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Impact of plant root functional traits and associated mycorrhizas on the aggregate stability of a tropical Ferralsol

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ABSTRACT

In many tropical regions, such as New Caledonia, soil erosion from anthropogenic activities and subsequent ecological restoration are major issues that require detailed soil and vegetation data for the production of management plans. To determine if some plant species are more useful for stabilizing soil aggregates and thus reducing erodibility, we examined three species endemic to New Caledonia, and measured how root traits and associated mycorrhizas and fungi influenced Ferralsol aggregate stability (MWD). The three species are hosts to different types of mycorrhizas and were: (i) the sedge *Costularia arundinacea* (Sol. Ex Vahl) Kük., an AMF (arbuscular mycorrhizal fungi) host, (ii) the shrub *Tristaniopsis glauca* Brongn. & Gris and (iii) the tree *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill., both of the latter are ectomycorrhizal fungi (ECM) hosts. Fungal abundance, aggregate stability, soil organic carbon (SOC), iron (Fe) and aluminium (Al) sesquioxides were measured in the soil beneath 20 individuals for each species, as well as in 20 control samples of bare soil. Root functional traits including root mass density (RMD), root length density (RLD) and percentage of fine roots were measured on all individuals. Results showed that plant species can significantly influence soil aggregate stability. MWD was greater in soil beneath *Costularia* characterized by high RMD, RLD, percentage of fine roots and fungal abundance, while MWD in the rhizosphere of *Tristaniopsis* and *Arillastrum* was similar to that of bare soil. Fe and Al were very high in all soil samples and are suspected of masking the influence of roots, fungi and SOC on MWD at the scale of isolated ECM-hosts. Therefore, MWD alone would not be a relevant predictor of restoration on such soil and further investigations should be carried out to identify a set of predictors useful for indicating the restoration of degraded soils on ultramafic substrates.

1. Introduction

In many tropical regions, ecological restoration is a major issue, especially on heavily eroded sites (Losfeld et al., 2015), and soil aggregate stability is viewed as a promising indicator of the restoration status in eroded ecosystems (Burri et al., 2009). Stable soil aggregates are more resistant to detachment and loss through erosion (Barthès and Roose, 2002; Pierson and Mulla, 1990), and therefore contribute to minimize soil erosion (Amézketa, 1999). Besides, soil aggregate stability is often considered as a critical indicator of ecosystem processes (Amézketa, 1999; Rillig et al., 2002), hypothesized to be positively related with primary productivity (Pellant et al., 2005) and conservation of soil fertility (Elliott, 1986). Thus, maintaining high aggregate stability would be essential for preserving soil productivity and minimizing soil erosion (Amézketa, 1999). Yet, limited empirical evidence is available to confirm that soil aggregate stability is a relevant predictor of ecosystem functions (Reinhart et al., 2015). Besides, despite the increasing number of studies focusing on ecosystem restoration, the process of stabilization remains poorly understood, especially in a tropical context.

The tropical archipelago of New Caledonia, in the south west Pacific ocean, is covered by Ferralsols on ultramafic substrates, which, at the same time, provide major nickel reserves, host a unique terrestrial biodiversity (Myers et al., 2000) and are prone to soil erosion (Dugain,

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1953). Over 1200 plant species, 97% of which are endemic to New Caledonia, are ultramafic-obligate (Isnard et al., 2016), highlighting the necessity to preserve and manage soils hosting this unique flora. However, to our knowledge, limited studies have explored aggregate stability on these particular soils and the putative use of aggregate stability as a restoration indicator. Therefore, our study focuses on this knowledge gap and will provide valuable data for managers requiring indicators of soil evolution during restoration processes. Demenois et al. (2017b) showed that in a Ferralsol on an ultramafic substrate, aggregate stability was positively influenced by iron (Fe) sesquioxides, certain root traits (e.g. root mass density, root length density and percentage of fine roots) and soil organic carbon (SOC).

The positive effect of fine roots on soil aggregate stability consists of i) enmeshing fine particles into stable macro-aggregates; ii) drying the localized soil environment around the roots, iii) drawing soil particles together; iv) supplying decomposable organic residues; v) supporting a large microbial population in the rhizosphere; vi) providing food for soil animals and vii) releasing polyvalent cations (Pojasok and Kay, 1990). However, the effect of fine roots on aggregate stability is variable and depends largely on soil type (Le Bissonnais et al., 2017), differences in fine root quantity and architecture that will determine the overall influence of roots on aggregates (Carter et al., 1994), root exudation that is variable among plant species (Haynes and Beare, 1997; Hütsch et al., 2002) and decomposition of dead roots that is related to the amount and the decomposability of root material (Robinson and Jacques, 1958). In a comparative study of the effects of fine roots versus soil characteristics, Le Bissonnais et al. (2017) showed that between sites, soil chemical properties and SOC were the main drivers of stability, but that within a site, plant fine root traits, and in particular root biomass and root length density, influenced most aggregate stability. Similarly, plant species diversity and richness have been demonstrated to promote the formation and the stabilization of soil aggregates (Erktan et al., 2016; Pérès et al., 2013; Pohl et al., 2009), largely due to a more optimal temporal and spatial occupation of roots in the soil matrix. However, these studies were not carried out on Ferralsols and did not take into account the type of mycorrhizas associated with the plant communities.

Fungal transformants and exudates act by coating fine soil particles with a layer of organic matter and by adhering the particles embedded and held on the surface, forming micro-aggregates. Like, plant roots, fungal hyphae can bind and enmesh micro-aggregates into macro-aggregates ($>250\ \mu m$) (Graf and Frei, 2013; Tisdall, 1994). Mycorrhizal fungi also indirectly affect aggregate stability through their host plants, particularly by accelerating the development of their root network and by serving as a distribution vector for associated micro-organisms (Graf and Frei, 2013). Although the influence of arbuscular mycorrhiza (AMF) on aggregate stability has been demonstrated several times (Miller and Jastrow, 2000; Rillig, 2004; Wilson et al., 2009), the contribution of ectomycorrhizas (ECM) to the formation and stabilization of soil aggregates has not been elaborated in detail. ECM are usually more host-specific than AMF and are generally associated with woody species (Wang and Qiu, 2006). Studies that comprehensively describe the influence of ECM characteristics on aggregate stability (e.g. filamentous growth, mycelial networks that stretch beyond the rhizosphere and the production of polysaccharides and hydrophobines), are scanty (Caesar-Ton That et al., 2001; Graf and Frei, 2013; Tagu et al., 2001).

To determine if some plant species and their associated mycorrhizas and fungi are more useful for stabilizing soil aggregates, we examined bare soil and three plant species endemic to New Caledonia, and measured how root traits and fungal abundance influenced Ferralsol aggregate stability. Plant species comprised herbaceous and woody species and were host to either AMF or ECM. We hypothesized that at the species level, a herbaceous species (AMF-host) would have a greater effect than a woody species, because of the large quantity of fine roots present, which would also increase AMF biomass. As woody species have a lower quantity of fine roots (Le Bissonnais et al., 2017), and consequently lower ECM biomass, aggregate stability should be lower.

2. Materials and methods

2.1. Field site, plant material and field sampling

Work was conducted in the Massif du Grand Sud in New Caledonia at a site called Bois du Sud, located in a botanical reserve (22°10′S-166°46′E) (Fig. 1a), at an altitude of 200–230 m. Mean annual precipitation is 3000 mm and the minimal and maximal mean annual temperatures are between 20.5 °C and 26.6 °C (Météo France, 2016). The site was selected according to three main criteria: (i) a Ferralsols on ultramafic substrates typical of the Massif du Grand Sud, (ii) a slope $<30°$ subject to water erosion, and (iii) the three model species to be studied were all present. Although the site comprised only Ferralsols according to the soil map of New Caledonia (Fritsch, 2012), three topographic sub-areas were defined: gully, north-facing slope and east-facing slope sub-areas. Each sub-area might correspond to different habitats and also influence water infiltration and run-off, and erosion as a consequence.

The three selected plant species were: *Costularia arundinacea* (Sol. Ex Vahl) Kük. (Cyperaceae), *Tristaniopsis glauca* Brongn. & Gris (Myrtaceae) and *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill. (Myrtaceae) (Fig. 2). All three species are dominant on Ferralsols in New Caledonia and are known to influence the soil microbial richness, composition and abundance (Gourmelon et al., 2016). The three species are used for revegetation, erosion control and ecological restoration in New Caledonia (L'Huillier et al., 2010) and have a potential positive impact on aggregate stability when dominant in plant communities (Demenois et al., 2017a).

Costularia is an endemic perennial sedge frequently abundant in the herbaceous stratum on Ferralsols in New Caledonia. As a plant host, *Costularia* is known to be associated with arbuscular mycorrhiza (AMF) and plant growth promoting rhizobacteria (PGPR) (Lagrange et al., 2011). *Tristaniopsis* is an endemic shrub growing in open sclerophyllous shrubland where it is ubiquitous and dominant. It is associated with ectomycorrhizal fungi (ECM) (Amir and Ducousso, 2010). *Arillastrum* is an endemic tree which usually occurs in extensive, monodominant stands (Sebert, 1874; Virot, 1956). It grows exclusively on ultramafic substrates and is associated with ECM (Papineau, 1989).

Plant sampling on the site was almost systematic and for each species, twenty individuals were geo-tagged (Fig. 1b). Plants were at least 1 m distant from each other to limit the risk of confounding root samples from other plants. As the age of the individuals was unknown, only specimens <2 m in height were selected to standardize observations. *Costularia* were mainly sampled (18 out of 20 plants sampled) in the east slope sub-area, while *Tristaniopsis* were mainly (14 out of 20 plants sampled) in the north slope sub-area. *Arillastrum* were equally present in the three sub-areas. Additionally, 20 wooden poles were inserted into the soil, distributed among the three sub-areas, and geo-tagged to mark control samples. Controls were characterized by bare soil, without any plants present, and were within a radius of 0.5 m from the nearest pole. For each plant individual ($n = 20$ per species), and control points ($n = 20$ points), four soil samples were collected for root trait measurements, assessment of fungal abundance, chemical analyses and aggregate stability tests.

2.2. Root trait measurements

The method used to measure root traits of the three plant species consisted of collecting, for each plant and control sample, soil samples (0–15 cm deep) at the base of each plant, using a cylindrical corer (diameter 8 × length 15 cm) in order to obtain a soil volume of 754 cm^3. Roots were extracted from the soil core by washing them with tap water in a column of two sieves (2.0 and 0.1 mm mesh size). Roots