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REGULAR ARTICLE

Microbial response of distinct soil types to land-use intensification at a South-Indian rural-urban interface

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Abstract
Aims Rural-urban dynamics are leading to agricultural intensification practices, which affect microbial ecosystem functions in a soil-specific way. This study aimed to investigate what effects agricultural intensification has on soil microbial communities.
Methods The effects of N fertilization level (low and high) and crop type (maize and finger millet) on microbial communities were investigated, using a two-factorial split-plot design, at two fields (irrigated and rainfed) on typical soil types (Nitisol and Acrisol) mimicking an intensification gradient in the rural-urban interface of the Indian Megacity Bangalore.
Results The Nitisol had higher pH and clay content than the Acrisol. In combination with irrigation, this led to higher aboveground plant biomass (APB), soil organic carbon (SOC), microbial biomass (MB), fungal ergosterol and microbial necromass. High APB resulted in low total P content, due to P export in APB and high soil C/P and MB-C/P ratios in the Nitisol. Crop type and N fertilization level did not affect microbial parameters in the irrigated Nitisol, whereas crop type affected ergosterol and MBP and N fertilization level affected basal respiration in the rainfed Acrisol. Particulate organic matter (POM) was a major explanatory factor for most microbial parameters in both soils. In the Acrisol, drought reduced metabolic demand, which counteracted negative effects of low pH and clay on the MB. This was indicated by similar metabolic quotients and MBC/SOC ratios in both soils.
Conclusions These results indicate the current need for water and high-quality fresh plant inputs to improve the microbial contribution to soil fertility at Bangalore.

Keywords Nitrogen fertilization · Carbon cycling · Tropical agriculture · Metabolic quotient · $\delta^{13}C$ of particulate organic matter · Irrigation

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Introduction

Urbanization of rural areas leads to a higher resource demand and agricultural intensification, altering soil microbial dynamics globally, especially in the tropics

(Elmqvist et al. 2013; Steinhübel and von Cramon-Taubadel 2021). In Bangalore (India), in particular, rural-urban dynamics have led to the introduction of irrigation in originally rainfed agriculture, depletion of groundwater sources, intensified fertilization, especially with N, and changes in crop selection (Prasad et al. 2016; Patil et al. 2019; Prasad et al. 2019). In addition, aboveground biomass from crops is removed from the fields for energy or fodder production, and even the resulting manure is used as fuel for domestic activities elsewhere, reducing the C return to the soil (Prasad et al. 2016; Prasad et al. 2019).

Intensified N fertilization and irrigation increase plant primary production and the input of plant residues to the soil (Yue et al. 2016; Oldfield et al. 2019; Araya et al. 2021). In systems where aboveground crop residues are not retained, roots are an important C supply to soil, which illustrates the importance of crops with a higher root/shoot ratio for increasing C input in soils. Particulate organic matter (POM) is an indicator of the labile soil C fraction mainly composed of recent plant residues (Fontaine et al. 2007; Kauer et al. 2021). POM is strongly affected by management and highly correlated with annual root productivity (Ontl et al. 2015; de Freitas Iwata et al. 2021). However, a higher C input may not promote C storage per se. It is the soil microbial activity and demand for C and nutrients that drives soil organic matter (SOM) decomposition or stabilization (Sinsabaugh et al. 2009; Manzoni et al. 2010; Stone et al. 2013; Vidal et al. 2021). This highlights the importance of microbial stoichiometry (element ratios) and limitations in the soil, which determine the requirements of the soil microbial biomass for maintenance and growth (Sinsabaugh et al. 2009; Manzoni et al. 2010; Buchkowski et al. 2015; Schleuss et al. 2021). In general, N and P are considered the most limiting nutrients in temperate and tropical soils, respectively (Elser et al. 2007; Joergensen 2010; Vitousek et al. 2010). In terms of soil microbial community structure, growth and activity, there is evidence to suggest contrasting N addition effects (Wallenstein et al. 2006; Treseder 2008; Padbhushan et al. 2021; Wang et al. 2021; Huang et al. 2021). In this context, the metabolic quotient (qCO_2), which is the ratio of basal respiration to microbial biomass C (MBC), is an important index of SOM utilization to satisfy the microbial demand for maintenance energy (Anderson and Domsch 1993, 2010; Hartman and Richardson 2013).

Shifts in the microbial community structure play a role in C dynamics, due to reported differences in resource use of fungi and bacteria and potentially different contributions to SOM (Rousk and Bååth 2011; Scott et al. 2012; Kallenbach et al. 2016; Malik et al. 2016). This highlights the importance of the fungal to bacterial ratio as an indicator for SOM dynamics. This ratio can be estimated on the basis of amino sugars in soil, which are present in the cell wall residues of fungi and bacterial cells (Joergensen 2018; Liang et al. 2019). Muramic acid (MurN) is specific for bacterial necromass, and glucosamine (GlcN) can be corrected to be used as an indicator for fungal necromass (Joergensen 2018). Saprotrophic fungi and biotrophic arbuscular mycorrhizal fungi (AMF) also contribute differently to SOM, due to their trophic differences (Verbruggen et al. 2017; Zhang and Elser 2017). Saprotrophic fungi decompose SOM, while biotrophic AMF receive organic compounds from plants in exchange for nutrients taken up from the soil. In arable soils, saprotrophic fungi contain exclusively ergosterol, which is not present in the cell-membranes of AMF (Olsson et al. 2003). In this way, the ergosterol/fungal GlcN ratio has served as a reliable indicator of shifts between saprotrophic fungi and AMF (Faust et al. 2017).

Management intensification affects microbial SOM stabilization, but the pathways and variation across agroecosystems are difficult to predict, due to the many factors involved, which is especially true for dynamic tropical agroecosystems (Joergensen 2010; Banger et al. 2015; Srivastava et al. 2020). Consequently, this study addresses important knowledge gaps in microbial ecology and stoichiometry in relation to urbanization-driven intensification in the tropics, caused by N fertilization level and crop type modified by soil type and irrigation. We investigated the following hypotheses: (1) High N fertilization leads to higher plant biomass, increasing MBC and MBC/P ratios. (2) POM is an indicator of recent plant residue input, and positively correlates with microbial indices. (3) Unfavorable conditions like low pH or nutrient limitation lead to a higher qCO_2. (4) A more efficient SOM utilization by microbial biomass is positively correlated to indicators of fungal biomass (ergosterol, fungal C/bacterial C, ergosterol/MBC, and ergosterol/fungal GlcN ratios).

Materials and methods

Experimental design

The experimental fields were located at the GKVK campus, University of Agricultural Sciences, Bangalore (°58′20.79″N, 77°34′50.31″E) at an altitude of 920 m above sea level. The mean annual temperature is 29.2 °C (Prasad et al. 2016) and the mean annual rainfall is 902 mm, with a total rainfall of approximately 500 mm during the monsoon season from July to October (Murugan et al. 2019). The study was conducted on a drip-irrigated (4 mm depth) Nitisol and a rainfed Acrisol (IUSS Working Group WRB 2015). Both soil types were developed from granitic bedrock of the Precambrian shields and were assigned as Alfisols in the USDA (United States Department of Agriculture) classification system (Vineela et al. 2008; Prasad et al. 2016; Sathish et al. 2016).

Both fields were cultivated with lablab (*Lablab purpureus* (L.) Sweet), maize (*Zea mays* L.), and finger millet (*Eleusine coracana* Gaertn.) as main crops (Table 1) during the rainy season, and only the irrigated Nitisol was used for vegetable cultivation of cabbage (*Brassica oleracea* cv.), eggplant (*Solanum melongena* L.), and tomato (*Solanum lycopersicum* L.), respectively, during the dry season (Dayananda et al. 2019). Both field experiments, established in 2016, had the same factorial randomized split-plot design, consisting of crop type and N fertilization level as factors. Maize and finger millet were randomly assigned to the plots, in which subplots for low and high N levels were established, with four replicates per treatment (Fig. 1). The high N level treatments received 100% of the recommended urea rate, split into two halves, i.e., at the time of sowing and 4 weeks after sowing (Dayananda et al. 2019). The low N level plots received no N fertilizer input in the sampling year (Table 1). In addition, single super phosphate and potassium were applied to low and high N treatments equally during sowing, but the amounts were adapted to expected yields for crops at each field.

Soil sampling, soil characteristics and plant yields

In October 2018, soil samples were collected before harvest. In each treatment replicate, three soil cores (diameter: 4.2 cm) were randomly taken at 0–10 cm depth and mixed to a composite sample. The soil bulk density was 1.65 and 1.72 g cm_3^{-1} at 15 cm depth for the irrigated Nitisol and rainfed Acrisol, respectively (Stephan Peth, personal communication). Soil samples were sieved to 2 mm and divided into two portions, one fresh portion (approx. 11% and 5% water content after sieving for the irrigated and rainfed soils, respectively) was stored frozen at −18 °C for biological analysis, the other was oven-dried at 105 °C and ground for chemical analysis. Soil pH was measured in water at a ratio of 1:2.5. Total C

Table 1 Mineral fertilization and corresponding rotation crops since the establishment of the field experiments in 2016 for the plots I and II with high and low N fertilization, sampled in 2018 under maize and finger millet at an irrigated Nitisol and a rainfed Acrisol (modified from Dayananda et al. 2019)

Plot	Year	Crop	Low N (kg ha^{-1})	High N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})
Irrigated Nitisol						
I	2016	Finger millet	50	100	17.5	41.5
I	2017	Lablab	0	25	21.8	20.8
I	2018	Maize	0	150	32.7	41.5
II	2016	Lablab	10	25	4.4	8.3
II	2017	Maize	0	150	32.7	33.2
II	2018	Finger millet	0	50	21.8	41.5
Rainfed Acrisol						
I	2016	Finger millet	25	50	21.8	31.1
I	2017	Lablab	0	25	21.8	20.8
I	2018	Maize	0	150	21.8	31.1
II	2016	Lablab	10	25	4.4	8.3
II	2017	Maize	0	100	21.8	20.8
II	2018	Finger millet	0	50	17.5	31.1

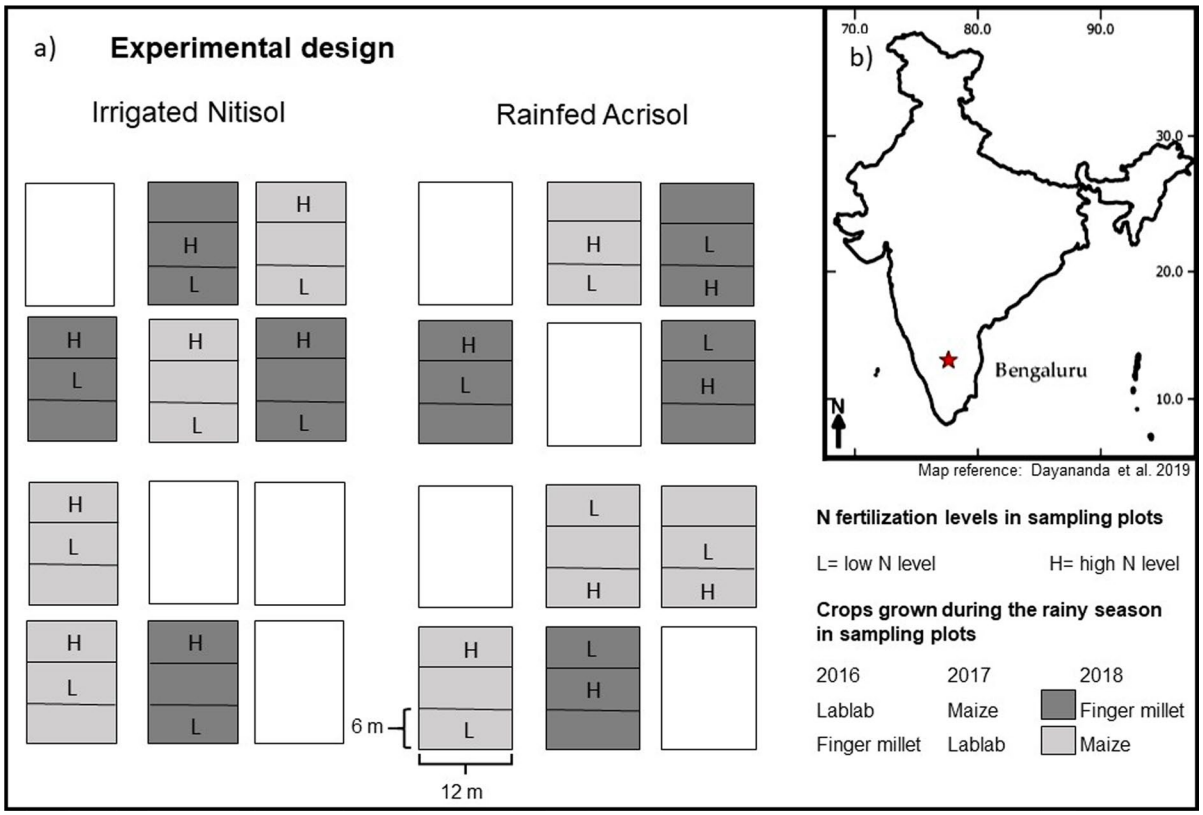

Fig. 1 **a** Description of the field experiments with a randomized split-plot design for crop type and N fertilization level treatments at the irrigated Nitisol and rainfed Acrisol. Finger millet and Maize plots are indicated in different colours, and subplots with low and high N fertilization level are indicated with L and H letters, respectively. **b** Location of Bangalore within India is indicated with a star

and total N were determined by gas chromatography, using a Vario MAX (Elementar, Hanau, Germany) elemental analyzer. Total C was considered equivalent to SOC, after verifying the absence of carbonate C. Total P and Total S were determined by HNO_3/microwave digestion, followed by inductively coupled plasma atomic emission spectroscopy (ICP-AES) at 213.618 nm wavelength (Vista-Pro radial, Palo Alto, USA). For soil texture, the sand fraction was determined by wet sieving after destruction of the organic matter with hydrogen peroxide, and dispersion with sodium metaphosphate. Clay fraction was quantified by the pipette method. Silt fraction was calculated as the difference of the sum of sand and clay to 100% (Stephan Peth, personal communication). Sampling of aboveground plant biomass (APB) and data of the specific treatments were performed and provided by Dayananda et al. (2019).

Microbial biomass indices

Microbial biomass C (MBC), N (MBN), and P (MBP) were determined by chloroform fumigation extraction, using soil samples adjusted to 50% of their water holding capacity after thawing for 5 d at 4 °C. For MBC (Vance et al. 1987) and MBN (Brookes et al. 1985), fumigated and non-fumigated samples were extracted from 5 g moist soil with 20 ml 0.5 M K_2SO_4, followed by measuring organic C and total N in the extracts with a multi C/N 2100S automatic analyzer (Analytik Jena, Germany). MBC was calculated as E_C/k_{EC}, where E_C = (organic C extracted from fumigated soil) − (organic C extracted from non-fumigated soil) and $k_{EC} = 0.45$ (Wu et al. 1990). MBN was calculated as E_N/k_{EN}, where E_N = (total N extracted from fumigated soil) − (total N extracted from non-fumigated soil) and $k_{EN} = 0.54$ (Brookes et al. 1985).

MBP was extracted from 2 g soil (on an oven dry basis) with 40 ml Bray I solution (0.025 M HCl + 0.03 M NH_4F) at pH 2.6 (Khan and Joergensen 2012). Phosphate was analyzed by a modified ammonium molybdate-ascorbic acid method (Olsen and Sommers 1982). MBP was calculated as E_P/k_{EP}/recovery, were E_P = (PO_4-P from fumigated soil) – (PO_4-P from non-fumigated soil) and k_{EP} = 0.40 (Brookes et al. 1982).

The fungal-cell membrane component ergosterol was extracted from 2 g moist soil with 100 ml ethanol by 30 min oscillating shaking at 250 rev. min^{-1} (Djajakirana et al. 1996), followed by reversed-phase high-performance liquid chromatography (HPLC) with 100% methanol as the mobile phase and detection at 282 nm.

Basal respiration was measured for one incubation week at 22 °C, after adjusting the water holding capacity of the soil to 40% and pre-incubating the soil for one week. The CO_2 was trapped with NaOH solution and then precipitated with 5 ml of a saturated $BaCl_2$ solution. The NaOH not consumed was back titrated with 0.25 M HCl, using a TITRONIC 500 (Xylem Analytics, Weilheim, Germany) system to the transition point of phenolphthalein at a pH of 8.3.

Amino sugars

Glucosamine (GlcN), galactosamine (GalN) and muramic acid (MurN) were measured after hydrolyzing 0.5 dry soil samples with 10 ml 6 M HCl for 6 h at 105 °C (Appuhn et al. 2004) as described by Indorf et al. (2011). Amino sugars were measured, using ortho-phthalaldehyde derivatization, by HPLC in a Dionex (Germering, Germany) Ultimate 3000 pump, a Dionex Ultimate WPS-3000TSL analytical autosampler with in-line split-loop injection and thermostat and an Ultimate 3000 fluorescence detector set at 445 nm emission and 330 nm excitation wavelength. Fungal GlcN was calculated by subtracting bacterial GlcN from total GlcN as an index for fungal residues, assuming that MurN and GlcN occur at a 1 to 2 M ratio in bacteria, with the formula: fungal GlcN (mg g^{-1}soil) = (mmol GlcN − 2 × mmol MurN) × 179.17 mg $mmol^{-1}$, where GlcN is the total GlcN and 179.17 is the molecular weight of GlcN (Engelking et al. 2007; Joergensen 2018). Fungal C and bacterial C for calculating the ratio of fungal to bacterial necromass were obtained by multiplying the contents of fungal GlcN and bacterial MurN by their conversion factors 9 and 45, respectively (Appuhn and Joergensen 2006).

Particulate organic matter

Particulate organic matter (POM) was obtained from 400 g of air-dried soil by wet sieving and flotation-decantation (Magid and Kjærgaard 2001; Muhammad et al. 2006) for the 400–2000 µm size-fraction. POM was dried at 40 °C for 48 h, weighed, ground, and analyzed for total C and N contents. The $^{13}C/^{12}C$ ratio of SOC and POM-C was measured by elemental analyser – isotope ratio mass spectrometry (Finnigan MAT, Bremen, Germany) and is expressed in δ-notation relative to the Vienna Pee Dee Belemnite (VPDB). To obtain estimates of the C contribution of C3 and C4 plants (%) to POM, $\delta^{13}C$ natural labelling was used in a two pooled-mixing model (Balesdent and Mariotti 1996), with the following equation:

$$C_{c4}(\%) = \frac{\delta^{13}\,C_{POM} - \delta^{13}\,C_{control}}{\delta^{13}\,C_{c4} - \delta^{13}\,C_{control}}$$

where $\delta^{13}C_{POM}$ represents the average signature of POM from all maize and millet plots in the irrigated Nitisol (−23.6 ± 0.7‰) and the rainfed Acrisol (−21.6 ± 0.7‰); $\delta^{13}C_{c4}$ is the average signature of pure maize and millet litter (−12.8 ± 0.4 ‰ and 12.6 ± 0.6 ‰ in irrigated and rainfed fields, respectively); $\delta^{13}C_{control}$ is a representative signature for tropical C3 plants (−27.6 ± 0.8 ‰) obtained by averaging the value provided by Diels et al. (2004) from a C3 plant and the average value from Swap et al. (2004) for C3 plants under an annual precipitation range between 650 and 970 mm.

Statistical analysis

Results were presented as arithmetic means on a soil dry mass basis. Variance homogeneity and normal distribution of the residuals were tested with the Levene test and Shapiro-Wilk test, respectively. The effect of treatments and their interactions on soil and microbial parameters were evaluated with a two-way analysis of variance employing the 'aov'-function in the 'stats' R package v. 3.5.3 in the R environment

Table 2 Soil physical and chemical properties on a soil dry mass basis as well as APB (aboveground plant biomass) at 0–10 cm soil depths at an irrigated Nitisol and a rainfed Acrisol, cropped with maize and finger millet under low and high N fertilization rates; probability values for the two-way ANOVA, using crop and N level as factors

Crop	N level	Clay[a] (%)	Soil pH (H_2O)	SOC (mg g^{-1} soil)	Total N	Total P (µg g^{-1} soil)	Total S	POM-C (µg g^{-1} soil)	POM-C/N	APB[b] (kg FM m^{-2})
Irrigated Nitisol										
Maize	Low	28	7.0	9.1	0.81	180	100	324	18.3	2.9
Maize	High	30	7.0	9.8	0.89	170	107	345	20.0	4.1
Millet	Low	32	7.3	9.5	0.85	220	111	375	19.5	1.6
Millet	High	28	7.2	9.3	0.84	190	100	349	20.0	3.4
Probability values										
Crop		NS	0.02	NS	NS	0.01	NS	NS	NS	0.04
N level		NS	NS	NS	NS	0.06	NS	NS	NS	0.004
SEM		2	0.1	0.4	0.04	10	10	31	1.0	0.43
Rainfed Acrisol										
Maize	Low	18	5.0	4.5	0.43	320	85	205	20.8	1.0
Maize	High	18	4.9	4.4	0.43	320	85	202	20.5	1.3
Millet	Low	18	5.5	5.3	0.50	410	86	260	21.5	0.4
Millet	High	17	5.2	4.8	0.46	380	87	276	21.8	1.1
Probability values										
Crop		NS	0.01	NS	NS	0.01	NS	NS	NS	0.07
N level		NS	NS	NS	NS	NS	NS	NS	NS	0.03
SEM		1.0	0.2	0.4	0.03	30	3	43	0.9	0.20

SEM = standard error of means for the crop and N fertilization treatments; NS = not significant; all interactions were not significant; [a] data from 0 to 5 cm depth (Stephan Peth, personal communication); [b] Fresh matter (FM) aboveground plant biomass from Dayananda et al. (2019)

(R Core Team 2019), except for MBP at the irrigated Nitisol, the residuals of which were not normally distributed and was tested with the non-parametric Kruskall-Wallis test ('kruskal.test'-function, 'stats' R package v. 3.5.3, R environment, R Core Team 2019). Multiple linear regression models were calculated for relevant microbial parameters as dependent variables and selected soil properties as independent factors, using the 'lm'-function in the 'stats' R package v. 3.5.3 in the R environment (R Core Team 2019). ANOVA and regression model simplification were applied in sequential steps to remove non-significant interactions and/or factors until the minimal adequate model was obtained. To test the relationship between MBC and ergosterol in the irrigated Nitisol and the relationship between the MB-C/N and ergosterol (%MBC) in the rainfed Acrisol, Pearson correlation was used. Pearson correlation was also used to test collinearity between soil properties prior to their selection for regression analysis.

Results

Soil properties of both soils differed, with higher pH and clay, SOC, total N, total S and POM-C contents of the irrigated Nitisol, but total P content 50% below that of the Acrisol (Table 2). The APB of the irrigated Nitisol exceeded that of the rainfed Acrisol by more than three times. In both fields, higher N levels significantly increased APB. Maize yield was higher than millet yield at the irrigated Nitisol. In both fields, soil pH and total P were higher in plots cropped with finger millet, regardless of the N fertilization level.

The irrigated Nitisol contained between 20% (MurN) and 80% (MBC, MBN, fungal GlcN, and GalN) more of the microbial biomass and necromass markers than the rainfed Acrisol (Table 3). MBP varied in a large range around a similar mean of 6.6 µg g^{-1} soil in both fields. N fertilization level did not affect any soil biological property at the irrigated Nitisol and increased only basal respiration at

Table 3 Mean of the microbial indices MBC MBN, MBP (microbial biomass C, N, P), ergosterol, MurN (muramic acid), fungal GlcN (glucosamine), GalN (galactosamine), and the CO_2-C (basal respiration rate) on a soil dry mass basis at an irrigated Nitisol and a rainfed Acrisol, cropped with maize and finger millet under low and high N fertilization rates; probability values for the two-way ANOVA, using crop type and N level as factors

Crop	N level	MBC	MBN	MBP	Ergosterol	MurN	Fungal GlcN	GalN	CO_2-C
		(μg g^{-1} soil)	(μg g^{-1} soil)	(μg g^{-1} soil)	(μg g^{-1} soil)	(μg g^{-1} soil)	(μg g^{-1} soil)	(μg g^{-1} soil)	(μg g^{-1} soil d^{-1})
Irrigated Nitisol									
Maize	Low	165	29	5.1	0.49	44	750	237	7.19
Maize	High	179	29	8.0	0.56	49	694	272	6.75
Millet	Low	166	28	9.7	0.59	49	772	293	6.61
Millet	High	180	31	4.7	0.55	50	782	266	7.00
Probability values									
Crop		NS	NS	NS	NS	NS	NS	NS	NS
N level		NS	NS	NS	NS	NS	NS	NS	NS
SEM		11	2	3.4	0.05	5	52	20	0.33
Rainfed Acrisol									
Maize	Low	80	13	5.2	0.21	35	363	126	3.99
Maize	High	95	14	5.1	0.15	40	423	143	5.21
Millet	Low	102	17	8.4	0.31	42	425	170	4.23
Millet	High	107	17	7.1	0.28	44	480	164	4.97
Probability values									
Crop		NS	NS	0.03	0.02	NS	NS	NS	NS
N level		NS	NS	NS	NS	NS	NS	NS	0.01
SEM		12	2	0.9	0.04	4	47	16	0.14

SEM = standard error of means for the crop and nitrogen treatments; NS = not significant; all interactions were not significant

Table 4 Stoichiometry of soil and microbial biomass (MB) at an irrigated Nitisol and rainfed Acrisol, cropped with maize and finger millet under low and high N fertilization rates; probability values for the two-way ANOVA, using crop type and N level as factors

Crop	N level	Soil C/N	Soil C/P	Soil C/S	MB-C/N	MB-C/P
Irrigated Nitisol						
Maize	Low	11.2	51	91	5.6	40
Maize	High	11.0	56	92	6.1	45
Millet	Low	11.2	43	87	5.8	21
Millet	High	11.1	49	94	5.8	40
Probability values						
Crop		NS	<0.01	NS	NS	NS
N level		NS	<0.01	NS	NS	NS
SEM		0.2	2	4	0.2	11
Rainfed Acrisol						
Maize	Low	10.3	14	53	6.4	19
Maize	High	10.1	14	51	7.1	19
Millet	Low	10.7	13	62	6.1	13
Millet	High	10.4	13	55	6.6	15
Probability values						
Crop		NS	NS	0.04	NS	NS
N level		NS	NS	NS	NS	NS
SEM		0.2	1	3	0.5	4

SEM = standard error of means for the crop and nitrogen treatments; NS = not significant; all interactions were not significant

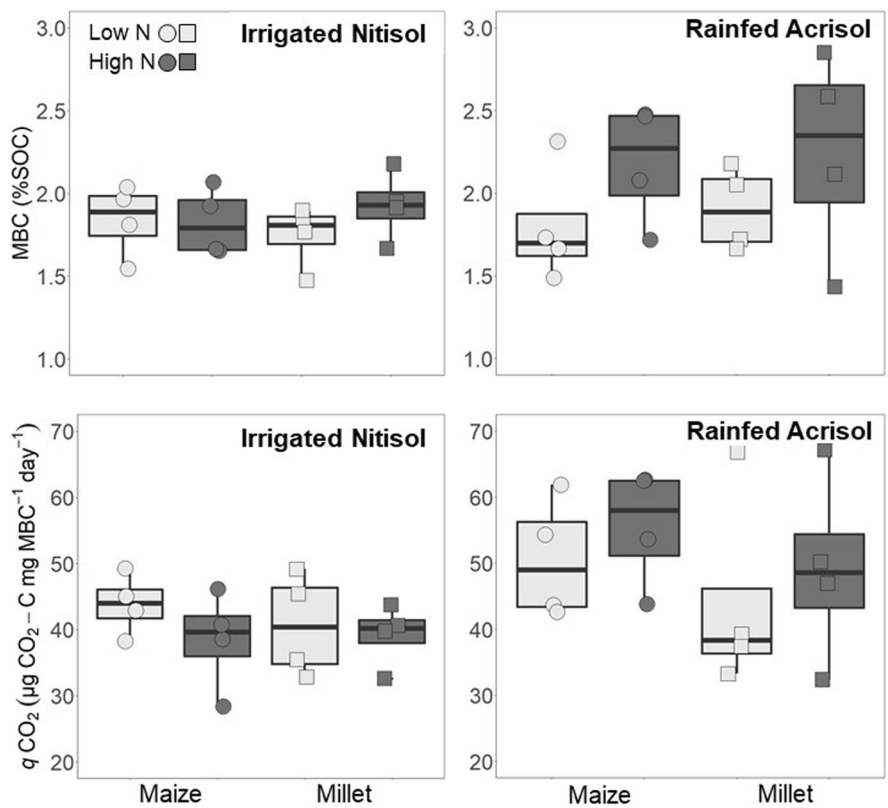

Fig. 2 Boxplots of the microbial biomass C (MBC)/SOC ratio and metabolic quotient qCO_2 at an irrigated Nitisol and a rainfed Acrisol, cropped with maize and finger millet under low and high N fertilization rates ($P > 0.05$); dots indicate the data of all replicates per treatment. Crop type is indicated by different shape, and N level is indicated by different colour

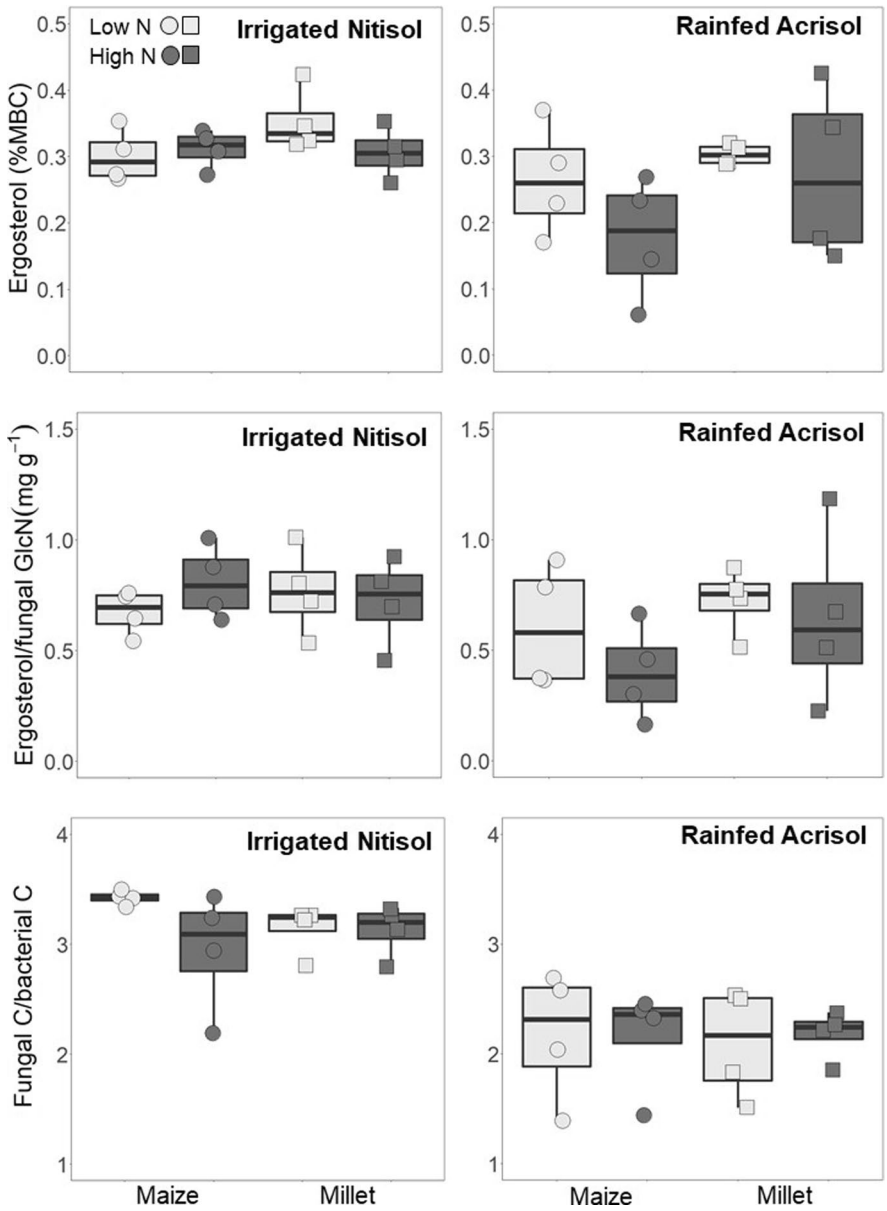

Fig. 3 Boxplots of the ergosterol/microbial biomass C (MBC) ratio, the ergosterol/fungal glucosamine (GlcN) ratio, and the fungal C/bacterial C ratio at an irrigated Nitisol and a rainfed Acrisol, cropped with maize and finger millet under low and high N fertilization rates ($P > 0.05$); dots indicate the data of all replicates per treatment. Crop type is indicated by different shape, and N level is indicated by different colour

the rainfed Acrisol. MBP and ergosterol were the two soil biological properties that showed a significant positive response to millet cropping, but only at the rainfed Acrisol.

Soil C/N and MB-C/N ratios varied around 10.5 and 6.5, respectively, at both fields, whereas soil C/P and MB-C/P ratios were four and three times larger, respectively, at the irrigated than at the rainfed field (Table 4). The MBC/SOC ratio varied around 1.8% at both fields and was not affected by any treatments, although there was a tendency that high N fertilization level increased this ratio at the rainfed Acrisol (Fig. 2). The metabolic quotient qCO_2 varied around 43 µg CO_2-C mg^{-1} MBC d^{-1} in both fields, with a tendency that millet cropping reduced the qCO_2 values at the rainfed Acrisol (Fig. 2). The ergosterol/MBC and ergosterol/fungal GlcN ratios varied around 0.29% and 0.75 mg g^{-1}, respectively, at both fields, exhibiting a considerably larger variation at the rainfed Acrisol (Fig. 3).The fungal C/bacterial C ratio varied around 3.3 at the irrigated Nitisol and

Table 5 Simple linear and multiple linear regressions between soil microbial indices as the dependent variable and soil physical and chemical properties and aboveground plant biomass as independent variables at two field experiments cropped with maize and finger millet under low and high N fertilization rates

Dependent variable	Intercept	Coefficient	Independent variables	R^2
Irrigated Nitisol				
MBC	666	−32.7	Soil-C/N	0.60**
		−1.4	Soil-C/S	
Ergosterol	0.06	0.001	POM-C	0.64***
Ergosterol (%MBC)	0.37	−0.003	Soil C/P	0.55**
		0.0003	POM-C	
Ergosterol/fungal GlcN	−0.47	0.002	POM-C	0.56**
		0.035	POM-C/N	
Fungal GlcN	1275.5	−27.04	POM-C/N	0.26*
MurN	94.56	−2.39	POM-C/N	0.25*
Rainfed Acrisol				
MBC	−45.19	6.19	Clay	0.55**
		0.13	POM-C	
MB-C/N	15.02	−1.65	Soil pH	0.42**
MB-C/P	−22.57	2.19	Clay	0.31*
Ergosterol	0.04	0.0008	POM-C	0.53**
Ergosterol (%MBC)	−0.47	0.14	Soil pH	0.32*
Ergosterol/fungal GlcN	0.45	0.002	POM-C	0.53**
		−0.3	APB	
Fungal C/bacterial C	7.05	−0.47	Soil C/N	0.31*
GalN	221.5	−44.19	APB	0.42**

* $P<0.05$, ** $P<0.01$, *** $P<0.001$;
MBC = microbial biomass C, MB-C/N = microbial biomass C/N ratio; MB-C/P = microbial biomass C/P ratio; POM = particulate organic matter; SOC = soil organic C; APB = aboveground plant biomass; MurN = muramic acid; GlcN = glucosamine; GalN = galactosamine

around 2.4 at the rainfed Acrisol, without treatment effects (Fig. 3).

At the irrigated Nitisol, MBC was mainly explained by the soil C/N ratio but also by the soil C/S ratio (Table 5). Ergosterol as well as the ergosterol/MBC and ergosterol/fungal GlcN ratios were all positively affected by POM-C, whereas the necromass markers fungal GlcN and bacterial MurN were both negatively affected by the POM-C/N ratio. At the rainfed Acrisol (Table 5), MBC was mainly explained by the clay content and POM-C, and ergosterol and the ergosterol/fungal GlcN ratio revealed a

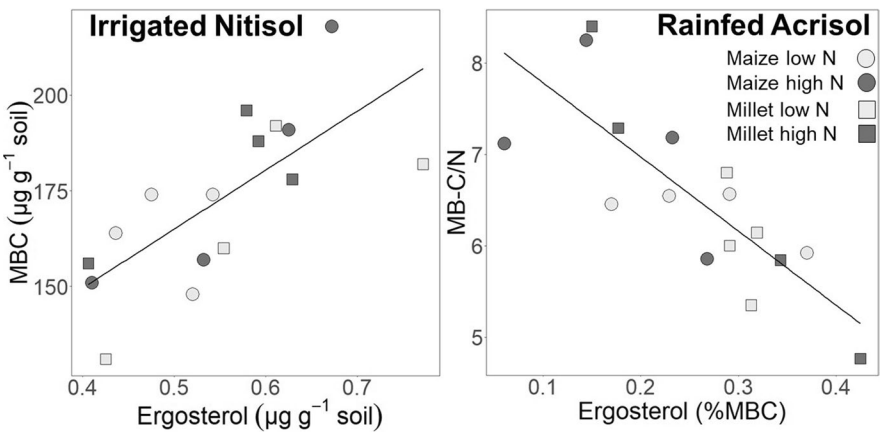

Fig. 4 Relationships between microbial biomass C (MBC) and ergosterol at the irrigated Nitisol ($y=154.1 \times x+87.9$, $R^2=0.52$, $P<0.01$) and between the microbial biomass C/N ratio (MB-C/N) and ergosterol/MBC ratio at the rainfed Acrisol ($y=-8.11 \times x+8.59$, $R^2=0.63$, $P<0.001$), cropped with maize and finger millet under low and high N fertilization rates. Crop type is indicated by different shape, and N level is indicated by different colour

Table 6 Isotopic δ ^{13}C signature of SOC (soil organic C), POM (particulate organic matter) and APB (aboveground plant biomass) at an irrigated Nitisol and a rainfed Acrisol, cropped with maize and finger millet under low and high N fertilization rates; probability values for the two-way ANOVA, using crop and N level as factors

Crop	N level	SOC-δ ^{13}C (‰)	POM-δ^{13}C (‰)	APB-δ^{13}C (‰)
Irrigated Nitisol				
Maize	Low	−21.7	−23.7	−12.3
Maize	High	−22.1	−24.5	−12.5
Millet	Low	−21.8	−23.3	−13.1
Millet	High	−21.8	−22.9	−13.1
Probability values				
Crop		NS	0.02	NA
N level		NS	NS	NA
SEM		0.22	0.36	NA
Rainfed Acrisol				
Maize	Low	−19.3	−21.7	−12.1
Maize	High	−19.1	−22.1	−12.1
Millet	Low	−19.5	−22.1	−13.4
Millet	High	−19.1	−20.6	−12.6
Probability values				
Crop		NS	NS	NA
N level		NS	NS	NA
SEM		0.18	0.61	NA

SEM = standard error of means for the crop and nitrogen treatments; NS = not significant; NA = not applicable, partly due to an insufficient number of replicates; all interactions were not significant

strong positive influence of POM-C. In contrast, soil C/N was the only predictor found for the fungal C/bacterial C ratio. APB was negatively related to the ergosterol/fungal GlcN and to GalN, while the ergosterol/MBC ratio was negatively influenced by pH and showed a negative relationship to the MB-C/N ratio (Fig. 4). The MB-C/P ratio was influenced by clay content and the MB-C/N ratio by soil pH (Table 5).

The mean soil $\delta^{13}C$ values varied around −21.9‰ and − 19.3‰ at the irrigated and rainfed field, respectively (Table 6). These mean values were 2.0‰ lower in the POM-C recovered at both fields. The C contribution from maize and millet residues to POM-C was on average only 27% in the irrigated Nitisol and 40% in the rainfed Acrisol, thus the contribution of former C3 plant material represented the larger contribution in the POM fraction.

Discussion

Soil and treatment effects on general microbial properties

The effects of soil type and water management considerably exceeded the experimental treatment effects on soil microorganisms. Nevertheless, the MBC and SOC contents, and the pH of the rainfed Acrisol were in line with those obtained previously on Nitisols and Acrisols under rainfed conditions in or around Bangalore, summarized as Alfisols (Vineela et al. 2008; Prasad et al. 2016; Sathish et al. 2016). At the irrigated, more fertile Nitisol, none of the microbial properties responded to the crop type or N fertilization level. In this soil, the negative effect of the soil C/N and soil C/S ratios on MBC indicate nutrient limitation. However, the fact that this effect was not reflected by an increased MB-C/N ratio suggests an additional limitation of C inputs, which were reduced under lower N availability. Effects of N fertilization level and crop type were observed in the acidic rainfed Acrisol. The higher total P content in millet plots was reflected by higher MBP. Similar amounts of P fertilizer applied in millet and maize plots but lower millet yields resulted in higher P uptake in microbial biomass under millet. In the rainfed Acrisol, microorganisms responded more sensitively to basic properties, i.e., variations in clay content and soil pH.

It was a striking feature of the current results that lower clay content and lower soil pH of the rainfed Acrisol did not result in much higher qCO_2 values and lower MBC/SOC ratios in comparison with

the irrigated Nitisol. This contrasts other studies, in which a lower pH (Anderson and Domsch 1993, 2010; Hartman and Richardson 2013) or lower clay content (Müller and Höper 2004) significantly increased the qCO_2, due to an increased demand for maintenance energy and reduced protection of SOM, respectively. However, such effects may have been counteracted by a drought-reduced microbial turnover in this study.

The irrigated Nitisol was characterized by extremely low total P contents, but the total P contents of the rainfed Acrisol were also low in comparison with other soils from India (Paul et al. 2018). The reason for the three times lower total P content of the irrigated Nitisol in comparison with the rainfed Acrisol could not be fully explained by the current study. Most likely, a similar P fertilization, but considerably lower yield resulted in less P uptake by crops and finally in a higher total P content of the rainfed Acrisol. This view is supported by the observation that the lower yield of millet cropping generally increased total P content and soil pH in comparison with maize, with a positive correlation between soil C/P and APB ($r = 0.64$) in the irrigated Nitisol. This indicates a rapid soil response to changes in the crop cultivated.

It should be considered that millet cultivation followed maize after lablab. Maize received more N from the preceding legume crop and from the higher urea fertilization than millet, which led to a small but significant decrease in soil pH at both fields. Consequently, the observed crop effects on soil properties were larger than those of the N fertilization level. This was especially true at the rainfed Acrisol, where millet cropping increased the contents of saprotrophic fungi by approximately 50% in comparison with maize, suggesting a larger C input by millet roots. On the basis of the current APB results and the calculated root/shoot ratios of 0.57 for millet (Goron et al. 2015) and of 0.16 for maize (Amos and Walters 2006), the resulting belowground root biomass at maturity was higher ($P < 0.05$) for millet (1.4 kg and 0.4 kg m^{-2} at the irrigated and rainfed field, respectively) compared to maize (0.6 kg and 0.2 kg m^{-2} at the irrigated and rainfed field, respectively). Although the rhizodeposits of the two crop species may be very similar, acid phosphatase and dehydrogenase activities are higher in finger millet than in maize cropping systems (Dotaniya et al. 2014). Acid phosphatases are also excreted by fungi (Dotaniya et al. 2019), which may additionally support the observed interactions between roots, the increase in saprotrophic fungi, and MBP under millet plots.

Specific effects on microbial stoichiometry

The strong P deficiency of the irrigated Nitisol led to wide MB-C/P ratios in comparison with other tropical soils (Joergensen 2010; Tischer et al. 2014). Large MB-C/P ratios were often observed in situations of low P availability in combination with relatively high C availability (Anderson and Domsch 1980; Kapoor and Haider 1982; He et al. 1997). The higher yield level at the current irrigated Nitisol aggravated P deficiency. In contrast to other studies (Heuck et al. 2015), high MB-C/P ratios were not related to high MB-C/N ratios, probably due to the combination of sufficient N fertilization and N_2 fixing lablab in the crop rotation.

At the rainfed Acrisol, clay positively affected the MB-C/P ratio, probably due to an increase in MBC, although no correlation was found between MB-C/P and MBC, both positively benefited from higher clay content. With increasing soil pH, the MB-C/N ratio decreased but the ergosterol/MBC ratio increased, indicating an increasing contribution of saprotrophic fungi to the microbial community. The MB-C/N ratio reflected the complex interaction with SOC, total N and P and not the ratio of fungi to bacteria suggested by Khan et al. (2016).

Specific soil and treatments effects on fungi

Irrigation led to a strong increase in crop yield, and most likely also in root input in comparison with the rainfed Acrisol. This increased MBC, MBN, and especially the ergosterol content, an indicator of saprotrophic fungi in arable soils (Joergensen and Wichern 2008). The positive relationship of ergosterol with POM-C was in line with the observation that fungal biomass is strongly dependent upon POM in soils with low carbon contents (Wachendorf et al. 2014).

At the irrigated Nitisol, the ergosterol/MBC ratio was negatively affected by the soil C/P ratio, suggesting that P availability specifically controls saprotrophic fungi. The current ergosterol/MBC ratios were generally in the range of other tropical arable soils (Joergensen and Castillo 2001; Joergensen 2010; Murugan and Kumar 2013). However, the strong

differences between the two fields in clay content and in soil pH had only minor effects on the ergosterol/MBC ratio in comparison with the results of others (Joergensen and Castillo 2001; Rousk et al. 2009; Wentzel et al. 2015).

The ergosterol/fungal GlcN ratio was relatively consistent in all treatments of the two fields, which supports the view that there is a strong relationship between fungal biomass and fungal necromass (Khan et al. 2016). In contrast, the fungal C/bacterial C ratio was markedly higher at the irrigated Nitisol, in line with the lack of response of bacterial biomass but positive response of fungi to soil moisture (Frey et al. 1999). Under rainfed conditions, GalN and fungal GlcN were more than 43% lower than in the irrigated Nitisol, whereas MurN only decreased by 25%. Drought apparently promoted the specific accumulation of bacterial residues. For this reason, Amelung et al. (1999) observed a relative increase in MurN in comparison with GlcN with decreasing mean annual precipitation. The markedly higher fungal C/bacterial C ratio at the neutral Nitisol in comparison with the acidic Acrisol contrasted other studies from India (Murugan and Kumar 2013) and many other regions (Rousk et al. 2011; Khan et al. 2016), suggesting that drought effects override pH effects.

Relevance of particulate organic matter at the two fields

Drought also promoted the accumulation of POM-C, which contributed 3.7% to SOC at the irrigated Nitisol and 5.0% at the rainfed Acrisol. POM contained only 27–40% C4 plant material, indicating that maize and millet were not main contributors to POM. Therefore, there was a lack of correlation between POM-C and APB. This result is surprising, considering that the C4 plants were the actual main crops for the study year in maize plots and for two consecutive years in millet plots, neglecting the small root input of vegetables during the dry period at the irrigated Nitisol. Hence, POM mainly consisted of plant residues not decomposed for several years. This contrasts the view that POM-C is always a very labile and readily bio-available pool, derived from less decomposed plant material of the previous crop (Benbi and Richter 2002; Wang et al. 2004; Heitkamp et al. 2009). The current results are even more surprising, considering the observation that POM-C generally had dominating positive effects on saprotrophic soil fungi, which were apparently unable to decompose these plant residues under the environmental conditions of the two fields. However, it is important to highlight that the crop yield in 2018 was particularly low compared to the previous year (Dayananda et al. 2019). This probably reduced the contribution of the current crop residues to POM and the correlation between the two variables, thus reducing the influence of APB on microbial indices.

The generally positive effects of POM-C on the ergosterol/fungal GlcN ratio indicate that this C-fraction promoted especially fungal biomass in comparison with fungal necromass. The negative effects of the POM-C/N ratio at the irrigated Nitisol on fungal GlcN and bacterial MurN suggest that not the amount but the quality of plant residues controls microbial necromass accumulation. APB at the rainfed Acrisol had negative effects on the accumulation of GalN, an indicator of microbial extracellular polymeric substances (Joergensen 2018). This suggests that microorganisms have to invest more energy in this fraction under drought conditions with a lower input of root and harvest residues.

Conclusions

Microorganisms in typical soil types at Bangalore are C and nutrient limited under major cereal cropping systems. The microbial response to intensification varied depending on soil pH and water availability. More favorable abiotic soil conditions and higher SOM of the irrigated Nitisol resulted in higher APB and MB in comparison with the rainfed Acrisol. N fertilization generally led to higher APB but had only minor effects on microbial biomass in both soil types. Crop effects were probably strengthened by indirect effects of higher N-fertilization of maize than millet, inducing a decrease of soil pH under maize. A low percentage of particulate organic matter from recent plant material indicates the additional importance of crop residues from previous rotations for soil microorganisms under tropical conditions. Fungal biomass and necromass were reduced in the rainfed Acrisol in comparison with the irrigated Nitisol. However, it was not possible to differentiate irrigation effects from land use history and soil effects, i.e., irrigation and rainfed treatments should be carried out on both

soil types. To address the entire rural-urban dynamics taking place in the soils at Bangalore, additional crops should be studied. In particular, the effects of vegetables, fruits and non-food crops, which are being increasingly cultivated due to increasing urban demand, have been largely unexplored.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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