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Short Communication

pH and exchangeable aluminum are major regulators of microbial energy flow and carbon use efficiency in soil microbial communities

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ABSTRACT

The microbial partitioning of organic carbon (C) into either anabolic (i.e. growth) or catabolic (i.e. respiration) metabolic pathways represents a key process regulating the amount of added C that is retained in soil. The factors regulating C use efficiency (CUE) in agricultural soils, however, remain poorly understood. The aim of this study was to investigate substrate CUE from a wide range of soils (n = 970) and geographical area (200,000 km^2) to determine which soil properties most influenced C retention within the microbial community. Using a ^{14}C-labeling approach, we showed that the average CUE across all soils was 0.65 ± 0.003, but that the variation in CUE was relatively high within the sample population (CV 14.9%). Of the major properties measured in our soils, we found that pH and exchangeable aluminum (Al) were highly correlated with CUE. We identified a critical pH transition point at which CUE declined (pH 5.5). This coincided exactly with the point at which Al^{3+} started to become soluble. In contrast, other soil factors [e.g. total C and nitrogen (N), dissolved organic C (DOC), clay content, available calcium, phosphorus (P) and sulfur (S), total base cations] showed little or no relationship with CUE. We also found no evidence to suggest that nutrient stoichiometry (C:N, C:P and C:S ratios) influenced CUE in these soils. Based on current evidence, we postulate that the decline in microbial CUE at low pH and high Al reflects a greater channeling of C into energy intensive metabolic pathways involved in overcoming H^+/Al^{3+} stress (e.g. cell repair and detoxification). The response may also be associated with shifts in microbial community structure, which are known to be tightly associated with soil pH. We conclude that maintaining agricultural soils above pH 5.5 maximizes microbial energy efficiency.

Soil organic matter (SOM) content is known to be strongly related with crop yield and the delivery of a wide range of ecosystem services in agricultural soils (Powlson et al., 2011). Consequently, identifying strategies which promote soil carbon (C) storage represents a central goal in sustainable soil management (Reeves, 1997; Machmuller et al., 2015). The design of effective C sequestration strategies, however, requires a good mechanistic understanding of the factors that regulate how C is processed by the soil microbial biomass (Schimel and Schaeffer, 2012; Kallenbach et al., 2019). The size, structure and activity of the soil microbial community is known to vary greatly in response to vegetation cover, soil properties, and management regime (Fierer, 2017; George et al., 2019). However, due to the central metabolic pathways being largely similar within either prokaryote or eukaryote communities, it is thought that substrate C is processed in a similar way in most agricultural soils (Rousk et al., 2009; Prosser, 2012). While it is recognised that there is a high degree of functional redundancy within the microbial community, the metabolic partitioning of C into either anabolic (growth and maintenance) or catabolic (respiratory) processes can vary widely between soils (Jones et al., 2018a). The factors regulating this immobilization-to-mineralization ratio (i.e. C use efficiency; CUE), however, remain poorly understood. It has been shown that CUE may be affected by the relative abundance of eukaryotes and prokaryotes within the community (Maynard et al., 2017; Soares and Rousk, 2019) and also potentially genome size (Saifuddin et al., 2019). In addition, studies at the local scale have shown that microbial CUE can vary in response to C supply (Gunina et al., 2017) as well as a range of climate, edaphic and plant variables (Jones et al., 2018b; Malik et al., 2018; Li et al., 2019; Silva-Sanchez et al., 2019). Whether these concepts can be universally applied at the broader scale and within ecosystem C models remains unclear (Zhang et al., 2018). In this context, our aims were to (1) determine the intrinsic variability in microbial CUE across a broad range of agricultural

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Table 1
Statistical description of microbial carbon use efficiency (CUE) and the other major soil properties for the sites from Western Australia investigated in this study.

Variable	*n*	Mean	CV (%)	Min.	Max.	Q1	Q3
CUE	970	0.646	14.7	0.273	0.954	0.591	0.700
pH	970	5.25	15.9	3.45	8.60	4.70	5.60
Total C (%)	970	1.56	88.1	0.22	14.76	0.84	1.74
Total N (%)	450	0.18	91.5	0.01	1.27	0.07	0.22
Clay (%)	970	7.9	79.1	0.1	37.7	3.5	10.5
Available N (mg N kg^{-1})	970	22.4	65.4	2.0	137.0	13.0	27.9
Available P (mg P kg^{-1})	970	27.8	52.4	1.0	135.0	18.0	35.0
Available S (mg S kg^{-1})	754	14.9	194.9	2.0	481.0	6.5	13.9
Available Ca (meq kg^{-1})	970	37.0	99.3	4.4	299	1.8	4.0
Available Al (meq kg^{-1})	970	0.80	159.4	0.00	12.4	0.0	1.0
Dissolved organic C (mg C kg^{-1})	970	93.8	61.6	16.8	800.1	61.3	110.4
Ca:Al ratio	970	54.1	121.6	1.1	540.0	16.6	63.6

n, sample number; CV, coefficient of variation; Min., minimum; Max., maximum; Q1, first quartile; Q3, third quartile.

soils (n = 970), (2) establish how this variability in CUE was related to major soil properties, and (3) establish whether differences in CUE can help explain differences in SOM retention in soil. A secondary aim of the work was to test whether soil pH influences the community's ability to use labile C.

Soil samples (0–10 cm) were collected from 970 individual sites across the south-west agricultural region (ca. 200,000 km^2) of Western Australia. All the soils had a similar parent material (Archaean granitic and gneissic parent rock of the Yilgarn Craton; Anand and Paine, 2002) and pedogenic age (> 2500 Ma). These highly weathered mineral soils are dominated by quartz and kaolinite and possess a low effective cation exchange capacity (eCEC). The region has an annual average temperature ranging from 15 to 21 °C and mean annual rainfall ranging from 327 to 747 mm. A summary of the major soil properties is shown in Table 1. Within each monitoring site (20 m^2) soil was collected from 10 random locations to form a 2 kg composite sample per location. Soils were collected field-moist, during summer fallow when the microbial biomass is known to be stable (Gonzalez-Quiñones et al., 2011). Sites represented land used for pasture, continuous cropping or mixed cropping. The soil samples were sieved (< 2 mm) and stored in aerobic containers until analysis. All soil analysis followed national guidelines as described in Rayment and Lyons (2011) unless otherwise stated. Soil pH was determined from a 1:5 0.01 M $CaCl_2$ solution. Exchangeable Al^{3+} and base cations (Ca^{2+}, Mg^{2+}, K^+, Na^+) were extracted from soil using 0.01 M silver thiourea and measured by inductively coupled plasma optical emission spectroscopy (Optima 5300DV ICP-OES; PerkinElmer Inc., Waltham, MA). Total organic C and total N were measured by combustion using an Elementar analyser (Vario Macro CNS; Elementar Analysensysteme, Langenselbold, Germany). Alkaline soils were first treated with acid to remove $CaCO_3$ before analysis of total organic C. Available P was extracted from soil using 0.5 M $CHNaO_3$ (pH 8.5; Colwell-P) with P in the extracts determined colorimetrically using the molybdate blue method of Murphy and Riley (1962). Extractable S was extracted from soil using 0.25 M KCl with S in the extracts determined by ICP-OES. Inorganic N was determined by extracting the soil with 0.5 M K_2SO_4 and NO_3^- and NH_4^+ determined colorimetrically on a Skalar San^{++} autoanalyzer (Skalar Analytical B.V., Breda, Netherlands). In this study, available N is defined as the sum of NO_3^- and NH_4^+. Soil particle size analysis (sand, silt, clay) was determined using sedimentation columns.

Microbial C use efficiency was determined as described in Jones et al. (2018a, b). Field-moist soil (5 g) from each site was placed in individual sterile 50 cm^3 polypropylene tubes. ^{14}C-labelled glucose (500 µl, 100 µM, 3.2 kBq ml^{-1}; 0.72 mg C kg^{-1}) was then pipetted onto the soil surface. This substrate was chosen as it represents the major C input to agricultural soils, is not sorbed to the solid phase, and can be used by almost all soil microorganisms (Gunina and Kuzyakov, 2015). The level of C substrate addition was chosen to reflect natural soil solution concentrations and microbial energy flow, but insufficient to induce large amounts of microbial growth (soil microbial biomass in these soils typically ranges from 50 to 500 mg C kg^{-1}; www.soilquality.org.au). After substrate addition, a polypropylene scintillation vial containing 1 M NaOH (1 cm^3) was suspended above the soil to trap the respired $^{14}CO_2$, and the tubes sealed. The soils were then incubated at 20 °C for 24 h, after which the NaOH trap was recovered and replaced. The incubation time was chosen to estimate how much of the substrate had entered the microbial biomass and is consistent with previous CUE methodologies (Jones et al., 2018a, b). After 72 h, when most of the substrate was assumed to have been taken up by the microbial community and partitioned into anabolic and catabolic pathways, the second NaOH trap was recovered. This time was selected based on many previous studies measuring the dynamics of low molecular weight C turnover by the microbial biomass which show that C partitioning is quasi-complete after 72 h (Glanville et al., 2016). After trap removal at 72 h, the amount of available ^{14}C remaining in the soil was quantified by extracting the soil with 25 ml of ice-cold 1 M NaCl (200 rev min^{-1}, 3 °C; Rousk and Jones, 2010), centrifuging the extracts (18,000 *g* 15 min) and recovering the supernatant. NaCl was chosen in place of KCl to minimize interference from ^{40}K when determining ^{14}C. The amount of ^{14}C in the NaOH traps and NaCl extracts was determined by liquid scintillation counting with Optiphase 3 scintillation fluid and a Wallac 1404 scintillation counter with automated quench correction (PerkinElmer Inc.). Microbial immobilization of the ^{14}C-substrate ($^{14}C_{imm}$) after 72 h was estimated as follows:

$$^{14}C_{imm} = {}^{14}C_{tot} - {}^{14}C_{NaCl} - {}^{14}CO_{2\text{–}72h} \quad (1)$$

where $^{14}C_{tot}$ is the total amount of ^{14}C-substrate added to the soil at time (t) = 0, $^{14}C_{NaCl}$ is the amount of ^{14}C recovered in the 1 M NaCl extracts and $^{14}CO_{2\text{–}72h}$ is the total amount of ^{14}C recovered as $^{14}CO_2$ after 72 h. Following Jones et al. (2018a,b), microbial CUE for the C substrate was then estimated as follows:

$$CUE = {}^{14}C_{imm} / ({}^{14}C_{imm} + {}^{14}CO_{2\text{–}72h}) \quad (2)$$

Assumptions of normality and homoscedasticity of the residuals were verified visually using diagnostic plots and a Shapiro-Wilk test in Minitab v18.0 (Minitab Inc., State College, PA). One-way ANOVA and principal component analysis were performed in Minitab v18.0 while curve fitting was performed in Sigmaplot v14.0 (Systat Software Inc., San Jose, CA). $P < 0.05$ was used as the level for statistical significance. Data in the text are presented as means ± SEM. All statistical analysis using pH values was undertaken after conversion back to H^+ concentration. The inflection point of the curve was calculated in the computing language Python using the NumPy package.

At the end of the experiment, our results showed that across all the samples, 34.5 ± 0.3% of the ^{14}C-labelled glucose added to the soil was recovered as $^{14}CO_2$ (n = 970). Of this, most was recovered in the first 24 h after substrate addition (83.4 ± 0.3% of the total $^{14}CO_2$), suggesting that the ^{14}C-glucose was rapidly assimilated by the soil microbial community. This was subsequently validated on a smaller subset of samples (n = 30) where the NaOH traps were changed at more regular intervals (see Supplementary information and Fig. S1). This finding is also in agreement with previous studies on soils similar to those employed here (Hoyle et al., 2008; Creamer et al., 2014). Extraction with 1 M NaCl at the end experiment showed that only small amounts of the ^{14}C-derived glucose could be recovered from the soil across all the samples (2.6 ± 0.1% of the total ^{14}C added) suggesting that the 97.4% of the ^{14}C-glucose had been taken up by the microbial biomass. The partitioning of ^{14}C by the microbial biomass into anabolic and catabolic processes showed that CUE varied widely (0.25–0.95) and followed a Gaussian distribution (Fig. 1; Table 1). The mean CUE value presented

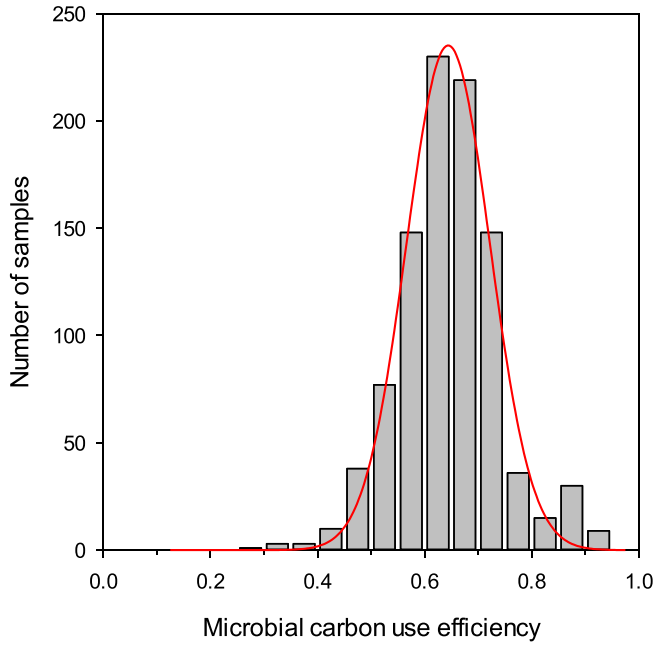

Fig. 1. Distribution in microbial C use efficiency (CUE) across the 970 samples used in this study. The line represents the fit of a Gaussian model to the experimental data (r^2 = 0.982).

here (0.646 ± 0.003; n = 970) was similar to that reported in soils from Europe (0.669 ± 0.005; n = 66; Jones et al., 2018a) and predicted from *in silico* metabolic modelling (0.62 ± 0.17; Saifuddin et al., 2019).

Our analysis revealed that CUE was strongly correlated with both soil pH and exchangeable Al content (P < 0.001; Fig. 2). In contrast, the relationship between CUE and either soil available S (P = 0.662), clay content (P = 0.542), available P (P = 0.083), total base cations (P = 0.080)and DOC (P = 0.03 were much less significant. A weak negative relationship was apparent between CUE and total soil C (P = 0.038), however, this only proved significant for a small subset of samples (< 5% of the total) which possessed high total C contents (total C ≥ 3%; Fig. S2). The relationship between CUE and pH showed a clear break point at pH 5.5 with CUE progressively declining as the soils became progressively more acidic (Fig. 2, upper panel). The inflection point in the sigmoidal relationship occurred at pH 4.88. The pH 5.5 break point coincided with the presence of Al^{3+} which started to dominate the soil exchange complex (Fig. 2, lower panel). As expected based on these results, there was also a strong relationship between CUE and exchangeable Al in soil (Fig. 3; Fig. S2).

While we acknowledge that our results cannot directly establish a causal relationship between microbial CUE and pH, our results are consistent with studies in plants and animals that have demonstrated large metabolic shifts in response to exposure to low pH and elevated Al concentrations (Zhao and Shen, 2018; Santore et al., 2018; Esparza et al., 2019). Notably in plants and aquatic organisms, the pH transition point at which metabolism starts to shift is almost the same as identified here (Fageria et al., 1990; Sayer et al., 1991; Serrano et al., 2008). Typically, one of the ways to overcome this exogenous stress is the production and secretion of compounds into the surrounding environment to complex and detoxify toxic Al^{3+} (e.g. extracellular polymeric substances, organic acids; Kobayashi et al., 2007; Auger et al., 2013; Hu et al., 2019). In addition, Al^{3+} can induce a range of other responses in organisms (e.g. interference with cell structure, signaling, membrane fluidity, enzyme function) as well as the activation of Al efflux mechanisms (Jones and Kochian, 1997; Auger et al., 2013). Consequently, exposure to Al leads to shifts in metabolism and a greater diversion of C into maintenance processes (e.g. reactive oxygen scavenging,

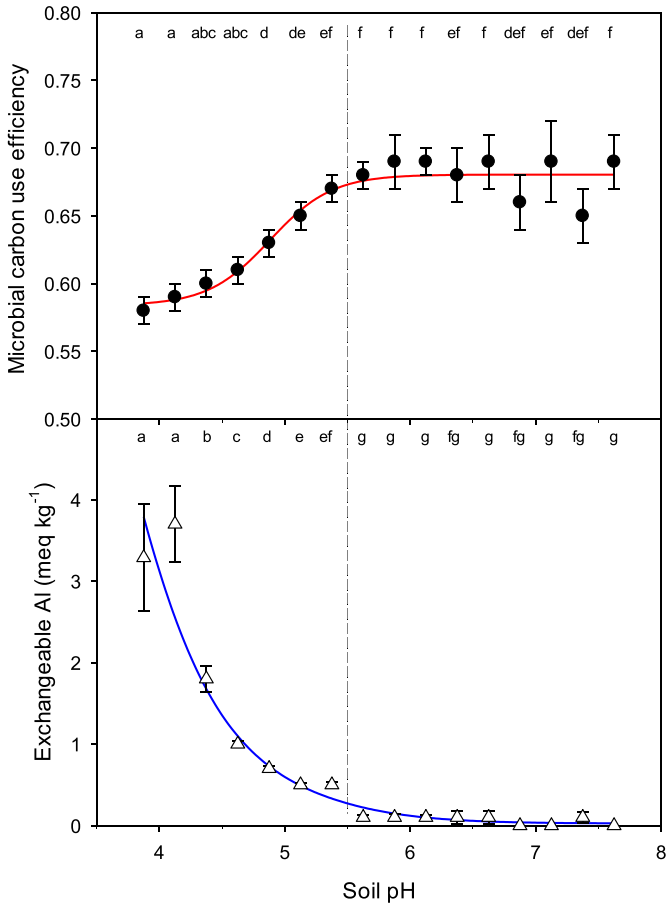

Fig. 2. Relationship between soil pH and microbial carbon use efficiency (upper panel), and soil pH and exchangeable Al (lower panel). Values represent means ± SEM. Different letters at the top of each panel represents significant differences between soil pH categories at the P < 0.05 level. The average number of values in each pH category is 68. The dotted line represents the soil pH value point at which there is a transition in the response of both CUE and exchangeable Al.

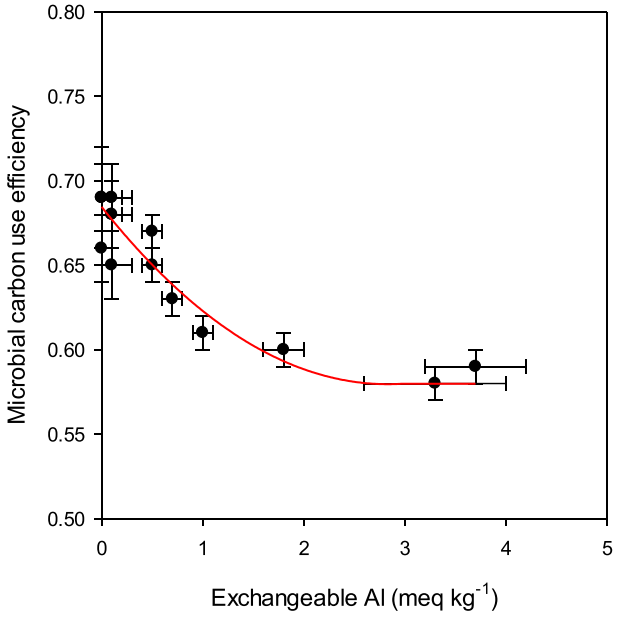

Fig. 3. Relationship between exchangeable Al and microbial carbon use efficiency. Values represent means ± SEM.

production of defense compounds, efflux pumps; Cumming et al., 1992; Auger et al., 2013). Furthermore, a recent metagenomic contrast of high and low pH soils, revealed elevated genes for metal resistance and membrane transport were notable features of acid soils (Malik et al., 2017). Such processes typically require ATP, meaning proportionally more C must be diverted into respiration. Further, Al may interfere with some respiratory pathways leading to re-routing of metabolism into more C inefficient pathways (Singh et al., 2009). As our results did not show any influence of pH on the speed of substrate use (Figs. S1 and S3), we also conclude that these changes in metabolism do not greatly affect the community's ability to use labile C, just the way it is partitioned internally.

Many studies have demonstrated the consistent dominance of pH in shaping belowground community composition at a range of spatial scales (Lauber et al., 2009; Griffiths et al., 2011; Tedersoo et al., 2014). Our pH-dependent CUE patterns could therefore also reflect differences in the dominance of certain microbial taxa. The highly weathered soils examined here have been shown previously to be bacterially dominated (Rui et al., 2017) suggesting that the dominance of certain bacterial groups at low pH (e.g. acidobacteria) may help explain the differences in CUE observed here. Intriguingly, past work has revealed a similar breakpoint of ~ pH 5.5 below which the acidobacteria become dominant (Jones et al., 2009; Griffiths et al., 2011). However, recent *in silico* predictions indicate that CUE may be highly variable in acidobacteria depending on substrate supply and genome size (Saifuddin et al., 2019). Further work should therefore establish if the activation of H^+/Al^{3+} tolerance mechanisms help explain the dominance of microbial taxa at low pH.

The Ca:Al ratio has often been used as a measure of stress in forest ecosystems (Farr et al., 2009), however, we found no relationship between Ca:Al and microbial CUE. In forest ecosystems, adverse effects on tree growth and nutrition occur at Ca:Al molar ratios < 1.0 (Cronan and Grigal, 1995), however, our values were generally much higher than this value. Consequently, as found for a range of plant species, this ratio may not be suitable as a stress indicator for microbial communities (Falkengren-Grerup et al., 1995; Rehmus et al., 2017).

Previous studies on very similar soils have shown that microbial uptake and partitioning of glucose-C can be highly dependent on soil nutrient availability (e.g. N, P and S; Creamer et al., 2014). This is also supported by similar studies showing CUE response to nutrient availability in other soils (Khan and Joergensen, 2019). Although we do not discount nutrient stoichiometry completely, it is more likely that this is of greater importance when much larger amounts of C are added to the soil, microbial growth is promoted and the demand for nutrients increases. For example, in the study by Creamer et al. (2014) the amount of glucose-C added was ca. 970 times higher than employed here. Here we used a low amount of C to more closely resemble steady state conditions. Further work is therefore required to understand the relationship between pH, nutrient stoichiometry and CUE at higher C addition rates.

In conclusion, we have established a clear relationship between CUE and pH across a wide range of agricultural soils. Although organic matter often accumulates in acid mineral soils under agricultural production (Hoyle et al., 2016), such as the ones studied here, this accumulation does not appear to be positively correlated with CUE. Our data shows that maintaining soil pH above 5.5 promotes greater microbial energy efficiency.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107584.

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