Genotypic variation in maize (Zea mays) influences rates of soil organic matter mineralisation and gross nitrification

New Phytologist

Research

Genotypic variation in maize (*Zea mays*) influences rates of soil organic matter mineralization and gross nitrification

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Received: *10 February 2021*
Accepted: *31 May 2021*

New Phytologist (2021) **231:** 2015–2028
doi: 10.1111/nph.17537

Key words: Genotype-by-management history interaction, genotypic variation, maize varieties, nitrification, no-tillage, plant–soil interactions, soil organic matter mineralization, southern Africa.

Summary

- Agricultural management practices that increase soil organic matter (SOM), such as no-tillage (NT) with crop residue retention, together with crop varieties best able to source nutrients from SOM, may help reverse soil degradation and improve soil nutrient supply and uptake by plants in low-input environments of tropical and subtropical areas.
- Here, we screened germplasm representing genetic diversity within tropical maize breeding programmes in relation to shaping SOM mineralization. Then we assessed effects of contrasting genotypes on nitrification rates, and genotype-by-management history interactions on these rates.
- SOM-C mineralization and gross nitrification rates varied under different maize genotypes. Cumulative SOM-C mineralization increased with root diameter but decreased with increasing root length. Strong influences of management history and interaction of maize genotype-by-management history on nitrification were observed. Overall, nitrification rates were higher in NT soil with residue retention.
- We propose that there is potential to exploit genotypic variation in traits associated with SOM mineralization and nitrification within breeding programmes. Root diameter and length could be used as proxies for root–soil interactions driving these processes. Development of maize varieties with enhanced ability to mineralize SOM combined with NT and residue retention to build/replenish SOM could be key to sustainable production.

Introduction

Soil degradation is a major threat to agricultural production (Tully *et al.*, 2015). This is particularly critical in tropical and subtropical regions (McKenzie *et al.*, 2015; Tully *et al.*, 2015). In sub-Saharan Africa (SSA), approximately 494 million ha of land (or >20% of land in most SSA countries) is affected by soil degradation, typically manifested in the form of soil erosion, soil organic matter (SOM) loss and nutrient depletion (McKenzie *et al.*, 2015). In southern Africa, specifically, maize (*Zea mays* L.) accounts for >75% of the area under cereal production (FAO, 2021), with yields amongst the lowest in the world (Cairns & Prasanna, 2018) and current climate variability has had a significant impact on recent production (Ray *et al.*, 2019). Restricted availability and use of fertilizer also is a key factor associated with this large yield gap (Cedrez *et al.*, 2020). This gap is largest in female-managed plots, with women applying less fertilizer to maize than male-managed plots (Burke *et al.*, 2018; Burke & Jayne, 2021). Ultimately, increasing fertilizer use in southern Africa will require changes in policy, infrastructure and local manufacturing (Cedrez *et al.*, 2020). Technologies such as maize varieties with tolerance to low nitrogen (N) conditions increase yields in this region, but unless higher concentrations of fertilizer are applied in the long term, they will further deplete soil inorganic N (Pasley *et al.*, 2020),thereby further degrading the soil and threatening food security for future generations in southern Africa.

In order to sustainably improve maize productivity in southern Africa, it is necessary to reverse soil degradation, for example through the build-up/replenishment of SOM (e.g. Amelung *et al.*, 2020). The physical, chemical and biological benefits of SOM accrual (Lal, 2015; Maron *et al.*, 2018) can confer greater resilience of cropping systems under climate change. Thus, crop management practices that enhance SOM are urgently needed. An example is no-tillage (NT) with retention of crop residues on the soil surface, as utilized in different forms of conservation agriculture (Thierfelder *et al.*, 2018), practiced on approximately 180 million ha of arable land worldwide with an increasing trend

(Kassam *et al.*, 2019). It has been shown that NT with residue retention gradually increases soil carbon (C), N and phosphorus (P) (compared with conventional tillage (CT) with crop residue removal) (Yang *et al.*, 2016), associated with replenishment of SOM. Selecting maize varieties in these systems that enhance SOM mineralization and N transformations could help ensure reliable and timely N supply from SOM and organic inputs (e.g. crop residues returned on soil surface) for plant uptake (Mwafulirwa *et al.*, 2017). However, there is limited knowledge of the abilities of maize varieties to foster SOM mineralization, or the potential for integrating these abilities into NT systems through balanced SOM replenishment and utilization (Janzen, 2006), thereby creating what we term a 'circular nutrient economy'.

Plant species and genotypes vary with respect to the degree to which they mediate SOM mineralization (Shahzad *et al.*, 2015; Mwafulirwa *et al.*, 2016; Yin *et al.*, 2019). For example, genotypes differ in amount and composition of rhizodeposits that shape rhizosphere microbial community structure (Paterson *et al.*, 2007) and increase microbial activities, including mineralization of SOM (i.e. rhizosphere priming effect; Kuzyakov *et al.*, 2000). There is significant potential for manipulating this root–soil interaction through breeding (Mwafulirwa *et al.*, 2016; Paterson & Mwafulirwa, 2021). A consequence of SOM mineralization is the mobilization of ammonium (NH_4^+) (following initial immobilization of N in microbial biomass and subsequent release via the microbial loop; Kuzyakov & Xu, 2013) and subsequent nitrification, both providing N available for plant uptake. Oxidation of ammonia (NH_3) to nitrite (NO_2^-), conferred by NH_3-oxidizing microbes, is typically the rate limiting step of nitrification (Wankel *et al.*, 2011), whereas rhizosphere bacterial communities play a key role in short-term changes in SOM dynamics (Haichar *et al.*, 2008; Fontaine *et al.*, 2011). Therefore, total bacterial abundance and the size of the NH_3-oxidizing groups (often measured by total bacterial 16S and ammonia monooxygenase (*amoA*) gene abundances, respectively) may reflect SOM mineralization and nitrification potentials in soil, affecting soil nutrient availability.

Traits such as root diameter, root biomass, root length, specific root length and root density define the nutrient absorption capacity of roots (McCormack *et al.*, 2015; Li *et al.*, 2016) and are known to affect rhizodeposition (Phillips *et al.*, 2011; Guyonnet *et al.*, 2018). There is a need to characterize genotypic variation in these traits, for example in maize, in the context of impacts on SOM and N dynamics, especially considering that root traits associated with mobilization of N from SOM will not necessarily be those that maximize fertilizer N use efficiency. For instance, in the global North, crop breeding under high-input conditions may have resulted in retention of root traits for capture of readily accessible mineral nutrients, such as from inorganic fertilizers, with loss of traits enabling efficient interactions with microbial communities mediating nutrient mobilization from SOM (Burton *et al.*, 2013; Huo *et al.*, 2017). However, maize breeding in southern Africa is focussed on selection under low-N conditions and there may be more genetic variation remaining within the primary gene pool for root-soil interactions. To explore this potential variation to control SOM and N cycling, it is necessary to (1) identify easily measurable traits with strong influence on root–soil interactions that can be used as proxies for these functional processes, (2) understand how plant traits, growth and soil process rates are affected by management practice and interactions with genotype, and (3) understand the temporal changes of these plant and soil parameters.

In this study, we first established genotypic variation in SOM-C mineralization within an association mapping panel selected to represent genetic diversity within tropical maize breeding programmes, and elucidated underpinning root traits associated with this function. We then examined nitrification rates and associated microbial gene abundances under maize genotypes selected for their varying abilities to mineralize SOM-C, and quantified genotype-by-management history (i.e. NT soil with crop residue retention on cropland vs CT soil with crop residue removal) interactions. We hypothesized that (1) genotypic variation associated with SOM-C mineralization and nitrification rates would be related to root traits, and (2) the influence of maize germplasm on nitrification rates and associated microbial gene abundances (bacterial 16S and *amoA*) would vary between soils with different management history.

Materials and Methods

Soil

Two soils were collected from the Domboshawa Research Centre (lat. −17.603°S, long. 31.604°E; 1545 m above sea level) in the highveld of Zimbabwe. The soils are classified as *Lixisols* (Mapfumo *et al.*, 2007). One soil was collected from an on-station trial that has been running since 2012 with contrasting soil management practices, from within plots with no-tillage (NT) and crop residue retention. The trial is planted with different maize varieties, fertilized with 83 kg nitrogen (N) ha^{-1}, 28 kg phosphorus pentoxide (P_2O_5) ha^{-1} and 14 kg potassium oxide (K_2O) ha^{-1}, supplied as basal dressing and topdressing. The second soil was collected from a conventionally managed field, with soil tillage (CT) and crop residue removal, bordering the NT plots. Approximately 10 soil subsamples (0–10 cm soil depth) were taken at random within each plot for NT soil and from adjacent locations in the bordering field for CT soil. The subsamples for each soil were thoroughly mixed into a composite sample and sieved through a 4-mm mesh on-site. The sieved soil samples then were packed in cooler boxes and transported to Aberdeen, UK, where they were stored at 4°C until experiment setup.

As general soil characterization, the CT and NT soils had silt + clay fractions of 16% and 20%, and sand fractions of 84% and 80%, respectively. Total carbon (C) concentration was 3.0 and 4.7 mg g^{-1} soil, total nitrogen (N) concentration was 0.2 and 0.4 mg g^{-1} soil, ammonium (NH_4^+)-N was 2.6 and 5.4 μg N g^{-1} soil, and nitrate (NO_3^-)-N was 10.0 and 1.7 μg N g^{-1} soil for CT and NT soils, respectively. Soil pH (H_2O) was 4.8 and 5.1, cation exchange capacity was 1.0 and 1.6 meq 100 g^{-1} soil, and electrical conductivity was 94 and 248 μS cm^{-1} for CT and NT soils, respectively.

Maize germplasm

Ninety-seven maize inbred lines were selected from the Drought Tolerant Maize for Africa association mapping panel (Wen *et al.*, 2011). This panel was developed to represent genetic diversity within the International Maize and Wheat Improvement Center (CIMMYT) and International Institute of Tropical Agriculture (IITA) maize breeding programs. These 97 lines were selected based on seed availability, seed quality and yield performance under drought, low-N, and combined drought and heat stress (Cairns *et al.*, 2013) from nine breeding programmes (Table 1). Information on the pedigrees of all of the lines is presented in Supporting information Table S1. Eight medium maturing commercial maize hybrids in Zimbabwe (SC513, SC633, Pan53, Pristine 601, ZAP55, ZAP61, PGS61 and 30G19) were included. These hybrids are grown widely in Zimbabwe. Seeds were imported to Aberdeen, UK, where they were stored at 4°C until sowing.

Experiment 1: Maize germplasm impacts on soil organic matter (SOM) mineralization

Set-up and measurements A screen of the 97 inbred lines and eight hybrids (i.e. 105 genotypes) was performed utilizing the CT soil. The soil was packed in microcosms (22.5 × 5.5 cm) to a bulk density of 1.44 g cm^{-3} to represent field bulk density and adjusted to 65% water holding capacity. A 5-cm layer of previously muffle-furnaced sand (0% organic matter) was packed to the bottom of each microcosm before packing the soil, as a strategy to reduce the quantity of soil to import. The systems were left to stabilize over a period of one week. After this initial soil stabilization period, plastic chambers made from syringe tubes (40 ml headspace) were inserted to 2.5 cm depth into the middle of microcosms for trapping CO_2 efflux from soil. The gas chambers were fitted with inlet and outlet stopper end tubes for controlled gas flow. Systems were maintained at 22°C and 70% relative humidity within a plant growth chamber (Mwafulirwa *et al.*, 2016). Each microcosm was sown with one plant including an unplanted control treatment. Plants were grown over 29 d without fertilizer addition. Owing to the large number of genotypes, space limitation and practicability to manage the experiment, treatments were replicated two to four times in a sequential randomized block design. Two hybrids and the control treatment were included in all blocks. Soil water content was maintained by adding deionized water on a mass basis twice a week. A 12-h daily photoperiod was set with 512 µmol m^{-2} s^{-1} photosynthetic active radiation (PAR) within the chamber. Continuous labelling of plants with ^{13}C-CO_2 started at the seedling growth stage, 1 wk after sowing. This was achieved by passing a continuous flow of ^{13}C-enriched CO_2 (20 atom% ^{13}C) through the plant growth chamber over the experimental period (Mwafulirwa *et al.*, 2016). CO_2 concentration, including ^{12}C-CO_2 and ^{13}C-CO_2, in the plant growth chamber was monitored multiple times each week.

Soil CO_2 fluxes were sampled at 16, 23 and 29 d after planting (DAP). To collect samples, the gas collection chambers were flushed with CO_2-free air for three minutes, obtaining outlet airflow <10 µl l^{-1} CO_2 concentration, then sealed for 40 min with stopper end tubes to accumulate soil CO_2 efflux in the headspace. Thereafter, approximately 25 ml air was sampled from the headspace with a gas syringe connected to the outlet tubing. Gas chambers remained open except during collection of soil CO_2 efflux. The sampled air was used to determine the CO_2 concentration and ^{12}C : ^{13}C ratios as described in Mwafulirwa *et al.* (2016). Calculation of total C respired for each treatment per sampling point was achieved using the CO_2-C concentration values and the soil under the surface area covered by the syringe tube. The total CO_2-C was partitioned to two component sources (SOM- and maize root-derived C) based on their $\delta^{13}C$ signatures. The maize root-derived C and SOM-derived C were determined according to Garcia-Pausas & Paterson (2011)and Mwafulirwa *et al.* (2016).

Plants were harvested as root and shoot fractions. Shoots were harvested by cutting at the soil surface, and then were freeze-dried. Roots were washed free of soil in deionized water and stored fresh in 50% ethanol at 4°C before analysis for average root diameter and total root length. For this, fresh roots were carefully spread onto a clear-bottomed reservoir filled with water to slightly cover the roots. Then, the roots were scanned on an Expression 1640XL flatbed scanner (Epson, London, UK), images were cropped to remove the border created by the reservoir, and total root length and average root diameter were measured using WINRHIZO software (Regent Instruments, Quebec City, Canada) (George *et al.*, 2014). Thereafter, roots were washed in deionized water and freeze-dried.

Table 1 Origin of maize lines used in Expt 1.

Breeding programme	Target of breeding programme	Number of lines
Zimbabwe	Drought and low N stress tolerance	31
Nigeria	Drought and striga tolerance	3
Colombia	Soil acidity	11
Highland	Yield potential	3
Entomology	Pest resistance	7
Subtropical	Yield potential	9
Tropical	Yield potential	19
Physiology	Drought and low N stress tolerance	14
Seed companies*	–	8

Cairns *et al*. (2013) and Wen *et al*. (2011) provide more detailed information of the maize lines, breeding programmes and breeding targets.
N, nitrogen.
*Hybrid varieties (from commercial seed companies) adapted to local conditions were included.

Experiment 2: Impacts of maize genotype and soil management history on nitrification

Setup and measurements Five maize inbred lines ((A.T.Z.T.R.L.BA90 5-3-3P-1P-4P-2P-1-1-1-B x G9B C0 R.L.23-1P-2P-3-2P-3-2P-1P-B-B-B)-B-76TL-1-2-4 (ATZTRI),

CL-G1837=G18SeqC2-F141-2-2-1-1-1-2-##-2 (CL-G18), (CML444/CML395//DTPWC8F31-1-1-2-2-BB)-4-2-2-2-2 (CML444x), La Posta Seq C7-F64-2-6-2-2 (LPSF64) and 95S43SR HG"A"-94-1-1-1 (95S43S)) and two hybrids (SC513 and 30G19), selected based on the range of variation in cumulative SOM-C mineralization in Expt 1 (Table 2), were used utilizing both CT and NT soils. The microcosm system, planting, growth conditions and growth period were as described for Expt 1, with the following exceptions: (1) microcosms were packed with soil only without a layer of muffle-furnaced sand, (2) NT soil was packed to bulk density of 1.38 g cm^{-3}, compared to 1.44 g cm^{-3} for CT soil, to reflect field conditions, (3) gas chambers and ^{13}C-CO_2 labelling were not used, and (4) each microcosm (planted or unplanted) received ^{15}N-enriched fertilizer ($^{14}NH_4{}^{15}NO_3$, 10 atom% ^{15}N), equivalent to 6 g N m^{-2} or 60 kg N ha^{-1}, at 14 DAP. Microcosms were arranged in a randomized complete block design with four replications, with two microcosms prepared per replicate to allow for two destructive plant and soil harvests. The fertilizer was mixed with deionized water during a watering event and spread onto the soil surface in droplets, ensuring distribution of the fertilizer within the soil. Four extra replicates of unplanted CT and NT soils also were fertilized in the same way and harvested within 15 min for determination of initial NO_3^--N concentrations and their ^{15}N-enrichment.

Plant root and shoot biomass were measured as described in Expt 1, at 23 and 29 DAP, with roots and shoots freeze-dried. Following plant harvests, the soil was thoroughly mixed by hand, and subsamples were taken and immediately stored at 4°C for determination of mineral N concentration and, in turn, gross nitrification by ^{15}N isotope pool dilution after the harvesting was completed. Further soil subsamples were taken and stored at −80°C for DNA extraction. Mineral N (NH_4^+-N and NO_3^--N) concentrations of the harvested soil samples were determined using an autoanalyzer (Traaks 800; Technicon, Saskatoon, Canada) following extraction of 10 g fresh soil with 50 ml of 2 M KCl solution. The remaining 2 M KCl soil extracts were stored frozen at −20°C until preparation for analysis of ^{15}N-enrichment, using a microdiffusion technique described by Goerges & Dittert (1998) recovering NO_3^--N. ^{15}N-enrichment of the recovered NO_3^--N was determined on an isotope-ratio mass spectrometer (IRMS; Sercon, Crewe, UK). Samples taken at 15 min after fertilizer application and 23 DAP were used for calculating the gross nitrification rate, according to Hart *et al.* (1994). The calculations are described in Methods S1.

Total DNA was extracted from 1 g soil using a phenol chloroform method as described in Deng *et al.* (2010) with the addition of a mutated DNA reference fragment to the lysis buffer. This allowed relative real-time assessment of gene copy count as described in Daniell *et al.* (2012), controlling for extraction efficiency and variable levels of inhibitors between treatments. Briefly, soil was reduced to a slurry in the extraction buffer before bead-beating with 1-mm steel beads and treatment with phenol chloroform and chloroform before precipitation with isopropanol and sodium acetate. Re-suspended pellets then were further purified through polyvinylpolypyrrolidone (PVPP). This method was selected as proprietary kits had performed poorly in preliminary experiments with soils from this system. Relative real-time PCR targeted the reference fragment using Mut-F and Mut-R primers (CCTACGGGAGGCAGGTC and ATTACCGCGGCTGC ACC; Daniell *et al.*, 2012) and 16S gene (CCTACGGGAGGC AGCAG and ATTACCGCGGCTGCTGG; Muyzer *et al.*, 1993) as described in Daniell *et al.* (2012), as well as the bacterial ammonium monooxygenase gene using amA1F (GGGGTTTCTAC TGGTGGT) and amoA2R (CCCCTCKGSAAAGCCTTCTTC) primers (Rotthauwe *et al.*, 1997).

Recent research has demonstrated that root traits and rhizosphere properties, including recruitment of microbiomes, during the seedling growth stage (*c.* 2–4 wk after planting) are predictive of relative rooting and rhizosphere characteristics in mature plants (e.g. Thomas *et al.*, 2016).

Statistical analyses

Univariate analyses were performed using the software GenStat v.18 (VSN International Ltd, Hemel Hempstead, UK). In Expt 1, repeated-measures ANOVA was used to test the effects of maize genotype and sampling date on root- and SOM-derived CO_2-C

Table 2 Selected maize lines used in Expt 2.

Entry number	Breeding programme	Germplasm	Short code	Pedigree	Cumulative SOM-derived CO_2-C (μg C g^{-1} soil)	Rank
211	Tropical	Line	CL-G18	CL-G1837=G18SeqC2-F141-2-2-1-1-1-2-##-2	29.72 ± 9.78	1
24	Zimbabwe	Line	CML444x	[CML444/CML395//DTPWC8F31-1-1-2-2-BB]-4-2-2-2-2	21.74 ± 5.15	13
–	Seedco*	Hybrid	SC513	–	20.42 ± 2.29	27
–	Physiology	Line	LPSF64	La Posta Seq C7-F64-2-6-2-2	17.45 ± 0.95	63
80	Highland		ATZTRI	(A.T.Z.T.R.L.BA90 5-3-3P-1P-4P-2P-1-1-1-B x G9B C0 R.L.23-1P-2P-3-2P-3-2P-1P-B-B-B)-B-76TL-1-2-4	16.99 ± 0.00	70
–	Pioneer*	Hybrid	30G19	–	16.19 ± 0.28	79
135	Subtropical	Line	95S43S	95S43SR HG"A"-94-1-1-1	12.37 ± 2.63	105

Selection was based on ranking of 105 maize lines and varieties across the range of variation in soil organic matter (SOM) carbon (C) mineralization measured in Expt 1, as SOM-derived surface soil CO_2-C efflux (mean ± 1SEM). Cairns *et al*. (2013) and Wen *et al*. (2011) provide more detailed information of the maize lines.
*Commercial seed companies.

efflux rates, with maize genotype as the fixed factor and sampling date as the repeated factor. One-way unbalanced treatment structure (general linear model) was used to assess the effects of maize genotype on cumulative root-derived C mineralization, cumulative SOM-C mineralization, root biomass, shoot biomass, root-to-shoot ratio, root diameter, root length and specific root length. In Expt 2, the effects of maize genotype, soil management history and sampling date on root biomass, shoot biomass, soil NH_4^+-N, soil NO_3^--N and bacterial 16S gene copy number in soil were assessed using three-way ANOVA. In addition, two-way ANOVA was used to evaluate the effects of maize genotype and soil management history on gross nitrification, and maize genotype and sampling date on *amoA* gene copy number in soil. For treatments with three or more levels (i.e. maize genotype in both experiments and sampling date in Expt 1), where statistically significant ($P < 0.05$) effects were found, the least significant difference (LSD) test was used to assess differences between individual means.

In Expt 1, the effects of root biomass, shoot biomass, root-to-shoot ratio, root diameter, root length and specific root length on cumulative root-derived C mineralization or cumulative SOM-C mineralization were tested using linear regressions (paired relationships). Linear regression also was used to assess the relationship between cumulative root-derived C mineralization and cumulative SOM-C mineralization. Furthermore, principal component analysis (PCA) was used to ordinate (eigenvalue scale) the samples to evaluate their associations with the measured traits of root biomass, shoot biomass, root-to-shoot ratio, root diameter, root length, specific root length, cumulative root-derived C mineralization and cumulative SOM-C mineralization. Because these variables were measured in different units, PCA was performed applying a correlation matrix to normalize data. In Expt 2, paired relationships between variables (root biomass, shoot biomass, NH_4^+-N concentration, NO_3^--N concentration, bacterial 16S gene copy number, bacterial *amoA* gene copy number and gross nitrification) also were evaluated using linear regressions. Furthermore, regression analysis was used to investigate relationships between individual root morphological traits or SOM-C mineralization measured in Expt 1 and gross nitrification measured in Expt 2 for corresponding maize genotypes. All regressions were considered significant at $\alpha = 0.05$. These multivariate analyses were performed using the free software PAST v.4.03 (Palaeontological Association, Oslo, Norway).

Results

Soil CO_2-C efflux and C mineralization in Expt 1

By 29 DAP there were significant ($P < 0.05$) differences among maize genotypes in cumulative SOM-C mineralized and cumulative root-derived C mineralized, measured as surface soil CO_2-C efflux (Tables 2, S1). Cumulative SOM-C mineralized varied from 12.4 to 29.7 μg C g^{-1} soil, whereas cumulative root-derived C mineralized varied from 0.6 to 53.6 μg C g^{-1} soil. Lines CL-G1837=G18SeqC2-F141-2-2-1-1-1-2-##-2 (CL-G18) and DTPWC9-F24-4-3-1, derived from the tropical and physiology breeding programmes in Mexico, were associated with the highest cumulative SOM-C mineralization and cumulative root-derived C mineralization, respectively.

There also was genotypic variation ($P < 0.05$) in SOM- and root-derived soil CO_2-C efflux rates at 16, 23 and 29 DAP, with no significant interaction of maize genotype-by-time. Rates of root-derived CO_2-C efflux increased over time (Table S2), in line with plant growth increasing root inputs to soil. By contrast, rates of SOM-derived CO_2-C efflux in planted and unplanted soil decreased over time, consistent with low fertility soil and depletion of the available SOM stock over the course of the experiment (Table S3). Nonetheless, rates of SOM-derived CO_2-C efflux in planted soils remained generally higher ($P < 0.05$) compared to the unplanted treatment, indicating a positive priming effects of maize genotypes on SOM throughout the experimental period.

Plant characteristics

In Expt 1, there was significant ($P < 0.05$) genotypic variation in root and shoot biomass, measured at 29 DAP. Root biomass varied from 0.03 to 0.4 g with an average of 0.2 g, whereas shoot biomass varied from 0.1 to 0.8 g with an average of 0.4 g (Table S1). However, there were no significant differences in root-to-shoot ratio among genotypes. Genotypic variation ($P < 0.05$) also was observed for average root diameter, root length and specific root length, ranging from 0.4 to 0.6 mm (0.5 mm average), 3.7 to 21.1 m (14.8 m average) and 40.3 to 175.5 m g^{-1} root biomass (81.5 m g^{-1} root biomass average), respectively (Table S1).

Likewise, in Expt 2 there were significant ($P < 0.05$) differences in root and shoot biomass among genotypes (Table 3; Fig. S1a, b). The overall range of root and shoot biomass was 0.1–0.8 g (0.4 g average) and 0.2–1.0 g (0.4 g average), respectively, indicating improved growth performance with fertilizer application, relative to Expt 1. In Expt 2, the NT soil with residue retention increased ($P < 0.05$) shoot biomass (0.5 ± 0.1 g for NT soil, 0.4 ± 0.03 g for CT soil) but did not affect root biomass (Table 3). Root biomass increased ($P < 0.05$) from 0.3 ± 0.03 g to 0.5 ± 0.04 g, measured at 23 and 29 DAP, respectively. There also was a significant ($P < 0.05$) increase in shoot biomass with time, with a significant interaction effect of genotype-by-time driven by greater separations in high biomass genotypes (Table 3; Fig. S1c).

Relationships between C mineralization and plant characteristics

Linear regression analysis in Expt 1 showed that cumulative SOM-C mineralization increased with average root diameter ($P < 0.0001$; Fig. 1a) and decreased with increasing root length ($P < 0.0001$; Fig. 1b) or specific root length ($P = 0.027$; Fig. 1c). Specific root length increased with decreasing average root diameter ($P < 0.0001$; Fig. 1d). By contrast, root biomass and root-to-shoot ratio did not significantly affect cumulative SOM-C mineralization (data not shown). A positive relationship was observed between cumulative SOM-C mineralization and cumulative root-

Table 3 Variance analysis for maize plant traits and soil parameters measured in Expt 2.

	Plant biomass *P*-values			Soil characteristics and gross nitrification *P*-values					
Source of variation	df	Root biomass (g)	Shoot biomass (g)	df	NH_4^+-N (μg N g^{-1} soil)	NO_3^--N (μg N g^{-1} soil)	16S (gene copies g^{-1} soil)	*amoA* (gene copies g^{-1} soil*)	Gross nitrification (μg N g^{-1} soil d^{-1})†
Maize genotype	6	**<0.001**	**<0.001**	7	**<0.001**	**<0.001**	**<0.001**	**0.025**	**0.017**
Management history	1	0.057	**0.026**	1	**<0.001**	**<0.001**	0.117	–	**<0.001**
Harvest time	1	**<0.001**	**<0.001**	1	**<0.001**	**<0.001**	0.607	0.997	–
Genotype × management history	6	0.955	0.261	7	**<0.001**	**<0.001**	0.624	–	**0.022**
Genotype × time	6	0.206	**0.047**	7	**<0.001**	0.475	**0.007**	0.418	–
Management history × time	1	0.500	0.308	1	**<0.001**	0.187	0.204	–	–
Genotype × management history × time	6	0.603	0.454	7	0.098	0.461	0.108	–	–

Significant *P*-values ($P < 0.05$) are shown in bold. df, degrees of freedom.
NH_4^+-N, ammonium-nitrogen; NO_3^-N, nitrate-nitrogen.
**amoA* was detected only in the no-tillage soil with crop residue retention, as it was below the detection limit in the conventional tillage soil with residue removal.
†Gross nitrification was measured at a single time point, i.e. at the first harvest time (23 d after planting).

derived C mineralization ($P = 0.0003$; Fig. S2a). Cumulative root-derived C mineralization was positively related to shoot biomass ($P < 0.0001$; Fig. S2b), root biomass ($P < 0.0001$; Fig. S2c) and root length ($P < 0.0001$; Fig. S2d), and negatively related to specific root length ($P < 0.0001$, Fig. S2e), but was not related to root-to-shoot ratio and average root diameter (data not shown).

The PCA plot (Fig. 2) shows an overview of the relationships measured in Expt 1. Based on the variation of SOM-C mineralization, seven maize genotypes (Table 2) were selected to assess microbial community size and nitrification in Expt 2. These genotypes are distributed over the PCA plot ordination space, associated with all observed variables, and fall within the 95% ellipse except for one score (Fig. 2). This indicates not only that the selection approach was valid for our stated purpose, but also that the selected genotypes are representative of the variation within the germplasm population for multiple variables.

Nitrification and soil characteristics in Expt 2

Overall, gross nitrification rates were increased ($P < 0.05$) by maize plants and the NT soil with residue retention (compared to unplanted soil and CT soil with residue removal, respectively), with a significant interaction between maize genotype and soil management history (Table 3; Fig. 3a). Maize genotype had no effect on gross nitrification in CT soil whereas soil management history did not significantly affect gross nitrification in unplanted soil and the hybrid 30G19 (Fig. 3a), driving the significant interaction. Compared with the maize genotype effect ($P = 0.017$, Table 3), soil management history had a strong effect ($P < 0.001$; Table 3) on gross nitrification.

The concentrations of NH_4^+-N and NO_3^--N in soil were affected ($P < 0.05$) by maize genotype, soil management history and time of sampling (Table 3). Soil NH_4^+-N and NO_3^--N concentrations were highest in unplanted soil followed by the line ATZTRI and lowest in the hybrids (SC513 and 30G19) (Fig. S1d,e), with both N forms decreasing with time (1.9 ± 0.3 and 20.8 ± 2 μg N g^{-1} soil for NH_4^+-N and NO_3-N, respectively, at 23 DAP, and 1.0 ± 0.3 and 12.8 ± 2.0 μg N g^{-1} soil for NH_4^+-N and NO_3-N, respectively, at 29 DAP). Compared with the CT soil with residue removal, the NT soil with residue retention decreased NH_4^+-N concentration (2.3 ± 0.4 and 0.6 ± 0.1 μg N g^{-1} soil for CT soil and NT soil, respectively) but increased NO_3^--N concentration (9.1 ± 1.3 and 25.2 ± 2.3 μg N g^{-1} soil for CT soil and NT soil, respectively). The two-way interaction of maize genotype-by-soil management history affected both NH_4^+-N and NO_3^--N concentrations (Table 3; Fig. 4). This was driven by the distinct separation of CT and NT soils for both N forms in unplanted soil and maize genotypes except line ATZTRI for NH_4^+-N and hybrid 30G19 for NO_3^--N. Two-way interactions of maize genotype-by-time and soil management history-by-time were significant for soil NH_4^+-N but not NO_3^--N, whereas the three-way interaction of maize genotype-by-soil management history-by-time was not significant for any of the N forms (Table 3).

Bacterial 16S gene copy number was significantly ($P < 0.001$) affected by maize genotype, but not soil management history or time but with a significant ($P < 0.05$) interaction between genotype and time (Table 3). This was driven by an increase in 16S copy number in 30G19 between days 23 and 29, driving the significantly higher overall gene copy count in this hybrid (Fig. 4c). The bacterial *amoA* gene was not detected in CT soil. However, in NT soil bacterial *amoA* gene copy number also varied ($P < 0.05$) among the maize genotypes with testcross lines typically showing lower *amoA* gene copy counts than the hybrids or the unplanted soil (Fig. S1f). Time of sampling and the interaction between genotype and time were not significant for *amoA* gene copy number (Table 3).

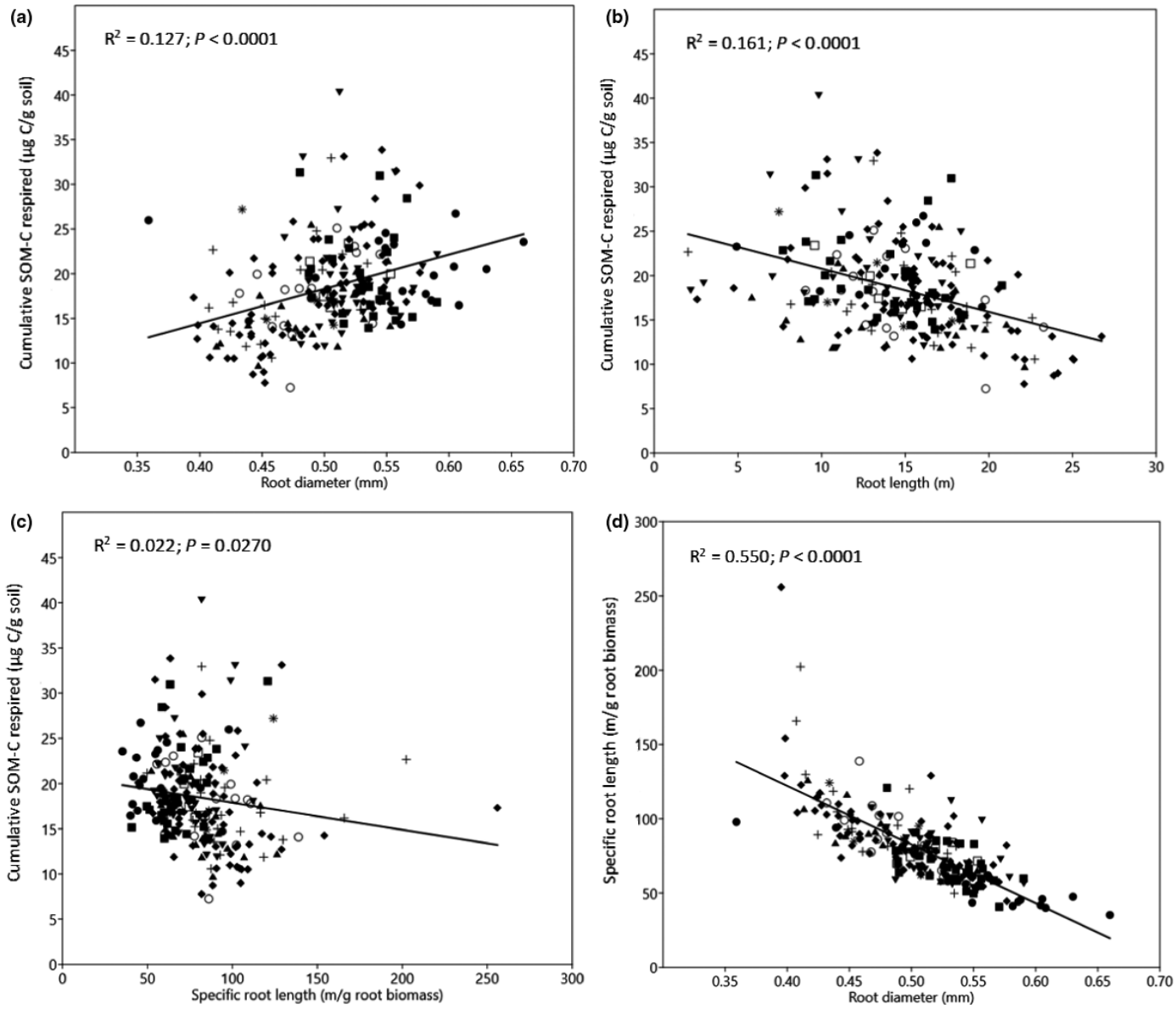

Fig. 1 Significant ($P < 0.05$) relationships between cumulative soil organic matter (SOM) carbon (C) mineralized, measured as surface soil CO_2-C efflux, and maize root diameter (a), root length (b) and specific root length (c), and the relationship between specific root length and root diameter (d) in Expt 1. Symbols represent different maize germplasm sources/breeding programmes: plus, Colombia; open circle, Entomology; star, Highland; dot, Hybrids; open square, Nigeria; filled square, Physiology; filled triangle, Subtropical; filled inverted triangle, Tropical; filled diamond, Zimbabwe.

Regression analysis, in Expt 2, showed that gross nitrification was not related to mineral N (NH_4^+-N and NO_3^--N) concentration or bacterial 16S and *amoA* gene copy numbers in soil, nor to maize plant root and shoot biomass (data not shown). Likewise, regression analysis showed that gross nitrification, measured in Expt 2, was not related to root morphological traits (i.e. root diameter, root length and specific root length) measured in Expt 1 for corresponding maize genotypes (data not shown).

Relationship between SOM mineralization and nitrification

Regression analysis showed no significant relationship between SOM-C mineralization and gross nitrification when measured in CT soil (data not shown) for corresponding genotypes and time. However, there was a significant relationship when SOM-C mineralization measured in Expt 1 was considered relative to gross nitrification in NT soil for corresponding genotypes and time (Fig. 3b).

Discussion

Genetic variation exists in ability of maize to mineralize SOM

Our results show genotypic variation in the ability of maize plants to influence soil organic matter (SOM) mineralization. The largest cumulative SOM-carbon (C) mineralization from soil planted with the tropical line CL-G18, 29 d after planting

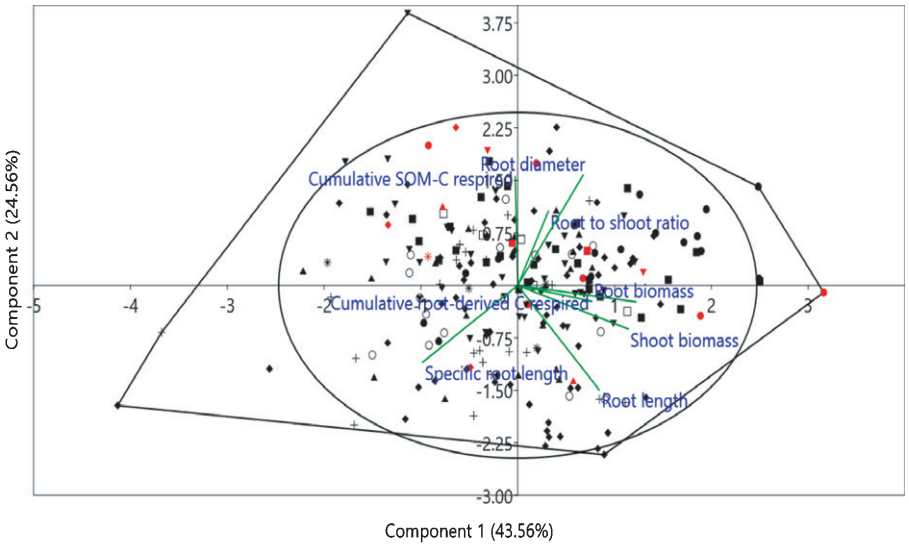

Fig. 2 Principal component analysis (PCA) ordination of the distribution of maize genotypes based on plant traits and root-derived carbon (C) and soil organic matter (SOM) C mineralized. Symbols represent different maize germplasm sources: plus, Colombia; open circle, Entomology; star, Highland; dot, Hybrids; open square, Nigeria; filled square, Physiology; filled triangle, Subtropical; filled inverted triangle, Tropical; filled diamond, Zimbabwe. Red symbols of the corresponding germplasm source show scores of the selected individual maize genotypes. Solid green lines show the loading (vectors) of the measured traits. The 95% ellipse is shown over the convex hull.

(DAP), was 2.4-fold greater than the lowest cumulative SOM-C mineralization associated with the subtropical line 95S43S. SOM-C mineralization was not directly related to root biomass, but was more closely linked to other root traits. In particular, we demonstrate for the first time that SOM-C mineralization increased with maize root diameter and was less under genotypes having longer, finer root systems.

It is possible that roots with larger diameter supported greater rhizodeposit quantities, as a result of their enhanced assimilate transport capacity (McCormack *et al.*, 2015), and that this was coupled to enhanced microbial activity in the rhizosphere (Uren, 2007), increasing SOM mineralization (Jackson *et al.*, 2019). That plants with short, thick roots may have been associated with greater root exudation could be a plant strategy to enhance microbially mediated nutrient mobilization where root growth/elongation is sacrificed under resource limitation (Brunner *et al.*, 2015). Positive relationships between C-substrate supply via root exudation and SOM priming also may be driven by microbial nitrogen (N)-demand (Dijkstra *et al.*, 2013) as a consequence of high C : N ratio of root-derived C-flow. Indeed, a number of studies have demonstrated that increased microbial N-demand can result in specific mobilization of N-rich components of SOM (i.e. N-mining; Craine *et al.*, 2007), a process that may be particularly important in the context of supporting crop N-demand from organic inputs (e.g. crop residues). These assumptions are in line with the low fertility soil used in this study and the positive priming effect observed throughout the experimental period. A study by Kumar *et al.* (2016), using soil cultivated with a modern maize variety, showed increase of SOM-C mineralization by ≤126% without N-fertilization. Thus, plant and microbially mediated SOM decomposition could play a beneficial role supporting plant productivity by unlocking nutrients bound in SOM or organic inputs over the crop growing period. However, alone this could ultimately further deplete SOM. Therefore, the declining but still positive SOM priming effect observed over the course of our study as affected by maize genotypes calls for complimentary SOM building measures in this soil, as we discuss in the next section. There also is a need to assess possible physiological trade-offs between short, thick roots with greater exudation for exploitation of SOM sources and deeper roots for drought tolerance.

Larger root diameter and lower specific root length also are common features of mycorrhizal plants. This results from enlargement of the root cortex with extra cell layers to accommodate the fungal structures (Fusconi *et al.*, 1999; Dreyer *et al.*, 2014) with lower biomass investment in root development in mycorrhizal plants (Marschner & Dell, 1994). Although mycorrhizal fungi found in many crop plants do not act as saprotrophs, they can access nutrients bound in SOM, and thereby promote its decomposition, through several strategies, mainly direct enzymatic breakdown, oxidation mechanisms and stimulation of heterotrophic microbes through provision of plant-derived C to the rhizosphere (Frey, 2019). The latter may be particularly important in maize, as arbuscular mycorrhizal fungi do not have the capacity for direct enzymatic breakdown of SOM (Frey, 2019).

In addition, we observed exceptions to the overall positive relationship between SOM-C mineralization and root diameter, in that hybrids had the largest root diameter but did not induce highest cumulative SOM-C mineralization (as compared with lines from the physiology breeding program which overall had large diameter and high cumulative SOM-C mineralization). Likewise, most genotypes with the largest cumulative root-derived CO_2 efflux (from root respiration and microbial mineralization of rhizodeposits) did not have higher cumulative SOM-C mineralization. This strongly suggests that plant factors besides quantity of root C deposition, such as intraspecies variation in rhizodeposit composition (that can differentially promote or inhibit microbial activity; Paterson *et al.*, 2007) or mycorrhizal symbiosis (Frey, 2019), likely also influenced SOM mineralization.

Genotype by soil management history interactions on nitrification, and the relationship between SOM mineralization and nitrification

The effects of plants, soil management history and microbial properties on SOM-C mineralization vs gross nitrification are

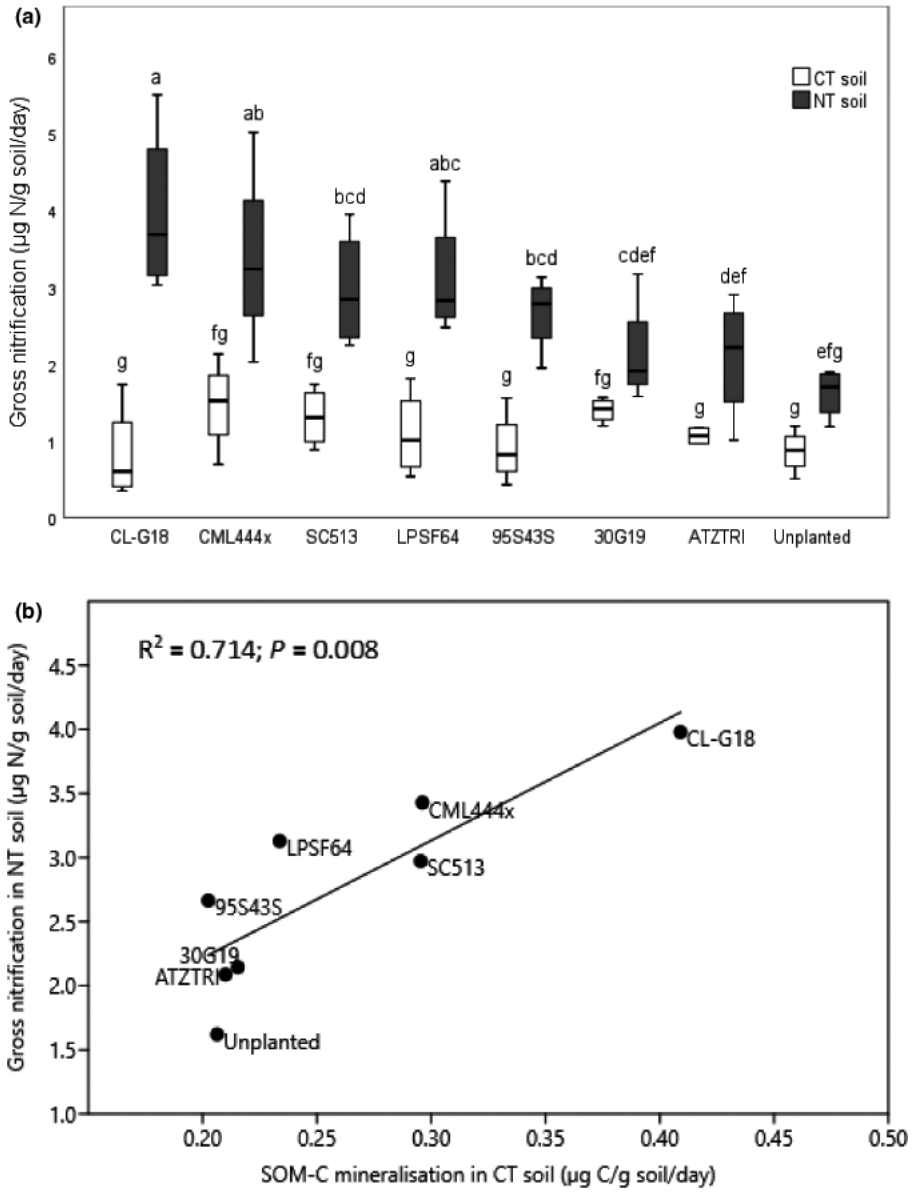

Fig. 3 Interactive effects of maize genotype and soil management history on gross nitrification rates in conventional tillage (CT) soil with crop residue removal and no-tillage (NT) soil with residue retention (a) and relationship between soil organic matter (SOM) carbon (C) mineralization in CT soil vs gross nitrification in NT soil (b). Letters indicate significant ($P < 0.05$) differences in gross nitrification between maize genotypes or soil management history. The horizontal line in a box plot indicates the median and the box indicates the upper and lower quartiles, with the vertical lines representing the minimum and maximum values.

summarized in Fig. 5. Increasing context-specific understanding of these effects will be vital for designing more sustainable cropping systems.

Studies indicate that variations in nitrification rate exist between plant genotypes (e.g. in ryegrass, clover or forage rape; Bowatte *et al.*, 2016) and management practices (e.g. Bi *et al.*, 2017). However, there is lack of understanding of plant genotype-by-management interactions on nitrification. In this study, gross nitrification was higher in the no-tillage (NT) soil with residue retention, with genotypes differentially affecting gross nitrification in the NT soil but not in the conventional tillage (CT) soil. It is likely that NT with residue retention history increased nitrification by modifying the soil environment, providing a source of labile SOM to microbial communities and, in turn, maintaining the supply of ammonium (NH_4^+) (resulting from decomposition of plant residues) for nitrification. That NH_4^+-N concentration was lower in NT soil compared to CT soil could be a consequence of the greater nitrification in the NT soil with residue retention depleting NH_4^+ in soil over the study period, consistent with the observed high concentration of NO_3^- in this soil compared to the CT soil. This also is consistent with bacterial *amoA* detected in NT soil, but this was below the detection limit in CT soil, highlighting the importance of NT and residue management for the abundance of nitrifier communities (e.g. as hypothesized above). This supports our second hypothesis that the influence of maize germplasm on nitrification rates and associated microbial gene abundances would vary as a function of soil management history. However, bacterial 16S gene abundance was not affected by soil management history, consistent with Ng *et al.* (2012) who found that NT did not alter bacterial abundance during a very early vegetative stage of wheat growth.

Notably, there was a strong relationship between genotypic effects on SOM-C mineralization in CT soil (Expt 1) and gross nitrification in NT soil (Expt 2). As SOM-C mineralization and

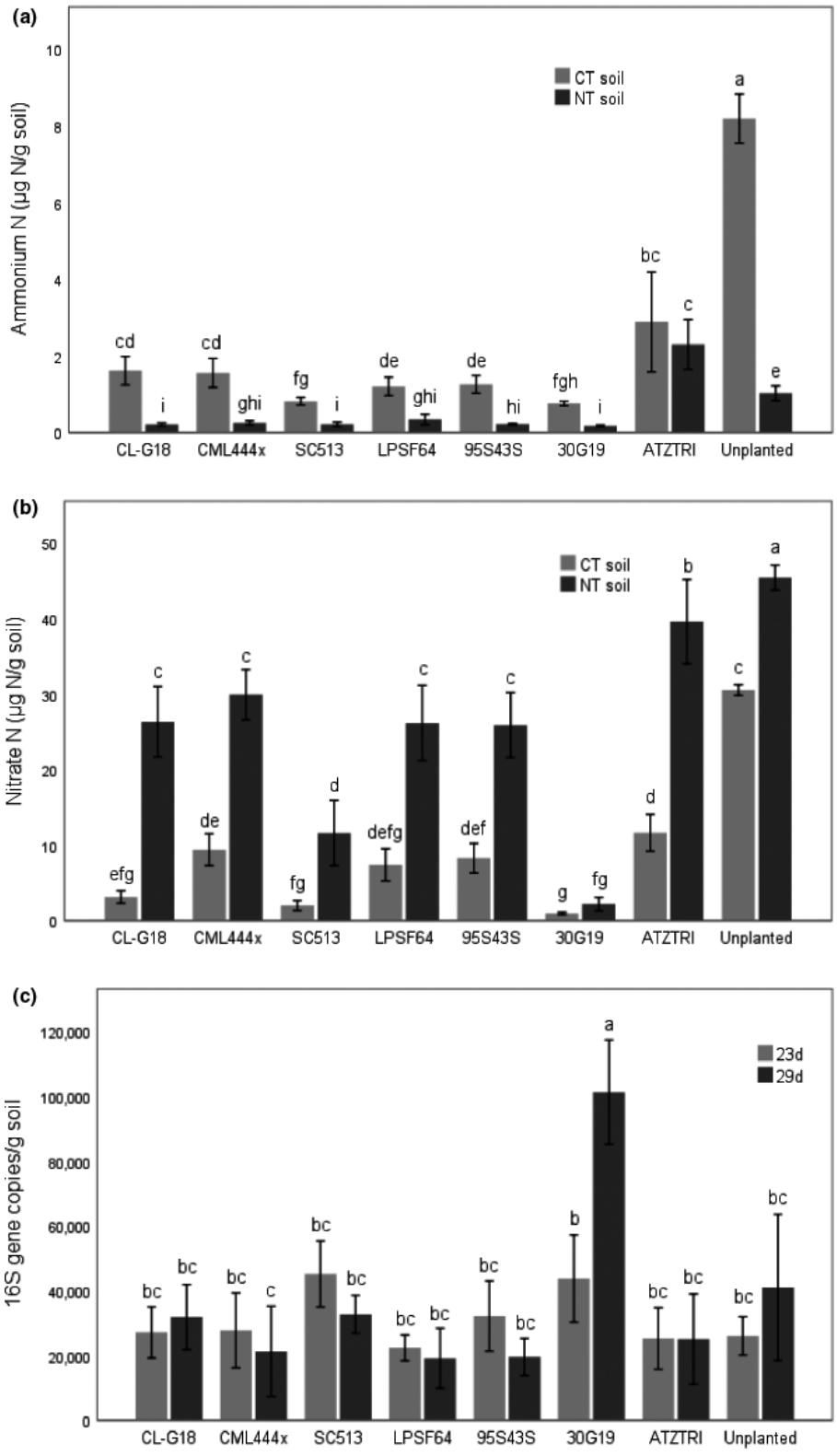

Fig. 4 Interactive effects of maize genotype and soil management history (conventional tillage (CT) with crop residue removal vs no-tillage (NT) with residue retention) on soil mineral nitrogen (N) (ammonium (NH_4^+)-N and nitrate (NO_3^-)-N: (a) and (b), respectively), and maize genotype and time of sampling on 16S gene copy number in soil (c) in Expt 2. Letters indicate significant ($P < 0.05$) differences between treatments. Bars show ±1 SEM.

gross nitrification were measured using soils with contrasting management history, care should be taken to derive conclusions based on this relationship. However, this relationship supports the positive impact of residue retention on N-supply to the total plant-available N pool. Moore *et al.* (2020) showed that in soil environments dominated with leaf litter, even small amounts of root C inputs could significantly stimulate microbial decomposition of complex C compounds. Surey *et al.* (2020) also

demonstrated the importance of organic matter inputs on soil N cycling. Furthermore, in previous ^{13}C and ^{15}N tracer studies it has been shown that rhizodeposition-induced mineralization of plant residues (Mwafulirwa *et al.*, 2017) and native SOM (Murphy *et al.*, 2015) can act to supply N for plant uptake.

Compared with genotypic variation, soil management history had a stronger effect on gross nitrification, with a significant interaction between genotype and soil management history. That there was no significant change in gross nitrification with planting for all genotypes in the CT soil and for genotypes 30G19 and ATZTRI in the NT soil, and that gross nitrification varied with soil management history for all genotypes but not hybrid maize 30G19 highlights the importance of a complimentary approach of crop breeding and management practices that retain organic matter or crop residues on cropland. Residue retention on cropland and NT can not only build SOM stocks and increase nitrification, but also decrease nutrient loss including nitrate (NO_3^-) through reduced leaching (Daryanto *et al.*, 2017). In this study gross nitrification was not related to bacterial *amoA* or 16S gene copy numbers in common with other studies. For example, Mao *et al.* (2011) investigating changes in N-transforming bacteria and archaea in soil during establishment of bioenergy crops (maize, switchgrass, *Miscanthus* × *giganteus* and mixed tallgrass prairie) also showed that nitrification was not significantly related to the quantity of bacterial *amoA*, and that the archaea community was the major ammonia oxidizer. The archaeal *amoA* gene was not measured in our study as fertilized soils are typically dominated by bacterial ammonia oxidizers (e.g. Shen *et al.*, 2011). Our finding of greater bacterial gene copy numbers in soil planted with the hybrid 30G19, especially for 16S, may be the result of larger plants and larger root diameter leading to greater rhizodeposition. High growth rate of the hybrid variety 30G19 (discussed below) also is in line with the interaction of maize genotype-by-time being important for 16S gene copy number, although this interaction was not significant for *amoA* gene copy number. That bacterial 16S and *amoA* gene abundances did not significantly change with time may be the result of uniform fertilizer application across treatments, short experiment duration or the fact that autotrophic ammonia oxidizers do not rely solely on C deposition from plants.

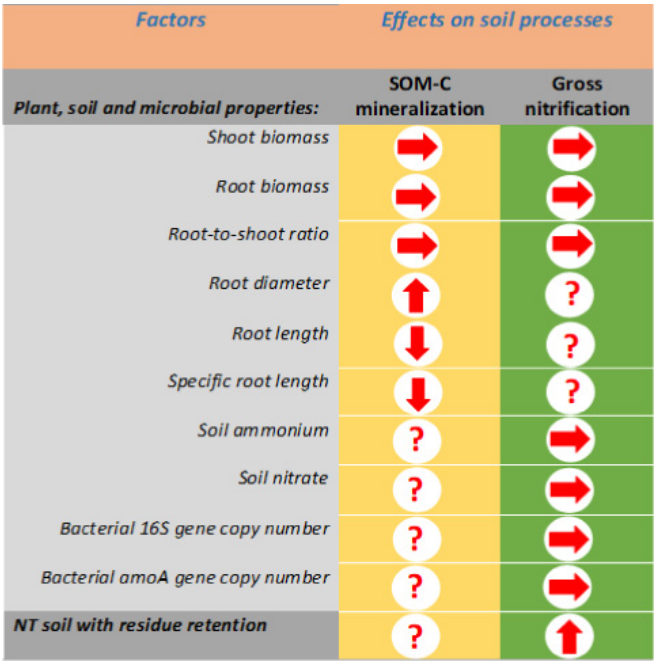

Fig. 5 Effects of maize plant, soil and microbial properties on soil organic matter (SOM) mineralization (Expt 1) and nitrification (Expt 2) and the impact of no-tillage (NT) soil with residue retention on nitrification (Expt 2). Upward pointing arrows indicate a positive effect, downward pointing arrows indicate a negative effect and horizontal arrows indicate no effect. Question marks designate lack of information, thus the effect was not assessed in the respective experiment. *amoA*, ammonia monooxygenase.

Implications for maize breeding

There is increasing attention on plant genotype-specific stimulation of microbial activity in agricultural soil and the impacts on SOM priming (e.g. Mwafulirwa *et al.*, 2016, 2017; Yin *et al.*, 2019), although the underlying factors mostly have not been elucidated. The large genotypic variation in traits associated with SOM mineralization observed here suggests that this functional process could be exploited within breeding programmes targeting low-input environments. The measurement of SOM mineralization via continuous ^{13}C-labelling requires dedicated facilities and is too costly to be realistically incorporated routinely into breeding programmes. However, SOM mineralization was significantly related to root morphological traits of root diameter and root length which, therefore, could be used as cheaper proxy traits for SOM mineralization, especially for context-specific breeding (e.g. under NT and residue retention with low inorganic fertilizer inputs). Lines from the tropical and physiology breeding programmes in Mexico were associated with highest C mineralization rates and could be explored for use as donors for breeding.

In this study, hybrid 30G19 had the largest root and shoot biomass, whereas ATZTRI (from the highland breeding program) had the smallest root and shoot biomass, with size of plants affecting nutrient uptake and residual concentrations of nutrients in soil. For instance, concentrations of soil NH_4^+-N and NO_3^--N were lowest after growth of 30G19 and highest for ATZTRI. This plant biomass data and the significant interaction effect of genotype-by-time on shoot biomass also show genotypic differences in plant growth rates. It is notable that soil management history influenced shoot biomass but not root biomass. On the one hand, shoot biomass increase in the NT soil with residue retention was clearly a consequence of direct nutrient availability in soil. On the other, the increase could be explained by a removal of the need to invest extra energy and biomass into roots due to the increased nutrient availability in this soil. Taken together, these findings indicate that maize root and shoot growth can be plastic in response to the nutrient status of soil (Junaidi *et al.*, 2018), and that their response to management can also depend on nutrient status of soil and plant genotype.

This indicates another potential selection/breeding target for specific managements.

Conclusions

Our study revealed maize genotype-specific effects on SOM-C mineralization and corresponding effects on nitrification. It provides the first demonstration that SOM mineralization increases with maize root diameter and decreases with increasing root length and specific root length. Therefore, there is the potential in maize breeding programmes for control of SOM mineralization using root diameter and root length as proxy traits of belowground C-deposition driving this functional process. Lines from the tropical and physiology breeding programmes in Mexico were associated with highest C mineralization and could be utilized as donor parents. An interaction effect of maize genotype-by-soil management history on nitrification was observed. NH_4^+-N and NO_3^--N concentrations in soil were lower and higher, respectively, in the NT soil with residue retention due to greater nitrification in this soil (compared to the CT soil with residue removal). Total available N was higher in the NT soil, likely as a consequence of its history of higher organic matter inputs. Combining management practices that build/replenish SOM and selection of genotypes that enhance SOM mineralization and organic N transformations could help ensure sustainable production and future food security of smallholder farmers in southern Africa. The extent to which varieties that enhance SOM cycling could enhance soil N supply under residue retention or aggravate SOM depletion in absence of residue retention requires further investigation.

Acknowledgements

This work was funded through the UK Global Challenges Research Fund administered by the Biotechnology and Biological Sciences Research Council (BB/P022936/1). We acknowledge the MAIZE CGIAR Research Program (www.maize.org) who supported this research with staff time. The CGIAR Research Program MAIZE receives W1&W2 support from the Governments of Australia, Belgium, Canada, China, France, India, Japan, Korea, Mexico, Netherlands, New Zealand, Norway, Sweden, Switzerland, UK and USA, and the World Bank. LM acknowledges the CGIAR Independent Science and Partnership Council (ISPC) for supporting an exchange visit to Zimbabwe. We thank A. Sim, B. Thornton, G. Martin, S. McIntyre, M. Procee, K. Buckeridge, M. Giles, S. Mitchell, S. Phiri and H. Chipala for their technical support. All authors declare no conflicts of interest with the current study.

Author contributions

All authors conceptualized the project and contributed to the data interpretation and writing of this manuscript. LM conducted the experiments and analyses and developed the figures and tables; and EMB, CT, EP, TJD and JEC were awarded the funding for this research.

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Data availability

The data used for this study is held in University of Edinburgh and CIMMYT repositories and can be made available on request.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Maize root and shoot biomass, ammonium and nitrate concentrations in soil and bacterial *amoA* gene copy numbers in soil as measured in Expt 2

Fig. S2 Significant relationships between maize plant traits and cumulative SOM-C mineralized as measured in Expt 1

Methods S1 Calculations for mineralization and nitrification.

Table S1 Traits measured in Expt 1 for 105 maize lines and hybrids.

Table S2 Maize root-derived CO_2-C surface soil efflux rates measured at 16, 23 and 29 DAP.

Table S3 Soil organic matter-derived CO_2-C surface soil efflux rates measured at 16, 23 and 29 DAP with maize.

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