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Social insects behind the microgranular structure of Ferralsols: Consequences for their physical fertility when cultivated

It was long accepted that the microgranular structure which is characteristic of many Ferralsols was mainly related to physico-chemical processes and to their mineralogical composition. It now appears, however, that this microgranular structure originates from the burrowing activity of termites and ants. Given its importance for the physical properties of Ferralsols, it will be necessary to study the different termite and ant species responsible for this microgranular structure and the characteristics of the burrowing activity associated with species. This is a major point to better understand the possible long-term consequences of agriculture on Ferralsol properties because it strongly affects soil faunal biodiversity

Most yellow or red soils found in the South American, African and Asian tropics are classified as Ferralsols in the World Reference Base (IUSS Working Group WRB, 2015). They correspond to Latosols in the Brazilian taxonomy (Embrapa, 2006), mainly to Ferrallisols in the Genetic Soil Classification of China and to Ferrosols in the Chinese Soil Taxonomy (Shi *et al.*, 2004 and 2006), and to Oxisols or Ultisols in the Soil Taxonomy (Soil Survey Staff, 2006). They represent a large land surface area with 750 million hectares worldwide (IUSS Working Group WRB, 2015), which corresponds in the tropics to about 14 % of the land surface area. They result from a long sequence of deep weathering under conditions that in most cases have prevailed for at least several tens of thousands of years (van Wambeke, 1992; Scholten *et al.*, 1997; Schaefer, 2001). In such soils, easily weatherable primary minerals such as feldspar and micas have disappeared, resulting in a fine material essentially made up of kaolinite and of iron and aluminium sesquioxides (Pédro, 1968; Melfi and Pédro, 1977, 1978). As a result, Ferralsols are characterized by extremely low native chemical fertility, resulting from very low nutrient reserves, low pH, high phosphorus retention by oxide minerals, and low cation exchange capacity (Yu, 1997; Kögel-Knabner and Amelung, 2014). On the other hand, most Ferralsols are characterized by a well-developed microgranular structure and consequently exhibit high physical fertility resulting from high porosity, low resistance to root penetration, high infiltration rate and high available water retention (Stoops, 1983; Trapnell and Webster, 1986; Bui *et al.*, 1989; Schaefer, 2001; Balbino *et al.*, 2002, 2004; Volland-Tuduri *et al.*, 2004, 2005; Reatto *et al.*, 2007, 2008, 2009).

The microgranular structure has long been recognized in Ferralsols and discussed as resulting from physico-chemical processes combining mechanical fragmentation of a compact soil material due to alternating wetting and drying in relation to change in the physico-chemical interactions between kaolinite and iron oxyhydroxides (Melfi and Pédro, 1977, 1978; Volkoff and Melfi, 1980; Karathanasis *et al.*, 1983; Cooper *et al.*, 2005). Although based on poorly defined processes, this explanation of the origin of the microgranular structure of Ferralsols has long been widely accepted by the scientific community. Some studies on Ferralsols from Congo and Ivory Coast, however, noted early the morphological similarity between the aggregates forming the walls of the termite mounds and of the underground cavities and channels on the one hand, and those forming the main components of the groundmass of the horizons of the Ferralsols studied on the other hand (Eschenbrenner, 1986), but these studies were not widely circulated in the scientific community. During the same period, Wielemaker (1984) highlighted the role of termites in mixing soil material in a range of Kenyan soils. He also showed the morphological similarity between the aggregates forming biological structures built by termites and the microgranular structure of the groundmass. During the 2000s, while basing their work mainly on observations made on Brazilian Ferralsols, several authors proposed that the microgranular structure might originate from the activity of soil-feeding termites and more broadly from social insects such as termites and ants (Schaefer, 2001; Reatto *et al.*, 2009).

More recently, while traces of termite activity had been observed early down to several tens of meters deep in lateritic profiles (Barros Machado, 1982; Tardy, 1992), several authors have shown the presence in the upper part of Ferralsols of material originating from the underlying saprolite present at 5 to 10 m depth (Bruand and Reatto, 2022; Bruand *et al.*, 2022 and 2023). These results indicated clearly that social insects, most likely termites, were at the origin of the microgranular structure of the Ferralsols studied, in that the presence of such material was the result of upward transport by termites or ants. Such transport could be motivated, as mentioned very early on, by the search for water which is only present at considerable depth at the end of the dry season (Tardy, 1992; Schaefer, 2001), or, as suggested much more recently, by the search for chemical elements such as sodium present in an exchangeable position on the 2:1 clay minerals of the saprolite whereas it is absent in the first top meters of the soil (Jouquet and Bruand, 2023).

Whatever may have been the earliest hypotheses to explain the formation of the microgranular structure, studies indicating that it must be considered as resulting from the activity of termites and ants for tens of thousands of years, even hundreds of thousands of years, are multiplying. They show that while rock weathering produces large amounts of fine material varying according to the mineralogical composition of the rock and topographic position, resulting in a material essentially made up of low-activity clay, and of iron and aluminium sesquioxides (Reatto *et al.*, 2008), termite and ants reorganize that material by their burrowing activity which produces a microgranular structure in the top first meters of the Ferralsols, limiting horizon differentiation. The variations in the organic carbon content in the first few decimeters are in fact the only ones enabling horizons to be distinguished. Ferralsols are characterized by the weakness of their horizonation (IUSS Working Group WRB, 2015) and this characteristic can likely be explained by the continual reworking of the soil by social insects, thus opposing the differentiation of horizons in these soils which result from a very long pedogenesis in a tropical climate.

The physical fertility (*e.g.* water permeability, resistance to root penetration, water retention) of Ferralsols, which is closely related to the development of the microgranular structure, appears to be therefore directly dependent on this activity of soil social insects (Lavelle and Spain, 2001; Bétard, 2021; Schaefer and Oliveira, 2022). It will therefore be necessary to attach the greatest importance to it when cultivating these soils. Any change in the soil faunal biodiversity in Ferralsol under native vegetation could have dramatic consequences on their capacity to infiltrate water and to be prospected by the roots. Initial studies taking into account the evolution of the biodiversity of social insect populations in Ferralsols following their cultivation showed that both the soil faunal biodiversity and microgranular structure development were significantly affected, with major consequences for Ferralsol fertility (Balbino *et al.*, 2002; Benito *et al.*, 2004). It is therefore recommended that studies specifying the dynamics of renewal of the microgranular structure in relation to the evolution of the populations of termites and ants be implemented. This requires that long-term field trials be conducted in different environments worldwide and that studies modeling the burrowing activity of termite and ant populations be conducted. Studies in mesocosms are also required to specify the dynamics of renewal of the microgranular structure for the species of termites and ants suspected of being the most active. This points out the need, as suggested by Jouquet *et al.* (2022), to redefine termite and ant functional groups based on their consequences on soil properties, particularly on the microgranular structure development in Ferralsols. The future of the physical properties of Ferralsols, and probably of many other soils affected by the burrowing activity of these social insects, depends on it.

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