought of Quercus ilex L., an evergreen sclerophyllous tree species widely distributed in the Mediterranean Basin (Barbero et al., 1992), has been extensively studied (Filella et al., 1998; Nardini et al., 2000; Ogaya and Peñuelas, 2003; Peñuelas et al., 2000; Sala and Tenhunen, 1996). Q. ilex is a keystone species in many Mediterranean ecosystems and is currently expanding its dominance by recolonising abandoned cropland and pastures and by out-competing Mediterranean conifers that are more sensitive to rising temperatures (Carnicer et al., 2013). Drought-induced declines in Q. ilex forests have been reported (Galiano et al., 2012; Camarero et al., 2015), but this tree possesses an array of functional and morphological traits (such as an extensive root system) for surviving periods of drought. Ecometabolomic studies of Q. ilex could thus identify the key metabolites involved in drought tolerance and resistance as well as measure how flexible are the individual metabolomes under stress conditions. We sampled once per season the leaves of differently sized mature Q. ilex trees of the same age from a forest exposed to a moderate experimental drought and analysed the elemental stoichiometries and metabolomes. We discuss three important issues of Q. ilex metabolic responses to environmental variables or factors by multivariate approximations: (i) we hypothesise that the depth of the upper soil layers (DUSL, typically the A + B horizons), where most of the biological activity and water uptake occur, may determine vegetation structure (VS) and overall metabolomic composition; (ii) we evaluate how different VSs, with special attention to trees growing in shallower soils, respond to the marked seasonality of the Mediterranean Basin and to experimental drought stress; and (iii) we apply the results of this study to illustrate the crucial necessity in ecometabolomic studies of controlling the factors potentially able to produce large metabolomic shifts in plants.
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