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Dryland forest management alters fungal community composition and decouples assembly of root- and soil-associated fungal communities

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ABSTRACT

Land management practices considerably influence ecosystem processes and functioning, particularly in dryland ecosystems where nutrient and water limitations have direct (via effects on productivity) and indirect (via effects on soil biota) effects on ecosystem properties. Fungi in soils and associated with roots play critical roles in soil nutrient cycling and plant nutrient acquisition, but their responses to land management practices in dryland ecosystems remain equivocal. Here we evaluate the responses of fungal communities in roots and soils associated with a *Eucalyptus saligna* plantation after six years of forest management practices (irrigation and fertilisation) and in two different microenvironments within treated plots, in the presence and absence of understorey grasses. We observed that the richness and evenness of fungal communities were higher in soil than in root samples, but these two parameters did not vary among any of the management treatments. Effects of fertilisation and irrigation on fungal community composition were observed and appeared to be related to variation in soil pH, moisture, and nitrogen availability. Both fertilisation and irrigation decreased the ratios of ectomycorrhizal fungi to total fungi and increased the frequencies of saprotrophic and/or plant pathogenic fungi. We observed that some OTUs were shared between soil and root-associated fungal communities but that fertilisation was associated with lower frequencies of shared OTUs, suggesting a decoupling of these communities. In the absence of grasses, where only tree roots were present, we observed fewer tight relationships between fungal occurrence in root and soil samples. Our findings highlight the importance of forest management practices for fungal community assembly processes in dryland ecosystems, which may have consequences for the predictability of fungal community dynamics and nutrient cycling.

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1. Introduction

Drylands, including arid and semi-arid ecosystems, are widely distributed around the world and cover *c*. 41% of Earth's terrestrial surface (Schimel, 2010). These ecosystems are characterized by low levels of soil moisture and nutrients owing to low precipitation and high evaporation (Delgado-Baquerizo et al., 2013), and are considered to be extremely vulnerable to anthropogenic perturbations and climate change (Singh et al., 2010; Martins et al., 2015). Microbial communities, particularly those associated with plant roots and rhizospheric soil, play a key role in ecosystem functions including biogeochemical cycling and affect plant growth and tolerance to biotic and abiotic stresses (Philippot et al., 2013; Singh et al., 2014). Given the critical importance of microbes to ecosystem services and the continuing expansion of drylands in many regions, it is important to generate an understanding of how microbes in dryland ecosystems respond to environmental shifts (Johnson et al., 2012; Hu et al., 2015).

Fungi fill important roles in carbon (C) cycling and plant nutrition in forest soils through their functioning as decomposers and mutualists (Tedersoo et al., 2014). Plant parasitic fungi can cause a range of plant diseases and negatively affect forest production, while mycorrhizal fungi facilitate water and mineral nutrient uptake by plants, and thus enhance fitness of plants experiencing environmental stress (Smith and Read, 2008). Therefore, understanding the responses of belowground fungal diversity and community composition in forest ecosystems facing environmental manipulation may aid sustainable forest management. This is particularly true if the disturbance influences taxa that are involved in regulating functional aspects of these ecosystems. Soil fungal

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diversity and community composition have been observed to respond to environmental variation associated with the plant community present (Peay et al., 2013) and fertilisation (He et al., 2008), while a global-scale study reported that soil fungal diversity could be largely explained by mean annual precipitation and soil calcium (Ca) concentrations across various ecosystems (Tedersoo et al., 2014). Therefore, fungi in managed dryland forests are expected to respond to practices associated with nutrient and/or water inputs, and understanding how these community responses are related to altered soil properties is essential for the prediction of outcomes related to plant nutrition, plant-soil-water interactions, and soil carbon cycling in other systems in other systems.

In addition, how fungal communities respond to management may depend on where they are observed given that soil- and root-associated fungal communities may be governed by differing assembly processes (Beck et al., 2015). Fungal communities associated with roots may be made up of members recruited from the surrounding soil fungal community (Danielsen et al., 2012), but there are conflicting observations in that root-associated fungal communities may be less diverse (Goldmann et al., 2016) or considerably more species-rich (Saks et al., 2014; Beck et al., 2015) than the surrounding soil fungal community. While the reasons behind these differences in fungal community assembly in soil versus roots still needs to be determined, they may have to do with the direct roles that root-associated fungi play in plant nutrition and fitness maintenance while soil-associated fungi influence plant nutrition and fitness indirectly via their effects on organic matter turnover and nutrient cycling.

Fertilisers are extensively applied in pursuit of higher crop yield, forage production, and wood output in agricultural, grassland, and forest ecosystems, respectively. Increased soil fertility alters the diversity, composition, and productivity of the aboveground plant community (Magnani et al., 2007; Fornara and Tilman, 2012) as well as some aspects of the belowground fungal community (Bradley et al., 2006; Veresoglou et al., 2012; Weber et al., 2013; Li et al., 2015; Nielsen et al., 2015; Zheng et al., 2016). These impacts on fungi may be due to direct effects on edaphic properties (Zheng et al., 2014) or indirect effects via changes in the abundance and/or composition of associated plant communities (Liu et al., 2012). Irrigation is also a common practice, especially in dryland systems, to alleviate water stress and promote productivity, with effects on edaphic properties and plant communities (Hawkes et al., 2011; Zhou et al., 2013; Li et al., 2015).

Soil fungal communities are expected to respond to changes in water availability. Nutrient diffusion is enhanced under increased water availability, which may reduce the dependence of host plants on mycorrhizal fungal mycelial uptake of these nutrients, and even of water (Augé, 2001). Water addition may also indirectly influence fungi via changes in plant community abundance and composition (Hawkes et al., 2011; Cregger et al., 2012; Li et al., 2015). Shifts in the aboveground plant community, together with changes in belowground resource availability due to altered plant litter, exudates, and soil characteristics may impact both mycorrhizal and saprotrophic fungi (Husband et al., 2002; Waldrop et al., 2006; Hawkes et al., 2011; Li et al., 2015). However, relatively little is known about the impacts of altered precipitation regimes on belowground dryland fungal communities compared to our current knowledge of plant responses and other microbes (Cregger et al., 2012; Zhang et al., 2013; Nielsen and Ball, 2015).

The main objective of this study was to explore the direct and indirect responses of fungal communities in dryland forests to long-term (six years) forestry management practices, namely fertilisation and irrigation. We sampled fungal communities from soil and roots in a dryland *Eucalyptus saligna* Sm. plantation. To evaluate the direct (via edaphic properties) and indirect (via plant responses) effects, we sampled soil and roots from patches that contained understorey grasses or were bare and only influenced by the tree roots and the management treatments. We hypothesized that management strategies would have strong effects on root-associated fungal communities, especially in patches with understorey grasses, because of the potential for both direct effects of edaphic properties and indirect effects associated with plant responses. Alternatively, root-associated fungal communities may be less affected by the treatments because the root environment already presents a strong environmental filter and altered edaphic properties contribute little to subsequent variation in root-associated fungal communities, leading to a decoupling of soil- and root-associated fungal communities (Beck et al., 2015). We also speculated that irrigation and fertilisation would have strong interactive effects in this ecosystem due to both water (Colombo et al., 2016) and soil fertility (especially phosphorus [P]; Nielsen et al., 2015) being limiting in local soils.

2. Materials and methods

2.1. Site and experimental design

The experimental field is located at the Hawkesbury Forest Experiment site (33°36′40″ S, 150°44′26.5″ E) in Richmond, NSW, Australia. The experiment consists of a series of plots planted with *Eucalyptus saligna* at a density of 1000 trees ha^{-1}. The plots also contain an understorey of grasses, with the space between tree rows dominated by *Eragrostis curvula* (Schrad.) Nees, *Microlaena stipoides* (Labill.) R. Br., and *Elymus repens* (L.) Gould, as well as smaller quantities of *Digitaria sanguinalis* (L.) Scop., *Setaria incrassata* (Hochst.) Hack., *Chloris truncata* R. Br., and *Dactylis glomerata* L. (Frew et al., 2013). Grasses are largely absent within tree rows as a result of a relatively dense layer of leaf litter and bark. Roundup was sprayed within tree rows, but not between rows, occasionally during the first two years of the study to facilitate tree establishment. The soil is a sandy loam and is characterized by low water holding capacity, low organic matter content (0.7%), low nitrogen ([N] < 1 mg kg^{-1}) and P (8 mg kg^{-1}) concentrations (Barton et al., 2010). Mean annual temperature at this site is 17 °C, and the mean annual precipitation is 801 mm. The ratio of precipitation to evapotranspiration at the site is 0.6; therefore, the site is classified as a dry sub-humid environment under UNEP classification (Millennium Ecosystem Assessment, 2005).

The field experiment consisted of four management treatments (fertilisation and ambient rainfall [F], fertilisation plus irrigation [IF], irrigation without additional fertiliser [I], and a control with ambient rainfall and without fertilisation [Control]), applied to experimental plots (38.5 × 41.6 m) in a randomized complete block design with four replicates for each treatment (resulting in 16 independent plots). Each plot was planted with 160 *Eucalyptus saligna* in 10 rows in April 2007, and experimental treatments were applied to the whole plot. At planting, 50 g of diammonium phosphate starter blend (N 15.3%, P 8.0%, potassium [K] 16.0%, sulphur [S] 7.7%, and Ca 0.3%) was applied to each tree to promote establishment. The Control treatment received no additional fertiliser or water. The first fertilisation in the F and IF treatments was undertaken with a solid N fertilizer (N 20.6%, P 3.0%, K 7.5%, S 3.8%, and Ca 4.4%) at a rate of 25 kg N ha^{-1} $year^{-1}$ in January 2008. Solid N fertiliser (N 21.6%, P 8.1%, K 12.0%, and S 0.6%), at a rate of 150 kg N ha^{-1} $year^{-1}$, was applied uniformly to the F treatment beginning in October 2008. The IF treatment received liquid fertiliser at a rate of 150 kg N ha^{-1} $year^{-1}$ (Nutrifeed19 and Liquid N, Amgrow Fertilisers, Lidcombe, NSW, Australia), beginning in October 2008. In both the I and IF treatments, grey water (pH 8.8, total N 0.6 mg L^{-1},

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