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Beneath the canopy: Linking drought-induced forest die off and changes in soil properties

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ABSTRACT

Climate warming and the occurrence of more severe dry spells are causing widespread drought-induced forest die-off events. Despite research on drought-triggered die-off processes is rapidly increasing, little is known on how soil conditions and rhizosphere features are affected by canopy dieback and tree death. We studied the soils in the rhizosphere of three coniferous forests where die-off was induced by a severe drought in 2012. We selected three forest types subjected to contrasting climatic and edaphic conditions dominated by three different tree species: silver fir (*Abies alba*; temperate conditions), Scots pine (*Pinus sylvestris*; continental and Mediterranean conditions) and Aleppo pine (*Pinus halepensis*; semi-arid and Mediterranean conditions). In each forest, we analyzed soil physical characteristics such as water retention capacity and soil texture, nutrient availability and microbial community structure (Phospholipid fatty acids, PLFA) below non-declining and declining or dying trees. We did not observe differences in nutrient availability between the two vigor classes. Conversely, we found strong differences in soil microbial community structure below non-declining and declining trees in the Silver fir and Aleppo pine stands. Soils in the Scots pine stand presented extremely low values of soil saturated sorptivity indicating a reduction of soil water infiltration after prolonged dry periods which could exacerbate drought stress. We conclude that forest dieback impacts the soil microbial community structure in the short term. Further research is required to understand the linkages between a reduced capacity of soil water infiltration after prolonged droughts, short-term changes in the soil microbiota, long-term nutrient imbalances and tree death. Soil conditions shall be considered as an important part of forest management strategies after drought-induced die off.

1. Introduction

The reports of forest die-off events triggered by dry spells have increased considerably during the last decades (Allen et al., 2010). Such rising trend is of major concern for many forests worldwide if global warming amplifies drought stress (Anderegg et al., 2013; Allen et al., 2015; Camarero et al., 2015). The consequences of drought-induced forest die-off can be complex, acting at several temporal and spatial scales (Ruthrof et al., 2016), namely from the simple replacement of some trees to large compositional changes at the community level or even shifts in productivity at the ecosystem level due to the increase of soil surface temperature and decline in evapotranspiration (Royer et al., 2011; Anderegg et al., 2012). While catastrophic and widespread die-off events that cause the death of most trees have more drastic effects on forests, gradual die-off processes affecting some individuals, while other neighbouring trees survive, have less obvious consequences on tree-soil interactions. How soils will respond to the forecasted increase in drought and related forest die-off disturbances is a pivotal question in current global-change ecology (Curiel Yuste et al., 2011; Brunner et al., 2015; Phillips et al., 2016; Baldrian 2017).

Many ecosystem goods and services provided by forests depend on ecosystem processes such as carbon (C) and nitrogen (N) cycling which are part of forest belowground processes (van Der Heijden et al., 2008; Curiel Yuste et al., 2011; Baldrian 2017). For example, the C stock in forest soils exceeds by far that in aboveground vegetation (Jobbágy and Jackson, 2000), and it is estimated that 40–70% of the C

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photosynthetically assimilated by forests is transferred to the rhizosphere (Hopkins et al., 2013). Along these lines, the C balance between aboveground vegetation and soil microbial respiration is controlled by N supply which controls C uptake by plants (Thomas et al., 2015; Wurzburger and Brookshire, 2017). Thus, nutrient cycles largely depend on the interaction between physicochemical soil properties, tree species identity and microbial communities.

The occurrence of abrupt disturbances such as forest die-off events caused by drought or pest outbreaks can have important influences on soil microbial communities and belowground nutrient cycling (Stursova et al., 2014; Pold et al., 2015). Pathogens causing forest die off (e.g. *Phytophthora* and *Heterobasidion* species) develop a substantial part of their life-cycles in the soil (Brasier et al., 1993; Oliva and Colinas, 2007). In addition, soil physical and chemical properties such as low water-holding capacity largely affected by soil hydrophobicity (water repellence), and nutrient deficiency can exacerbate the negative consequences of drought stress on tree vigour leading to forest die-off (Doerr et al., 2000; Pinto and Peñuelas, 2007; Hallett et al., 2011). However, these changes in soil conditions can arise because of forest die-off since tree species can modify soil organic matter content and water retention capacity (Lebron et al., 2007).

The influence of drought-related die-off on forest soil conditions may have different pathways. If phloem transport within declining trees is weakened, the composition of soil nutrients below the tree may change since C and N organic concentrations in the soil decrease (Dannenmann et al., 2009) while inorganic N concentration increases (Kreuzwieser and Gessler, 2010). This has been shown by girdling experiments causing tree death and altering the quantity and quality of C and N compounds reaching the rhizosphere (Stursova et al., 2014; Pold et al., 2015). In dry regions, drought can also reduce phosphorous (P) and potassium (K) uptake by trees increasing their concentration in the soil (Sardans and Peñuelas, 2007). If rhizodeposition, i.e. root exudates (organic compounds released into the soil by plant roots), is depressed then there may be a decrease of microbial biomass or activity in the rhizosphere (Dannenmann et al., 2009) or changes in the diversity of the soil microbiota (Schulze et al., 2005).

The processes involving the interaction between trees and soil microbes are very dynamic in space and time (Bahram et al., 2015; Baldrian, 2017). For example, soil microbes are able to utilize root exudates in minutes or few hours, but they will need several years to decompose dead wood (Baldrian, 2017). The decline and death of a tree reduces or stops the supply of carbohydrates from the roots to the soil via root exudation (Brunner et al., 2015). However, the subsequent fall of dead needles and branches could feed soil microorganisms with different carbon sources through decomposition (Kana et al., 2012; Mikkelson et al., 2016). Nevertheless, the use of this readily available organic matter by microorganisms depends on the composition and activity of microbial communities as well as on environmental conditions (Pisani et al., 2014; Kuzyakov and Blagodatskaya, 2015). Thus, it is expected that drought-triggered forest die-off is anticipated to induce changes in soil microbial structure (Curiel Yuste et al., 2012; Stursova et al., 2014; Lloret et al., 2015). Nonetheless, it is unclear if these post-drought changes in the soil microbiota are similar among forests showing die-off but presenting different soil types and subjected to contrasting climate conditions.

Drought could also alter physical and chemical soil features (structure, water holding capacity, pH, hydrophobicity, nutrient availability) and decrease the enzymatic activity of the soil microbiota (Dannenmann et al., 2009; Curiel Yuste et al., 2011; Baldrian et al., 2013), leading to a negative feedback on tree nutrition by reducing nutrient mineralisation by bacteria (Kreuzwieser and Gessler, 2010). For instance, in *Eucalyptus* forest showing die-off this was associated with changes in the soil bacterial functional diversity linked to a decrease in the utilization of carbohydrates, amino acids and amines by the soil bacterial communities in sites with declining tree health (Cai et al., 2010). Furthermore, forest die-off usually leads to a reduction in canopy cover, which could increase the radiation reaching the ground and enhance evaporation further exacerbating soil dryness and contributing to more extreme microclimatic conditions in the uppermost soil, where most fine roots are found, thus reducing the rhizosphere microbiota activity (Sardans et al., 2008).

Tree species composition has important influences on forest soil physical and chemical characteristics (Augusto et al., 2015). As a consequence, there can be a large variation in soil microbial community composition between different forest types (Baldrian, 2017). Drought may impact forest soil differently depending on the forest type studied and its prevailing climatic conditions (Aponte et al., 2013). For example, while climate warming may enhance soil enzyme activity in temperate hardwood forests of central Europe (Baldrian et al., 2013), it might have contrasting influences on drought-prone Mediterranean forests (Sardans and Peñuelas, 2007; Sardans et al., 2008). However, the soil physical properties as well as soil nutrient content and microbial community structure may also vary at the scale of centimetre in forest soils (Koorem et al., 2014; Nacke et al., 2016). Thus, forest soils may differ between neighbouring declining and non-declining trees growing in the same stand (Curiel Yuste et al., 2012; Mikkelson et al., 2016).

Here we compare belowground soil properties (physical features, nutrient availability, microbiota composition) of coexisting declining or recently dead vs. non-declining trees in three forest types which experienced a drought-induced die-off in 2012. These forests are dominated by Scots pine (*Pinus sylvestris*), Silver fir (*Abies alba*) and Aleppo pine (*Pinus halepensis*), respectively, and they are subjected to contrasting climatic conditions. After the drought in 2012, we monitored the canopy cover, a proxy of tree vigour (Dobbertin, 2005), of surviving trees. In 2015, we measured soil physical and chemical characteristics and characterized the soil microbial structure. We hypothesize that despite strong differences in nutrient supply rates and soil microbial structure linked to different forest characteristics (soil type, climate condition), die-off will be followed by a shift in nutrient availability and microbial community structure in the rhizosphere of declining and recently dead trees.

2. Materials and methods

2.1. Study sites and sampling protocols

We studied the populations of three conifers inhabiting three sites situated in Aragón (north-eastern Spain) and subjected to contrasting climatic conditions (Camarero et al., 2015). Particularly, we studied: a Scots pine (*Pinus sylvestris* L.) forest located in the Iberian System (Corbalán, Teruel) subjected to a continental Mediterranean climate (Table 1), a silver fir (*Abies alba* Mill.) forest situated in the Pyrenees (Paco Ezpela, Ansó) where temperate conditions prevail, and an Aleppo pine (*Pinus halepensis* Mill.) forest situated in the Middle Ebro Basin (Peñaflor, Zaragoza), close to the Monegros steppe, characterized by a semi-arid Mediterranean climate (see sites' features in Table 1). The Iberian system and the Pyrenees represent the southernmost distribution limit of Scots pine and Silver fir in Europe. The Ebro Basin is one of the driest regions in Europe. Climate warming and the occurrence of severe droughts during the late 20th century and early 21st century (1986, 1994–1995, 2005, 2012) have caused die-off events affecting the study forest types (Camarero et al., 2015; Vicente-Serrano et al., 2010; Supporting Information, Fig. S1).

The Corbalán Scots pine forest present no evident signs of human management during the last 50 years (Camarero et al. 2015). The Paco Ezpela silver-fir forest present signs that intense logging activity was undertaken in the past such as stumps and wood trails (Sangüesa-Barreda et al., 2015). Nevertheless, these management activities ceased in the early 1950s (Camarero et al., 2015). The Peñaflor Aleppo pine stands were part of a large recreational forest which in the past was reserved for the sole use of the aristocracy for hunting and recreation