



Soil texture modulates the response of ammonia-oxidizing prokaryotes to biochemical quality of organic inputs in tropical agricultural soils



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ABSTRACT

Soil texture modulates the response of ammonia-oxidizing bacterial (AOB) and archaeal (AOA) communities to biochemical quality of organic inputs in tropical agricultural soils. To verify this assumption, we used the soil organic matter long-term field experiments in Kenya established on contrasting soils (i.e., clayey Humic Nitisol, sandy Ferric Alisol) in 2002. Since the start of the experiments, soils were continuously treated (4 Mg C ha⁻¹ year⁻¹) with biochemically different organic inputs including *Tithonia diversifolia* (TD; C/N ratio: 13, Lignin: 8.9%; Polyphenols: 1.7%), *Calliandra calothyrsus* (CC; 13; 13; 9.4) and *Zea mays* stover (ZM; 59; 5.4; 1.2). In 2013, soils (0–15 cm) were sampled at young growth (EC30) and flowering (EC60) stages of maize and subjected to DNA-based community analysis of AOB, AOA and 16S rRNA genes. Soil texture exerted stronger effects on the dynamics of the assayed genes than organic input quality with AOB being more responsive than AOA. Clayey soil with its predominant soil organic matter background and large surface area of clay minerals revealed generally higher AOB and AOA abundance than the sandy soil. In the sandy soil, N-rich TD and cellulose-rich ZM promoted AOB abundance, while it was decreased under CC due to N limitation induced by high contents of polyphenols and lignin. N limitation under ZM revealed a clear community differentiation of AOB between ZM versus TD and CC in the clayey soil. For the sandy soil, AOA community composition was distinct between CC versus TD and ZM. To provide a more detailed mechanistic understanding of active AOB and AOA in response to organic input quality, we recommend for prospective research RNA-based along with enzymatic analyses as complement to those shown in this study. This should be approached using controlled experiments to eliminate interfering environmental effects including rainfall and soil moisture, respectively.

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1. Introduction

Tropical agro-ecosystems are generally resource limited justifying the use of organic inputs as complements to mineral fertilizers to replenish soil nutrients (e.g., nitrogen (N)) for crop growth (Chivenge et al., 2009; Mtambanengwe et al., 2006; Rasche and Cadisch, 2013). Small-holder farmers can rely on a broad array of organic inputs (e.g., crop residues, prunings from shrubs and trees) differing in their biochemical quality. Organic input quality is commonly defined by the contents of N, lignin, polyphenols and also cellulose (Kunlanit et al., 2014; Palm et al., 2001). It was acknowledged that decomposition of organic matter by soil

microorganisms, which play a key role in providing organically bound nutrients to crops, is regulated by organic input quality (Rasche and Cadisch, 2013). In this respect, organic inputs such as *Tithonia diversifolia* (TD; C/N ratio: 13, Lignin: 8.9%; Polyphenols: 1.7%) accelerated decomposition availing N early in the cropping season, while more recalcitrant resources such as *Calliandra calothyrsus* (CC; 13; 13; 9.4) showed delayed decomposition patterns (Palm et al., 2001). The delayed decomposition of CC was mainly associated with the formation of polyphenol protein bonds limiting the accessibility of organic N by microbial decomposers (Millar and Baggs, 2004). Recently, it was shown that such polyphenol-induced N limitation prompted a critical stress response through increase in abundance of proteolytic bacteria in sandy agricultural soils (Rasche et al., 2014).

It remains yet to be understood to which extent microbial driven nitrification is regulated by organic input quality. This may count

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for both nitrifying prokaryotes (ammonia-oxidizing archaea (AOA)) and (ammonia-oxidizing bacteria (AOB)) whose community dynamics are generally assessed on the basis of the functional marker *amoA* gene (α -subunit of the enzyme ammonia-monooxygenase) (Prosser and Nicol, 2008; Zhang et al., 2013). Existing observations of organic input quality effects on AOA and AOB community dynamics have not displayed clear response patterns. For example, low C/N ratios, hence easily decomposable organic materials (e.g., *Brassica napus*, cereal straw) in comparison to high C/N ratio inputs (e.g., compost, peat) with a gradual decomposition pattern promoted the abundance of AOA in both sandy and clay loam soils (Strauss et al., 2014; Wessén et al., 2010). Conversely, no treatment effect was observed on AOB abundance. Muema et al. (2016) in a clayey soil reported a promotion of AOB abundance by both low and high C/N ratio inputs (i.e., *Tithonia diversifolia*, *Zea mays*), respectively, while AOA abundance remained unaffected by inputs of different biochemical quality. Hai et al. (2009) found a promotion of AOA and AOB abundance in sandy soils after treatment with nutrient rich semi-decomposed cattle manure (low C/N ratio), while both groups were decreased by sorghum straw with a high C/N ratio. On the other hand, Muema et al. (2015) and Wessén et al. (2010) observed a clear community composition differentiation of both, AOB and AOA in a clayey and clay loam soils, respectively, treated with biochemically distinct organic inputs.

These contradictory results clearly imply that the response of nitrifying communities to organic input quality may be determined by other factors including physic-chemical soil characteristics (Kögel-Knabner et al., 2008). Clayey compared to coarse textured sandy soils show a generally higher accumulation potential of soil organic matter (SOM) either through physical protection of freshly added organic inputs or via organo-mineral associations (Dieckow et al., 2009; Kögel-Knabner et al., 2008). These characteristics of fine-textured clayey soils induced a higher abundance of total bacteria than in sandy soils as attributed to the higher surface area of clay particles promoting bacterial growth as well as providing protection from predation (Kögel-Knabner et al., 2008; Neumann et al., 2013; Poll et al., 2003). With respect to nitrifying soil microorganisms, Pereira e Silva et al. (2012) reported a higher abundance of AOB and AOA in clayey than in sandy soils, supporting the mechanisms of clayey soil linked promotion of microbial populations (Kögel-Knabner et al., 2008). Other observations evidenced that AOA in fine textured soils preferentially utilize native SOM (Stopnišek et al., 2010; Zhalnina et al., 2012; Zhang et al., 2010) explaining their increased abundance over sandy soils. In contrast, Wessén and Hallin (2011) found AOA abundance to be negatively correlated with clay content which supported the concept of AOA being generally adapted to nutrient limitation in soils (Levičnik-Höfferle et al., 2012; Valentine, 2007). It remains however speculative if organic inputs of similar biochemical quality induce consistent responses of nitrifying communities in soils with distinct textures.

Our objective was therefore to primarily determine the interrelations between soil texture and organic inputs of contrasting biochemical quality on the abundance and community composition of AOB and AOA in tropical agricultural soils. We hypothesized a higher AOB and AOA abundance in clayey than sandy soils regardless of organic input quality. This appears justified by the strong SOM background of clayey soils as determined by the acknowledged beneficial characteristics of clay minerals in sequestering organic substrates fostering microbial proliferation (Gentile et al., 2011a; Kögel-Knabner et al., 2008). Furthermore, alteration of community composition, i.e. AOB and AOA, was proposed in a clayey but not sandy soil due to its high nutrient status. Consequently, we argue that the general resource limitation in sandy soils is compensated with the addition of high quality

organic inputs (low C/N) availing high amounts of organic C and N to AOB and AOA, promoting their abundance and community composition alteration early in the cropping season. This is in contrast to intermediate (high polyphenol and lignin contents) and low (high C/N) quality inputs hindering their fast decomposition. In this respect, we hypothesized at later crop growth stages a promotion of AOB and AOA abundance along with a community composition alteration in sandy soils as a consequence of gradual decomposition of intermediate and low quality inputs availing C and N substrates to the decomposer communities.

2. Materials and methods

2.1. Sites description and experimental design

The study was carried out at the soil organic matter (SOM) long-term field experiments in Embu (0° 30' S, 37° 30' E) and Machanga (0° 47' S, 37° 40' E) which were established in 2002. Embu site (1380 m above sea level (a.s.l)) is located in Embu district in the central highlands of Kenya (130 km northeast of Nairobi). Machanga site (1060 a.s.l) is located in Mbeere district, approximately 200 km northeast of Nairobi. Embu site has an annual mean temperature of 20 °C and a mean annual rainfall of 1200 mm, while Machanga site is characterized by frequent droughts due to erratic and unreliable rains with a mean annual temperature of 26 °C and an average annual rainfall of 900 mm. Rainfall at both sites occurs bimodal with long rains received from mid-March to June and short rains from mid-October to December. The soil at Embu is defined as a Humic Nitisol (FAO, 2006) dominated by kaolinite minerals derived from basic volcanic rocks. The texture of the topsoil layer (0–15 cm) was characterized by 17% sand, 18% silt and 65% clay and contained 29.3 g kg⁻¹ organic C, 2.8 g kg⁻¹ total N and a pH of 5.8 (H₂O) at the start of the experiment (Chivenge et al., 2009; Gentile et al., 2011a). Machanga site is characterized by a sandy soil derived from granitic gneisses and is classified as Ferric Alisols (FAO, 2006). The texture of the top layer (0–15 cm) contained 67% sand, 11% silt and 22% clay with 5.3 g kg⁻¹ organic C, 0.6 g kg⁻¹ total N and a pH (H₂O) of 6.1 at the onset of the experiment (Gentile et al., 2011a). Moreover, Machanga soil was reported to be deficient in major crop nutrients such as N and P (Gentile et al., 2011a), while the Embu soil was considered fertile with greater total carbon and nitrogen (TC, N_t), as well as higher exchangeable bases measured at the onset of both experiments (Chivenge et al., 2009; Gentile et al., 2011a).

The two SOM long-term field experiments were implemented to primarily study the effect of continuous annual application of biochemically contrasting organic inputs and their combination with mineral N fertilizer on the productivity of maize (*Zea mays* L.) crop, used as a test crop, as well as soil C and N dynamics (Chivenge et al., 2011, 2009; Gentile et al., 2011a; Rasche et al., 2014). This presented work however, focused only on organic input treatments excluding the effect of fertilizer N by not considering the plots that received mineral N fertilizer. The experiment was laid out in a randomized complete block design (RCBD) with three replicates with plot sizes of 6 m × 5 m and 6 m × 6 m in the clayey and sandy soil, respectively. Further details of the field experiment set-up can be retrieved from Chivenge et al. (2009) and Gentile et al. (2009). Three organic input types were considered in this study: high quality *Tithonia diversifolia* (C/N ratio: 13, Lignin: 8.9%; Polyphenols: 1.7%), intermediate quality *Calliandra calothyrsus* (13; 13%; 9.4%) and low quality *Zea mays* (59; 5.4%; 1.2%) (Gentile et al., 2011b). At the onset of long rains in each year, these organic inputs (leaves, petioles and small branches for *C. calothyrsus* in addition to stems for *T. diversifolia* and *Z. mays* stover) were collected and analyzed for dry matter and total C and N content. Dry matter and total C data were then used to determine the amount of

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