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UNDERSTANDING FINE SEDIMENT DYNAMICS IN AQUATIC SYSTEMS

Do temperature and moisture conditions impact soil microbiology and aggregate stability?

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Abstract

Purpose Studies predicting the impacts of climate change on erosion have considered numerous variables, such as rainfall erosivity and vegetation cover, but have not considered potential changes in soil erodibility. Erodibility is an intrinsic property of the soil, strongly correlated with the stability of soil aggregates. It is influenced by soil physico-chemical attributes, including the microbiological community. The study aim was to determine how shifts in temperature and moisture conditions, which other studies have shown affect microbiological communities, might affect aggregate stability.

Methods Using an experimental approach with laboratory microcosms, aggregates from a sandy loam soil and a clay soil were incubated at three temperatures and three moisture conditions in a factorial experimental design. Aggregate stability was quantified using rainfall simulation. Microbiological indicator metrics were measured to evaluate treatment microbiological impacts, including community composition (PLFA), biomass carbon, and respiration.

Results Temperature and moisture content affected aggregate stability significantly, but differently for the two soil types tested. For the sandy loam soil, aggregate stability decreased significantly with increasing moisture content. For the clay soil, aggregate stability increased significantly with increasing temperature. For both soil textures, temperature and moisture content affected microbiological community composition and respiration. Regression analysis indicated that microbiological properties were significant predictors of aggregate stability.

Conclusion Our results emphasise the dynamic nature of soil aggregate stability. Changes in microbiological metrics suggest possible biological mechanisms for aggregate stability changes, which should be investigated further to better understand the potential impacts of climate change on soil erodibility and erosion.

Keywords Soil erosion · Erodibility · Climate change · Microbial community · Biostabilisation

1 Introduction

Climate change is predicted to impact the frequency, severity, and extent of soil erosion, threatening soil sustainability (Nearing et al. 2004; Mullan 2013). Whilst the potential impacts of climate change on rainfall erosivity have been well studied (Nearing 2001), few studies have considered the impacts on soil erodibility, i.e. the susceptibility of soil to erosive forces (Favis-Mortlock and Boardman 1995). Soil erodibility is an intrinsic property of the soil, determined by the soil properties (e.g. soil texture, organic matter, and biological activity) that influence the forces internal to the soil (e.g. gravity, cohesion, and adhesion) that resist surface erosion. It is represented methodologically as an erosion threshold (i.e. rainfall intensity or overland flow that initiates erosion) or, once the threshold has been surpassed, an erosion rate. Soil erodibility has been found to be strongly correlated inversely with aggregate stability; thus, aggregate stability has been widely used as an indicator of soil erodibility (Bryan 1968; Salvador Sanchis et al. 2008). Aggregate formation and stability are controlled by numerous abiotic and biotic factors that affect the binding of soil particles and aggregates (Six et al. 2004; Bronick and Lal 2005; Regelink et al. 2015). For example, soil microbes can aid aggregation through the physical enmeshment of particles by fungal hyphae (Degens et al. 1996; Lehmann and Rillig 2015) and by the production of exudates (e.g. extracellular polymeric

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substances; EPS) that promote particle adhesion (Tisdall and Oades 1982; Ritz and Young 2004; Blankinship et al. 2016). By working at the aggregate scale, researchers can focus on how soil properties affect erodibility, before scaling up to consider the interactions and feedbacks caused by other environmental or anthropogenic factors important at field scale.

Despite several proposed relationships between seasonal conditions and aggregate stability (e.g. Bullock et al. 1988), there is limited empirical evidence to support the prediction of climate change impacts on aggregate stability. Seasonal variations in aggregate stability have been observed (Lavee et al. 1996; Amézketa 1999; Cosentino et al. 2006; Salvador Sanchis et al. 2008), which suggest that it is responsive to changes in environmental conditions. However, there is a lack of consensus in the literature. Aggregate stability has been observed to both increase and decrease with changes in temperature and moisture content (Denef et al. 2001; Cosentino et al. 2006). Whilst some of the differences between studies could be explained by different methodologies and soil properties (Amézketa 1999) or climate-associated influences on aggregation creation and breakdown due to freeze-thaw or wetting-drying, it remains unclear how shifts in temperature and soil moisture, individually and in combination, might affect aggregate stability, and, in turn, erodibility.

Previous research has demonstrated that microbiological communities and the exudates they create are highly responsive to physical and environmental conditions (e.g. particle size distribution, soil moisture, light, and temperature) (Cosentino et al. 2006; Knapen et al. 2007; Nunan 2017; Baveye et al. 2018; Walker et al. 2018; Li et al. 2019; König et al. 2020). For example, changes in soil temperature and moisture have been shown to affect the composition of the microbiological community (Evans and Wallenstein 2014; Supramaniam et al. 2016), through a variety of mechanisms (e.g. changes in metabolic activity, available oxygen, resource availability and accessibility, microbial motility, and soil microstructure connectivity) (Franzluebbers 1999; Or et al. 2007b; Moyano et al. 2013). These changes would affect microbiological groups, including fungi, gram-positive bacteria, and gram-negative bacteria, differently due to structural and physiological differences, such as hyphal connectivity to resources and cell wall structure (Nazih et al. 2001; Uhlířová et al. 2005; Schimel et al. 2007). The variation in the effects of climatic conditions on microbiological groups affects ecological strategy and resource allocation and, in turn, modifies hyphal growth and EPS production and characteristics (Roberson and Firestone 1992; Evans and Wallenstein 2014). Thus, shifts in the abundance of fungi, gram-positive, and gram-negative bacteria associated with climatic conditions may have a varying effect upon aggregate stability. Therefore, whilst we know that a changing climate will affect the microbiological community, and microbiological communities and their exudates affect erodibility and aggregate stability, we have not yet explored the response of aggregate stability (Cosentino et al. 2006).

The aim of this study is to determine how shifts in temperature and moisture conditions, which have been shown to affect microbiological communities, affect soil aggregate stability. A laboratory experiment was designed to test the following hypotheses: (i) aggregate stability will be greater under higher temperatures; (ii) aggregate stability will be lowest under the driest soil conditions and greatest at intermediate moisture content; (iii) interaction between temperature and moisture treatments will yield the highest aggregate stability under the warmest and intermediate soil moisture conditions; and (iv) the effects of temperature and moisture on aggregate stability will be influenced by soil texture and duration of climate incubation. This research was inspired by the long history of research on biological aggregation and its effects on erodibility in aquatic sediment, with was a core area of research for Dr. Ian Droppo, for whom this special issue is dedicated.

2 Methods

2.1 Soil collection and preparation

Two surface soils (depth 0–150 mm) were used in this experiment: a sandy loam and a clay from the Silsoe Experimental Farm (Bedfordshire, England, National Grid Reference TL075356/TL075351). The sandy loam soil is from the Bearsted series (6% organic matter, 69% sand, 20% silt, 11% clay), and the clay soil is from the Evesham series (6% organic matter, 42% sand, 15% silt, 44% clay). These soils were selected because they had the same organic content, were managed by the same farmer, and were in close proximity (< 500 m apart), thus would have a similar microbiological species pool, even if community composition varied. The two soils were used because particle size distribution and clay content have been shown to alter numerous physical and chemical soil properties (e.g. porosity, soil pH, hydration characteristics and organic matter and cation interactions), which may affect the responses of the microbial community to temperature and moisture and influence soil aggregation processes (Bronick and Lal 2005; Regelink et al. 2015). On collection, the field moist soil was gently broken apart by hand following planes of least resistance, taking care to avoid compaction and smearing. Soils were then air-dried for 72 h away from direct sunlight and sieved to obtain aggregates with diameters between 2 and 5.6 mm. Any plant material retained was gently removed by hand.

The sieved aggregates (25 g, 2–5.6 mm) were assigned to microcosms, which consisted of a 2-mm aperture mesh (Wondermesh) fitted across a hoop (95 mm in diameter) and enclosed in an air-tight container (185 × 130 × 45 mm, $l \times w \times d$) with a cotton wool wetting bed to facilitate soil moisture content through capillary rise. To minimise the

level of initial disruption and the risk of slaking caused by the methodological addition of moisture, the wetting bed within the microcosms was designed to generate a slow rate of initial wetting. The aggregates were spread across the microcosm mesh in a single layer with minimal contact between aggregates to enable the investigation of single aggregate mechanisms. Nine treatments were prepared for each soil texture in a 3 × 3 multifactorial design, with three levels of temperature (5 °C, 15 °C, and 30 °C) and three levels of moisture content representing wet, intermediate, and dry conditions. Temperature was controlled by placing the microcosms in environmental chambers, whilst moisture content was controlled by adjusting the wetness of the wetting bed. For the wet treatment, 80 ml of deionised water was added to the wetting bed, and aggregates reached a moisture content of 32% (sandy loam) and 44% (clay) moisture content. In the intermediate treatment, 60 ml of water was added, and aggregates reached a moisture content of 14% (sandy loam) and 20% (clay). No water was added for the dry treatment resulting in a moisture content of < 2% (sandy loam) and < 7% (clay). Microcosm containers were opened regularly to allow air circulation at the same time as moisture content maintenance. To evaluate the effects of incubation duration, microcosms were held under the treatment conditions for 1 week, 2 weeks, or 4 weeks. For each treatment, paired microcosms were analysed for aggregate stability by rainfall simulation; microbiological community composition by phospholipid fatty acid (PLFA) analysis; microbial respiration rate by rapid automated bacterial impedance technique (RABIT); and microbial biomass carbon by chloroform fumigation extraction. Microcosms were paired for the different destructive laboratory analyses, and there were three sets of replicates per treatment.

2.2 Aggregate stability and rainfall simulation

There are numerous methods used to measure aggregate stability, with many methodologies based on the wet-sieving approach (Kemper and Koch 1966; Le Bissonnais 1996; Amézketa 1999). Whilst variants of this method enable the distinction of aggregate breakdown mechanisms, the process is highly mechanical and far removed from natural erosion processes. Comparatively, rainfall simulation has been reported to be the most realistic method for measuring aggregate stability (Almajmaie et al. 2017), and so, this method was selected here to determine aggregate stability. Aggregates held in the microcosms were subjected to a rainstorm generated by a 9-m gravity-fed hypodermic needle rainfall simulator (Allton et al. 2007; Jeffery et al. 2010). Before each rainfall event, all microcosms were air-dried for 24 h (to standardise moisture conditions at the time of rainfall application to less than 7%) and weighed. The microcosms were subjected to a simulated rainfall event of 33 mm h^{-1} for 5 min, which represents a gentle rainfall event with a return period of less than 6 months (NERC 1975). After the rainfall simulation, samples were air-dried for 48 h and weighed.

The percentage of stable aggregates was calculated using the following equation (Almajmaie et al. 2017):

$$\text{Aggregate stability (\%)} = \frac{(\text{dry weight of aggregates post rainfall} - \text{microcosm structure})}{(\text{dry weight of aggregates pre rainfall} - \text{microcosm structure})} \times 100$$

Percentage data for aggregate stability was normalised using an arcsine transformation for statistical analyses.

2.3 Phospholipid fatty acid analysis

Phospholipid fatty acid (PLFA) analysis was used to characterise microbiological community composition, as current understanding of microbiological stabilisation potential is limited to broad taxonomic classes. PLFAs were extracted based on the procedures by Frostegård et al. (1993), Frostegård and Bååth (1994), and Bardgett et al. (1996), based on the method developed by Bligh and Dyer (1959). Aggregates for PLFA analysis were frozen at − 20 °C and freeze-dried. PLFAs were extracted from 10 g of aggregates. Fatty acid methyl esters (FAMEs) were identified by gas chromatography (GC) retention time. Results were expressed as a percentage of the total area of the identified peaks on the chromatogram, which was then used to assess relative abundance of fungi, gram-negative bacteria, and gram-positive bacteria. PLFAs 16:1ω5, 18:2ω6, and cis18:1ω9 were used as indicators for fungal biomass (Frostegård et al. 1993, 2011; Frostegård and Bååth 1994). Trans16:1ω11, cis16:1 ω7, cyc17:0iso, cis17:1ω8, cis17:0, trans17:1ω8, and cis19:0 represented gram-negative bacteria. Finally, i15:0, ai15:0, i16:0, 17:0 i17:0, and ai17:0 represented gram-positive bacteria (Bardgett et al. 1996; Zelles 1999; Ruess and Chamberlain 2010). Other PLFAs determined were 14:0, 15:0, i16:1, 16:0, Me17:0iso, Me17:0iso2, cyc17:0iso. 17:0br, 17:1ω 7, 17:0(12Me), 18:1ω7t, 18:1ω13, 18:0, 19:1ω6, 18:0(Me), 20:4(5,8, 4, 11,14), 20ω5(3), and 20:0.

2.4 Microbial respiration rate

Environmental conditions could affect aggregate stability through changes in the microbial metabolic rate, in which greater activity and, potentially, more exudates would be produced when the respiration rate is higher (Costa et al. 2018). Microbial respiration rate was calculated based on the indirect impedance technique and rapid automated bacterial impedance technique (RABIT; Don Whitley Neil, UK) according to Ritz et al. (2006). This method measures the decrease in conductance of alkaline agar over time as the agar absorbs microbially produced CO_2 (Ritz et al. 2006; Butler et al. 2011, 2012). First,

RABIT cells were created by immersing electrodes in 1 ml of potassium hydroxide agar. Next, 1g of soil was weighed into a glass boat and sealed inside the RABIT cell. Samples were stored at 4 °C, then allowed 2 h at 25 °C within the RABIT equipment to allow for equilibration prior to measurement. The basal microbial respiration rate was determined over between 2- and 4-h incubation at 25 °C. The RABIT technique requires a constant temperature, as respiration rates are measured via electrical conductivity; thus, temperature was different from the incubation, but consistent across the temperature treatments. Respiration rates were corrected for dry mass of soil to account for soil moisture conditions consistent with the incubation treatment at the time of measurement. For each sample, three methodological replicates were included. Falsely terminated tests were removed from the dataset, as were outliers (identified as 1.5 times the interquartile range above or below the upper and lower quartiles). Microbial respiration rate was measured after the treatment incubation rather than during incubation due to the destructive nature of sampling and measurement. As such, the measurement of microbial respiration reflects the response of the microbial community to the consistent temperature during RABIT measurements post-incubation, mediated by previous thermal stress conditions during the incubation and substrate availability.

2.5 Microbial biomass carbon

Similar to respiration rates, an increase in microbial biomass carbon might reflect a greater absolute abundance of microbes and/or exudates, which previous studies have found could affect aggregate stability (Degens et al. 1996; Schloter et al. 2003). It was estimated for three replicates for each treatment, based on the chloroform extraction procedure developed by Jenkinson (1976) and Vance et al. (1987). A subsample equivalent to 12.5 g air-dry weight was placed in a 50-ml Duran bottle and fumigated for 24 h, whilst another subsample was not fumigated as a control. Dissolved carbon was extracted from both samples by shaking the subsamples in 50 ml of 0.5 M K_2SO_4 for 30 min and filtering through Whatman filter papers. Concentrations of dissolved organic carbon were measured using a segmented flow analyser. Carbon flush was assessed as the concentration of DOC from fumigated samples minus the concentration of DOC from the non-fumigated samples. Biomass carbon was estimated using a conversion factor of 0.45 (British Standards Institution 1997).

2.6 Statistical analysis

Analysis of variance (ANOVA) and Tukey's HSD post hoc tests were used to assess differences in aggregate stability, microbial biomass C, and microbial respiration rate between treatments. Pearson correlation analysis was used to test correlative associations between variables including aggregate stability, temperature, soil moisture, and microbial properties. Multiple regression analysis for both soil textures was completed using the stepwise method. R3.2.5 was used for statistical analysis (R Core Team 2018) using stepAIC from the MASS package (Venables and Ripley 2002) and the ggplot2 package (Wickham 2016), and results were considered significant at $p \leq 0.05$.

3 Results

In both sandy loam and clay samples, the duration of incubation (1 week, 2 weeks, or 4 weeks) had no significant effect on aggregate stability ($p > 0.05$, data not shown). As the focus of this study was on aggregate stability, statistical analyses were completed on pooled results as a single dataset. Furthermore, as there were no significant observed interaction effects between temperature and moisture content on aggregate stability (ANOVA, $p > 0.05$), the main effects of the climatic conditions are considered individually, i.e. the main effects of temperature considered across all moisture contents and conversely.

3.1 Aggregate stability

Aggregate stability responded differently to the temperature and moisture content treatments for the two soils tested (Fig. 1). For the sandy loam soil, aggregate stability was significantly different between moisture treatments ($p < 0.001$), with the highest aggregate stability in the dry treatment (Fig. 1B). There was no significant difference in aggregate stability between temperature treatments ($p > 0.05$, Fig. 1A). Meanwhile, for the clay soil, aggregate stability significantly increased with increasing temperature ($p < 0.005$; Fig. 1C), but there was no significant effect on aggregate stability for the moisture content treatments ($p > 0.05$; Fig. 1D).

3.2 Microbiological variables

The microbiological data provide evidence that the temperature and moisture content treatments produced changes to variables associated with metabolic activity and community composition. It was not possible to monitor respiration during the incubation, so it was measured post-incubation. The results show that the microbial community had higher respiration rates after incubation under the 5 °C treatment than the 15 °C and 30 °C treatments. It also increased with increasing moisture content in the sandy loam soil aggregates (Fig. 2A, B) and clay aggregates (Fig. 3A, B). For both temperature and moisture content, these results suggest that the high respiration rates measured post-incubation may

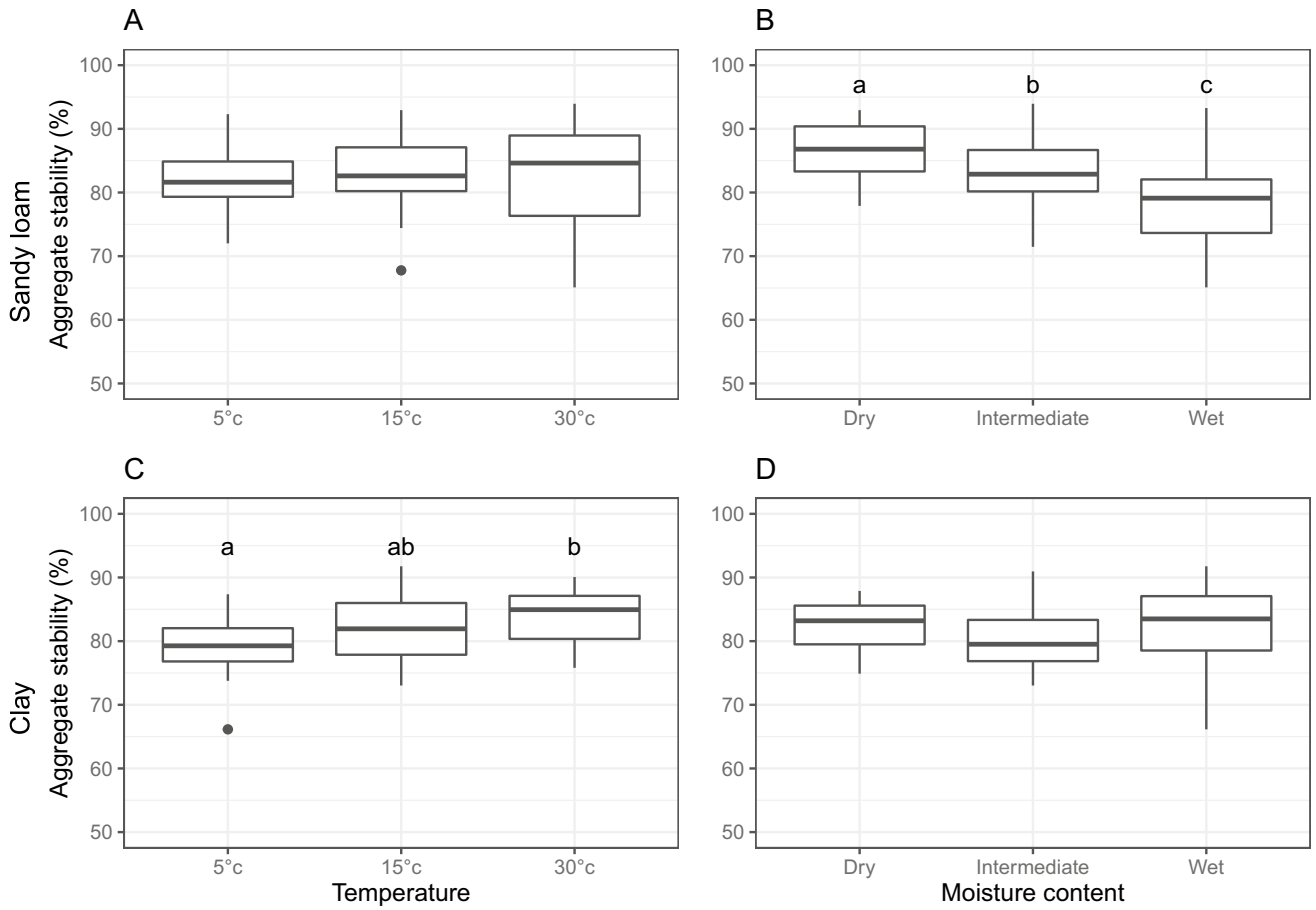

Fig. 1 Aggregate stability by **A**, **C** temperature and **B**, **D** moisture content for **A**, **B** sandy loam and **C**, **D** clay. Different letters signify statistically significant difference for arcsine transformed percentage aggregate stability

have been caused by lower metabolic activity during incubation, a ramping up of metabolic rates at more favourable thermal conditions, or a more bioavailable carbon sources at the time of measurement. Microbial biomass carbon was not significantly affected by temperature or moisture content in the sandy loam (Fig. 2C, D). However, in the clay soil aggregates, microbial biomass carbon significantly increased with increasing moisture content (Fig. 3D).

The relative abundances of gram-positive and gram-negative bacteria were not significantly affected by temperature or moisture content in the sandy loam soil aggregates (Fig. 4A–D). In the clay soil aggregates, increasing temperature significantly increased gram-positive bacteria abundance, with the relative abundance of gram-positive bacteria significantly higher at 30 °C (Fig. 5A). In contrast, gram-negative bacterial abundance decreased with increasing temperature, as the relative abundance of gram-negative bacteria was significantly higher at 5 °C and decreased with increasing temperature (Fig. 5C). In both soils tested, moisture content did not significantly influence the relative abundance of gram-positive or gram-negative bacteria (Figs. 4 and 5).

In the sandy loam soil aggregates, the relative abundance of fungi was significantly higher in the driest treatment, but fungal abundance was not significantly affected by temperature (Fig. 4E, F). In the clay soil aggregates, temperature and moisture content conditions did not significantly influence fungal abundance (Fig. 5E, F).

3.3 Statistical analyses

For the sandy loam soil, aggregate stability was significantly negatively correlated with moisture content, but had no significant correlation with temperature (Table 1). Temperature was significantly negatively correlated with the relative abundance of fungi. Moisture content was significantly positively correlated with microbial respiration and significantly negatively correlated with the relative abundance of fungi. Aggregate stability showed significant positive correlations with microbial biomass carbon and relative abundance of gram-negative bacteria.

Pearson correlation analysis on the clay aggregates showed a significant positive correlation between aggregate stability

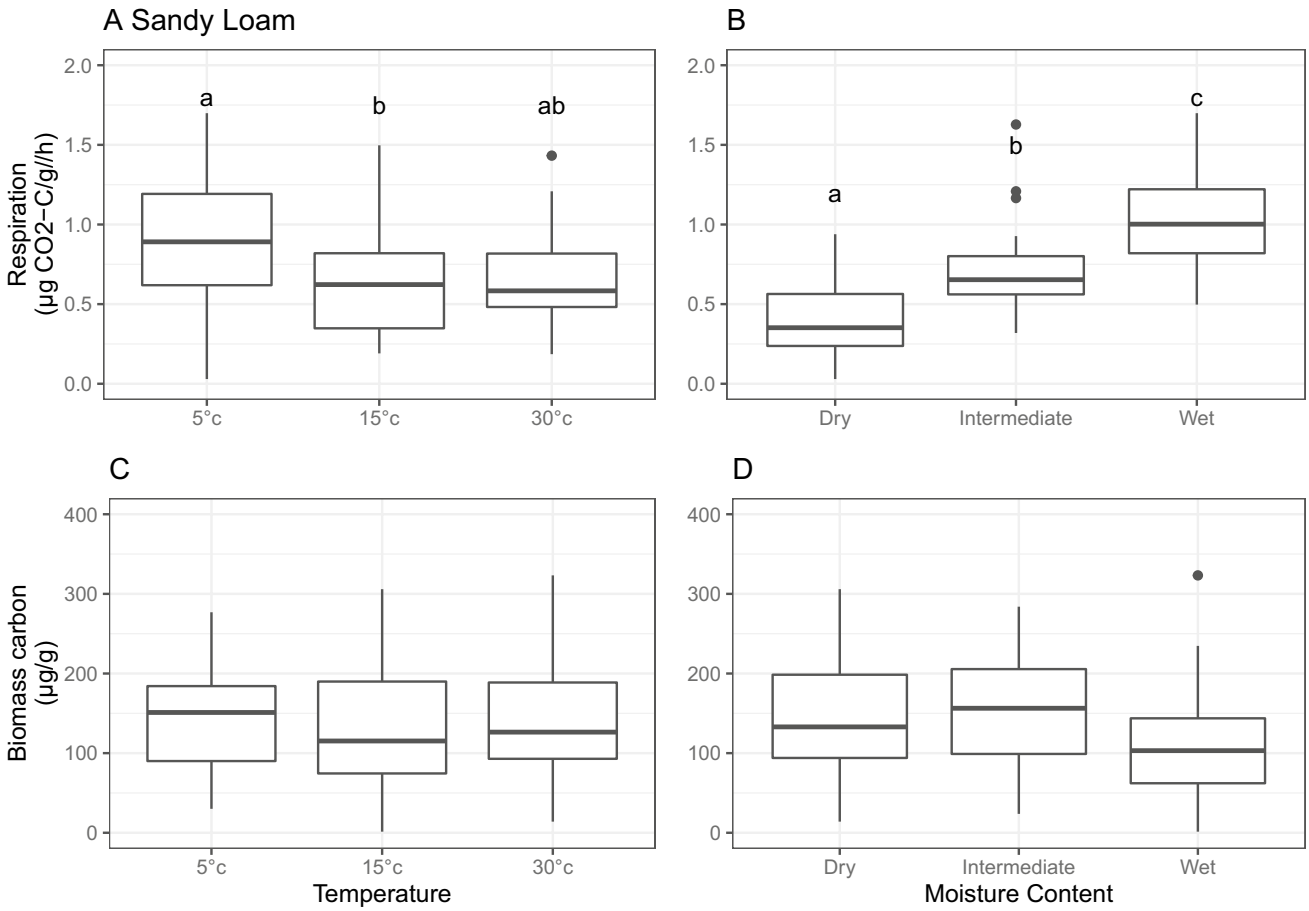

Fig. 2 Microbial respiration (**A**, **B**) and microbial biomass carbon (**C**, **D**) by temperature and moisture content for sandy loam aggregates. Different letters signify statistically significant differences

and temperature (Table 2). Contrary to the sandy loam soil results, aggregate stability was not correlated with moisture content. Temperature had a significantly negative correlation with microbial respiration and the relative abundance of gram-negative bacteria, but temperature was significantly positively correlated with the relative abundance of gram-positive bacteria. Moisture content had a significant positive correlation with microbial respiration and microbial biomass carbon. Aggregate stability was also shown to be significantly negatively correlated with the relative abundance of gram-negative bacteria.

Multiple regression analysis showed that several microbiological properties were significant predictors of aggregate stability (Table 3). However, there were substantial differences between the sandy loam and clay minimally adequate models. For the sandy loam soil aggregates, stability was best predicted by microbial respiration, biomass carbon, and gram-negative abundance (adjusted $R^2 = 0.209$, $p < 0.001$). Meanwhile, for the clay soil aggregates, it was best predicted by the relative abundance of gram-negative bacteria (adjusted $R^2 = 0.064$, $p = 0.013$).

4 Discussion

The aim of the experimental laboratory study was to determine how shifts in temperature and moisture conditions, which affect the microbiological community, affect soil aggregate stability. The main findings were (i) the effects of temperature and moisture on aggregate stability differed between the two soil types tested but not the duration of incubation (hypothesis 4); (ii) aggregate stability differed significantly by pre-rainfall incubation temperature for the clay soil tested, with the hottest temperature having the greatest stability and relative abundance of gram-positive bacteria (hypothesis 1); (iii) aggregate stability differed significantly by pre-rainfall incubation soil moisture for the sandy loam soil tested, with the driest sandy loam aggregates having the greatest stability and relative abundance of fungi (hypothesis 2); and (iv) no significant interaction effects were observed for moisture and temperature treatments in this factorial experiments for the two soils tested (hypothesis 3).

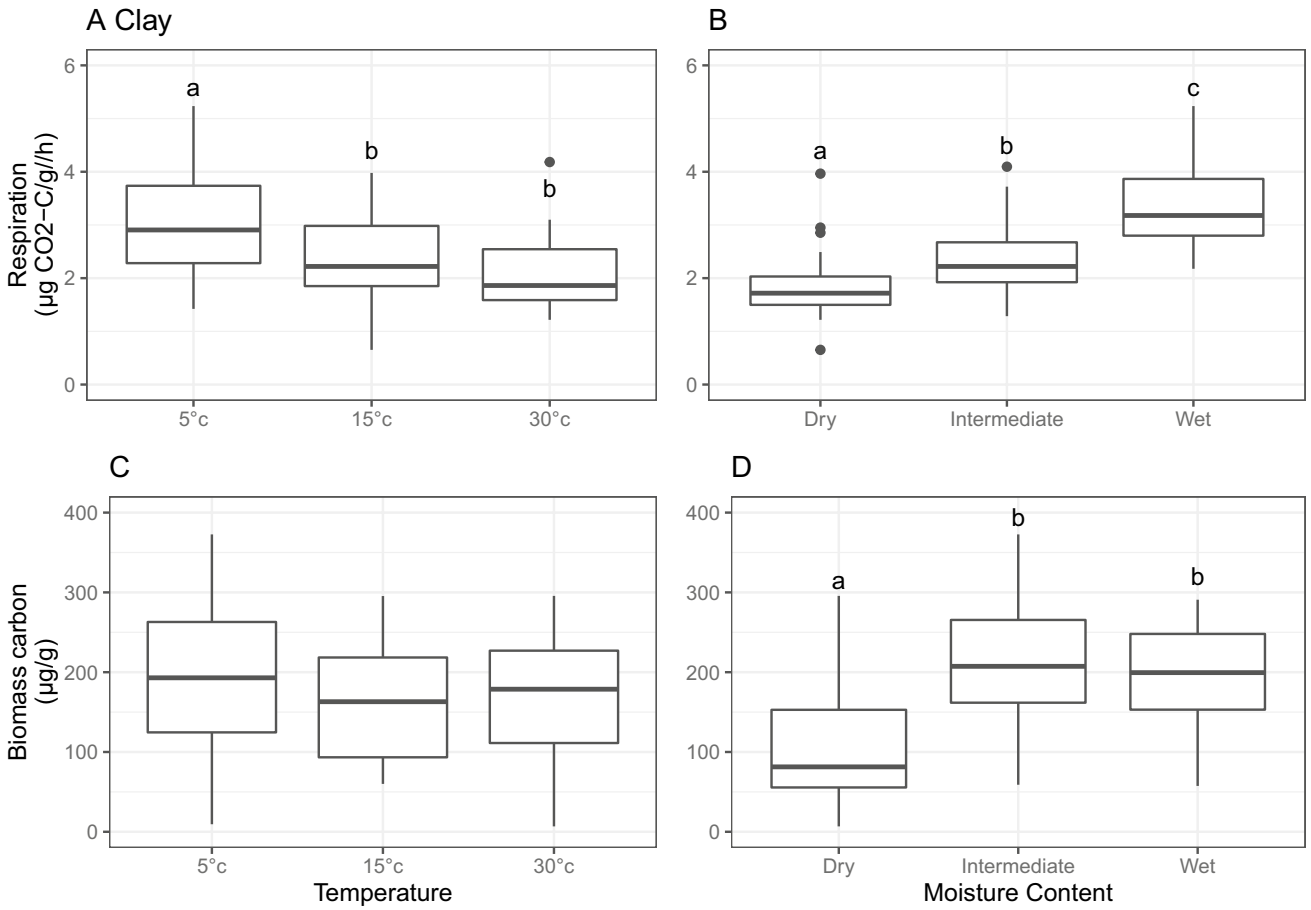

Fig. 3 Microbial respiration (**A**, **B**) and microbial biomass carbon (**C**, **D**) by temperature and moisture content for clay aggregates. Different letters signify statistically significant differences

In this study, aggregate stability increased significantly with increasing temperature for the clay soil tested (Fig. 1A, C). This positive relationship between aggregate stability and temperature for the clay aggregates is not supported by theory on the physico-chemical effects of temperature, which hypothesises that aggregate stability would decrease with increasing temperature as interparticle bonds are weakened through several physical and chemical mechanisms (Plum and Esrig 1969; Dexter et al. 2010; Kelishadi et al. 2018). Increased temperature is hypothesised to cause an increase in the internal energy of particles resulting in the expansion of entrapped air and double layers in clay, thereby disrupting interparticle bonds and reducing structural stability. However, fieldwork has provided some empirical support for our findings. Lavee et al. (1996) investigated aggregate stability along a climatological transect and found that aggregate stability was highest under temperatures of 15 °C and lower for temperatures between 0 and 10 °C and temperatures exceeding 35 °C. This unimodal peak in aggregate stability was suggested to be a combination of the physical effects of temperature and biotic activity, though soil microbiological properties were not measured in that study. A similar unimodal distribution in aggregate stability was found across an 800-m elevation gradient in an alpine meadow, which was related to the combined effects of temperature and moisture on microbiological activity and soil carbon (Li et al. 2017).

Aggregate stability decreased significantly with increasing moisture content for the sandy loam soil (Fig. 1A, C). This soil moisture effect on sandy loam aggregates is independent and unrelated to the more widely reported impact of moisture content at the time of rainfall (Cousen and Farres 1984; Ben-Hur and Lado 2008; Almajmaie et al. 2017). Moisture content was equilibrated for all treatments by air-drying prior to the rainfall event. Thus, these results indicate that moisture content during incubation affects processes internal to the aggregate that affect its stability.

The microbiological data confirms that the temperature and moisture treatments did affect community compositional and functional indicator metrics. However, similar to aggregate stability, the results differed between the two soils tested. For both soils, the only microbiological data

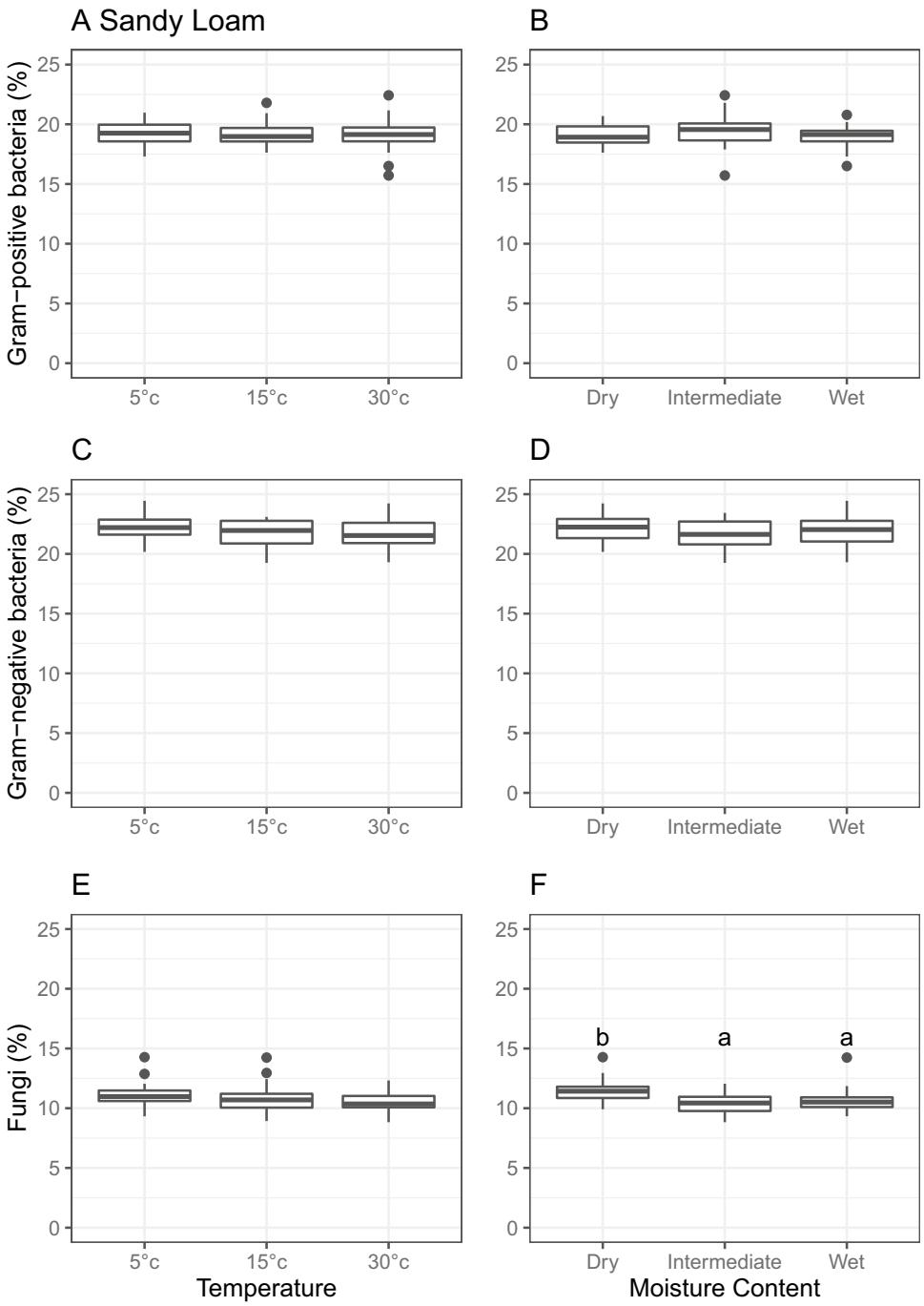

Fig. 4 The relative abundance (%) of gram-positive bacteria (**A**, **B**) gram-negative bacteria (**C**, **D**), and fungi (**E**, **F**) by temperature and moisture content for sandy loam aggregates. Different letters signify statistically significant differences

that align strongly with the changes in aggregate stability are the PFLA results (Figs. 4 and 5). For the sandy loam soil, the higher aggregate stability recorded in the dry treatment (Fig. 1B; Table 2) was associated with a significantly higher abundance of fungi (Fig. 4F). Similarly, for the clay loam soil, the higher aggregate stability recorded for the warm (30 C) treatment (Fig. 1C; Table 1) was associated with significantly higher gram-positive and lower gram-negative bacteria abundances (Fig. 5A, C; Table 1).

For the moisture effect observed in the sandy loam soil, previous studies have found the fungal hyphae are more tolerant of low soil moisture (Jennings 1987; De Boer et al. 2005) and that fungal biomass correlates with higher aggregate stability due to hyphal growth and particle enmeshment (Degens et al. 1996; Lehmann and Rillig 2015; Lehmann et al. 2020). Reduced aggregate stability is observed consistently in studies that inhibit the growth of the fungal component of the soil microbiological community using fungicides (Beare et al. 1997; Bossuyt et al. 2001; Tang et al. 2011). However,

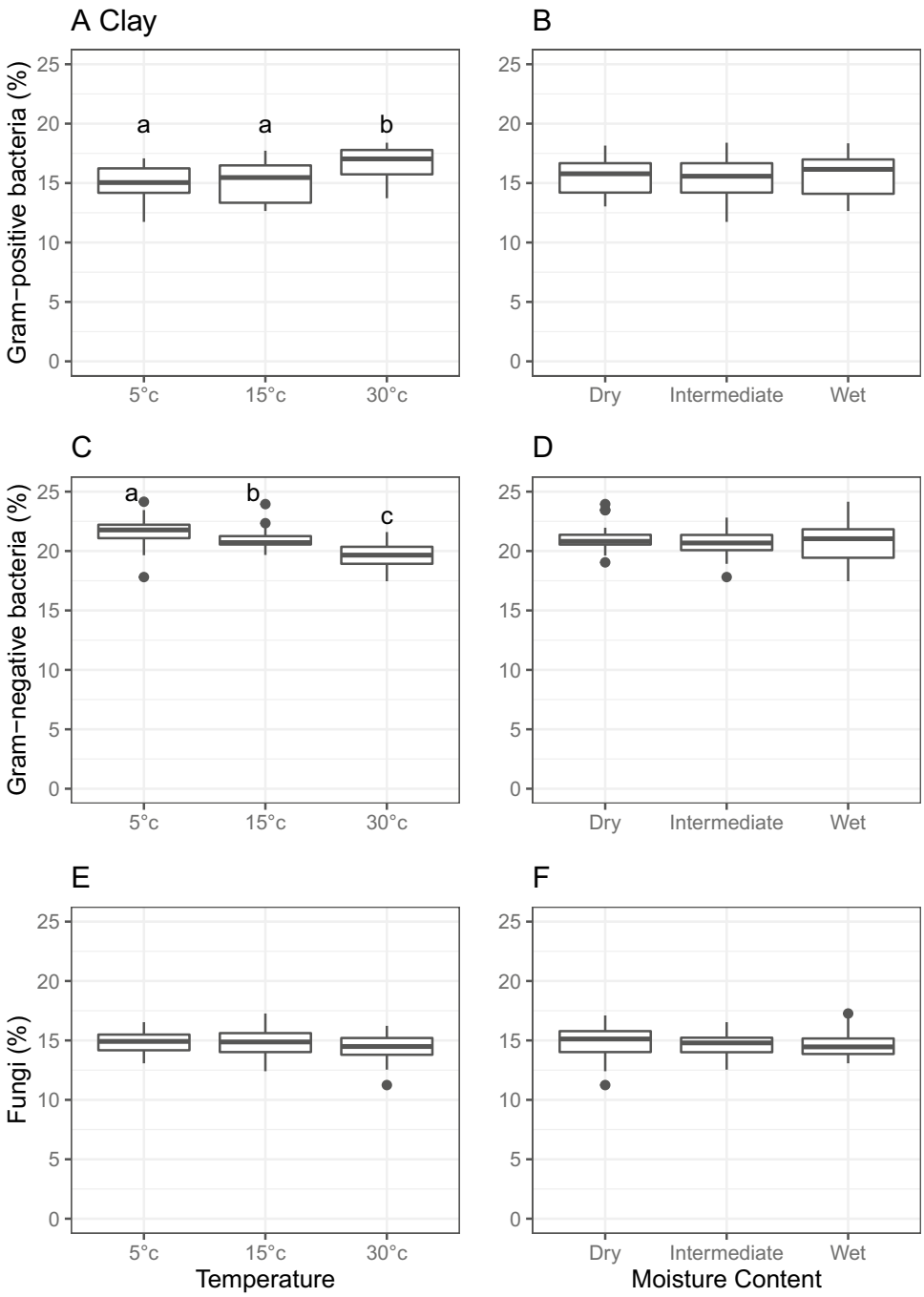

Fig. 5 The relative abundance (%) of gram-positive bacteria (**A**, **B**) gram-negative bacteria (**C**, **D**), and fungi (**E**, **F**) by temperature and moisture content for clay aggregates. Different letters signify statistically significant differences

soil moisture could affect aggregate stability through both physico-chemical and biological mechanisms. For example, the higher proportion of micropores to macropores in the clay soil aggregates may have made the aggregates less susceptible to fissure than the sandy loam aggregates (Peng and Horn 2005; Borken and Matzner 2009). These physical differences may also underlie biological-mediated responses to soil moisture that affect aggregate stability. Moisture content conditions influence numerous soil properties critical for microbiological life, including soil hydration status, oxygen availability, pore connectivity, bacterial motility, and thus, resource accessibility (Skopp et al. 1990; Or et al. 2007a; Moyano et al. 2013). These mechanisms could explain why respiration and microbial carbon biomass were identified as significant predictors in the regression analysis for the sandy loam soil (Table 3). Thus, there is evidence that changes in soil moisture affects aggregate stability, at least in the sandy loam soil tested; further research is needed to examine in detail the physico-chemical and biological mechanisms that might be responsible.

Table 1 Pearson correlation analysis for sandy loam aggregates

	Aggregate stability (arcsine)	Temperature	Moisture content	Incubation duration	Microbial respiration (μg CO_2-C g^{-1} h^{-1})	Microbial biomass carbon (μg g^{-1})	Gram-positive bacteria (mol%)	Gram-negative bacteria (mol%)
Temperature	0.065							
Moisture	− 0.529***	-						
Incubation duration	0.018	-	-					
Microbial respiration (μg CO_2-C g^{-1} h^{-1})	− 0.304**	− 0.213	0.655***	0.192				
Microbial biomass carbon (μg g^{-1})	0.253*	− 0.001	− 0.171	0.065	− 0.049			
Gram-positive bacteria (mol%)	− 0.070	− 0.036	− 0.050	0.115	− 0.157	− 0.013		
Gram-negative bacteria (mol%)	0.273*	− 0.112	− 0.115	− 0.296**	0.068	− 0.022	− 0.151	
Fungi (mol%)	− 0.070	− 0.250*	− 0.314**	0.057	− 0.220*	− 0.102	− 0.229*	− 0.155

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

For the temperature effect observed for the clay soil, the shift in the relative abundances of gram-positive and gram-negative bacteria is supported by previous research, which suggests that temperature-induced substrate constraints limit gram-negative bacteria, whilst gram-positive bacteria are better adapted to acquire resources at higher temperatures (Biasi et al. 2005; Feng and Simpson 2009). Whether these shifts in microbiological abundance are responsible for the differences in aggregate stability is unknown. Similarly, respiration post-incubation differed by temperature for the clay soil, with lower rates in higher temperature treatments (Fig. 3A). These results suggest that respiration rates were potentially higher during the hot temperature incubation, leading to substrate depletion prior to or during the

Table 2 Pearson correlation analysis for clay aggregates

	Aggregate stability (arcsine)	Temperature	Moisture content	Incubation duration	Microbial respiration (μg CO_2-C g^{-1} h^{-1})	Microbial biomass carbon (μg g^{-1})	Gram-positive bacteria (mol%)	Gram-negative bacteria (mol%)
Temperature	0.373***							
Moisture	0.031	-						
Incubation duration	− 0.112	-	-					
Respiration (μg CO_2-C g^{-1} h^{-1})	− 0.138	− 0.430***	0.657***	− 0.001				
Microbial biomass carbon (μg g^{-1})	− 0.133	− 0.104	0.396***	0.056	0.380***			
Gram-positive bacteria (mol%)	0.099	0.412***	0.036	− 0.008	− 0.130	− 0.154		
Gram-negative bacteria (mol%)	− 0.275*	− 0.603***	− 0.165	− 0.059	0.163	0.007	− 0.518***	
Fungi (mol%)	− 0.047	− 0.213	− 0.027	0.180	0.098	0.240*	− 0.522***	− 0.115

*$p < 0.05$; ***$p < 0.001$

Table 3 Multiple regression analysis for aggregate stability and microbial predictor variables for the sandy loam and clay aggregates, using stepwise method

Predictors	Aggregate stability arcsine (sandy loam)			Aggregate stability arcsine (clay)		
	Coefficient estimates	Std. error	*p* value	Coefficient estimates	Std. error	*p* value
Intercept	0.36	0.22	0.1	1.3	0.14	< 0.001
Respiration (μg CO_2-C g^{-1} h^{-1})	− 0.1	0.03	0.0025			
Microbial biomass carbon (μg g^{-1})	0.0004	0.00016	0.016			
Gram-negative bacteria (mol%)	0.029	0.0097	0.0036	− 0.17	0.0065	0.013
Observations	81			81		
R^2/adjusted R^2	0.239/0.209			0.076/0.064		
p value	< 0.001			0.013		

post-incubation testing (Moyano et al. 2013). A higher respiration rate during incubation could generate higher microbial abundances and exudates (Degens et al. 1996), but this mechanism is not supported by the data from this study (Fig. 3C). Furthermore, there are other significant differences in respiration rates for other treatments and the sandy loam soil that do not correspond to changes in aggregate stability (e.g. Figs. 2A and 3B). Thus, whilst microbial biomass carbon and respiration reflect microbial turnover of carbon and biomass synthesis and growth (Degens et al. 1996) and have often been used as indicators of microbially mediated processes (Schloter et al. 2003; Ritz et al. 2009; Truu et al. 2009), further research is necessary to determine how environmental conditions affect aggregate stability through changes in microbiological community composition, spatial arrangement, and biomechanical properties of the biologically generated organic compounds and structures.

This study was inspired by Dr. Ian G. Droppo's long and rich research career. His aquatic sediment research advanced our scientific understanding of the biological mechanisms for suspended sediment aggregation and the influence of chemical and physical factors on floc strength and sediment erodibility (Liss et al. 1996; Droppo 2001, 2004; Droppo et al. 2007, 2008, 2015, 2016; Grabowski et al. 2011, 2012). This whole system perspective on sediment composition and consideration of particle interactions has been influential in refocusing fundamental erosion and transport research at the floc and aggregate scale and broadening the factors investigated (e.g. Chen et al. 2022). Dr. Droppo has also helped to unify research soils and sediments, through his pioneering research on floc/aggregate characterisation (Droppo et al. 2005) and the transformation of eroded soil into riverine flocs (Grangeon et al. 2014). Through this research, we hope to encourage more cross-disciplinary and integrative research, informed by Dr. Droppo's work, to support renewed investigation into the dynamic and responsive nature of soil erodibility. To do this, we recommend further research on the mechanistic connections between environmental conditions, soil properties, microbiological community composition, and their stabilising functions. We recommend a renewed focus at the aggregate scale to determine how changes in environmental conditions (trends and increased variability) impact on the production of biogenic stabilising structures and functions to affect particle interactions at the aggregate scale. This work should attempt to separate out abiotic and biotic controls, for example, by identifying causal relationships through the comparison of sterile and non-sterile soil microcosms, and use advanced methods to monitor changes in communities (e.g. quantitative PCR, amplicon sequencing, and/or metagenomics) and their metabolic activity (e.g. CO_2 respiration during incubation, metabolomics). This fundamental research should link to larger scale work to consider how these factors in turn influence the hydrological and geomorphological processes that determine overland flow, erosion mechanisms (e.g. sheet and rill erosion), and sediment transport.

5 Conclusions

In this study, controlled laboratory experiments were used to determine how shifts in soil temperature and soil moisture, which alter the soil microbiology, affect the stability of soil aggregates. The key results were that these two climate-related conditions affected the two tested soils differently. Soil moisture had a significant effect on aggregate stability for the sandy loam soil, but temperature had a significant effect on the clay soil. The sandy loam soil aggregates were most stable following incubation under the driest condition and least stable under the wettest condition. Importantly, these results are different from the oft-reported effect of soil moisture on aggregate stability at the time of rainfall, as moisture content was equilibrated before stability testing. The clay soil aggregates were most stable following incubation under the hottest temperature (30 °C) and least stable at the coolest temperature (5 °C). The two soils differed in texture but were otherwise as similar as possible for natural soil samples (e.g. same organic content, managed by the

same farmer, and found in close proximity (< 500 m apart)). The changes in aggregate stability aligned with shifts in the microbiological community, a higher relative abundance of fungus in the sandy loam aggregates under dry conditions and more gram-positive bacteria in the clay soil aggregates under hot conditions. These results highlight the need to investigate further the interactions and feedbacks between climatic conditions, soil properties, microbiological communities, and aggregate stability. The study adds to a growing body of literature that documents that aggregate stability is a dynamic soil property responsive to shifts in climate, which must be investigated in greater detail and at larger spatial scales to better understand their implications for soil erodibility and the prediction of soil erosion with climate change.

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Data availability Data from this study are openly available from Cranfield University's Online research data repository (CORD) at DOI: https://doi.org/10.17862/cranfield.rd.23668803.

Declarations

Competing interests The authors declare no competing interests.

References

Allton KE, Harris JA, Rickson RJ, Ritz K (2007) The effect of microbial communities on soil hydrological processes: a microcosm study utilising simulated rainfall. Geoderma 142:11–17. https://doi.org/10.1016/j.geoderma.2007.06.004

Almajmaie A, Hardie M, Acuna T, Birch C (2017) Evaluation of methods for determining soil aggregate stability. Soil Tillage Res 167:39–45. https://doi.org/10.1016/j.still.2016.11.003

Amézketa E (1999) Soil aggregate stability: a review. J Sustain Agric 14:83–151. https://doi.org/10.1300/J064v14n02

Bardgett RD, Hobbs PJ, Frostegard A (1996) Changes in soil fungal : bacterial biomass ratios following reductions in the intensity of management of an upland grassland. Biol Fertil Soils 261–264

Baveye PC, Otten W, Kravchenko A et al (2018) Emergent properties of microbial activity in heterogeneous soil microenvironments: different research approaches are slowly converging, yet major challenges remain. Front Microbiol 9:1929. https://doi.org/10.3389/fmicb.2018.01929

Beare MH, Hu S, Coleman DC, Hendrix PF (1997) Influences of mycelial fungi on soil aggregation and organic matter storage in conventional and no-tillage soils. Appl Soil Ecol 5:211–219. https://doi.org/10.1016/S0929-1393(96)00142-4

Ben-Hur M, Lado M (2008) Effect of soil wetting conditions on seal formation, runoff, and soil loss in arid and semiarid soils - a review. Aust J Soil Res 46:191–202. https://doi.org/10.1071/SR07168

Biasi C, Rusalimova O, Meyer H et al (2005) Temperature-dependent shift from labile to recalcitrant carbon sources of arctic heterotrophs. Rapid Commun Mass Spectrom 19:1401–1408. https://doi.org/10.1002/rcm.1911

Blankinship JC, Fonte SJ, Six J, Schimel JP (2016) Plant versus microbial controls on soil aggregate stability in a seasonally dry ecosystem. Geoderma 272:39–50. https://doi.org/10.1016/j.geoderma.2016.03.008

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15:808–824. https://doi.org/10.1111/j.1365-2486.2008.01681.x

Bossuyt H, Denef K, Six J et al (2001) Influence of microbial populations and residue quality on aggregate stability. Appl Soil Ecol 16:195–208. https://doi.org/10.1016/S0929-1393(00)00116-5

British Standards Institution (1997) BS 7755 4.4.2:1997 Determination of microbial mass: part 2: fumigation-extraction method

Bronick CJ, Lal R (2005) Soil structure and management: a review. Geoderma 124:3–22. https://doi.org/10.1016/j.geoderma.2004.03.005

Bryan RB (1968) The development, use and efficiency of indices of soil erodibility. Geoderma 2:5–26

Bullock MS, Kemper WD, Nelson SD (1988) Soil cohesion as affected by freezing, water content, time and tillage. Soil Sci Soc Am J 52:770–776. https://doi.org/10.2136/sssaj1988.03615995005200030031x

Butler E, Whelan MJ, Ritz K et al (2011) Effects of triclosan on soil microbial respiration. Environ Toxicol Chem 30:360–366. https://doi.org/10.1002/etc.405

Butler E, Whelan MJ, Ritz K et al (2012) The effect of triclosan on microbial community structure in three soils. Chemosphere 89:1–9. https://doi.org/10.1016/j.chemosphere.2012.04.002

Chen WL, Grabowski RC, Goel S (2022) Clay swelling: role of cations in stabilizing/destabilizing mechanisms. ACS Omega 7:3185–3191. https://doi.org/10.1021/acsomega.1c04384

Cosentino D, Chenu C, Le Bissonnais Y (2006) Aggregate stability and microbial community dynamics under drying-wetting cycles in a silt loam soil. Soil Biol Biochem 38:2053–2062. https://doi.org/10.1016/j.soilbio.2005.12.022

Costa OYA, Raaijmakers JM, Kuramae EE (2018) Microbial extracellular polymeric substances: ecological function and impact on soil aggregation. Front Microbiol 9:1–14. https://doi.org/10.3389/fmicb.2018.01636

Cousen SM, Farres PJ (1984) The role of moisture content in the stability of soil aggregates from a temperate silty soil to raindrop impact. Catena 11:313–320. https://doi.org/10.1016/0341-8162(84)90029-8

De Boer W, Folman LB, Summerbell RC, Boddy L (2005) Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiol Rev 29:795–811. https://doi.org/10.1016/j.femsre.2004.11.005

Degens BP, Sparling GP, Abbott LK (1996) Increasing the length of hyphae in a sandy soil increases the amount of water-stable

aggregates. Appl Soil Ecol 3:149–159. https://doi.org/10.1016/0929-1393(95)00074-7
Denef K, Six J, Bossuyt H et al (2001) Influence of dry-wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biol Biochem 33:1599–1611
Dexter AR, Richard G, Czyz EA, Giot G (2010) Changes in the matric potential of soil water with time and temperature. Soil Sci 175:320–328. https://doi.org/10.1097/SS.0b013e3181e83d98
Droppo IG (2001) Rethinking what constitutes suspended sediment. Hydrol Process 15:1551–1564
Droppo IG (2004) Structural controls on floc strength and transport. Can J Civ Eng 31:569–578
Droppo IG, D'Andrea L, Krishnappan BG et al (2015) Fine-sediment dynamics: towards an improved understanding of sediment erosion and transport. J Soils Sediments 15:467–479. https://doi.org/10.1007/s11368-014-1004-3
Droppo IG, Exall K, Stafford K (2008) Effects of chemical amendments on aquatic floc structure, settling and strength. Water Res 42:169–179
Droppo IG, Krishnappan BG, Lawrence JR (2016) Microbial interactions with naturally occurring hydrophobic sediments: influence on sediment and associated contaminant mobility. Water Res 92:121–130. https://doi.org/10.1016/j.watres.2016.01.034
Droppo IG, Nackaerts K, Walling DE, Williams N (2005) Can flocs and water stable soil aggregates be differentiated within fluvial systems? Catena 60:1–18. https://doi.org/10.1016/j.catena.2004.11.002
Droppo IG, Ross N, Skafel M, Liss SN (2007) Biostabilization of cohesive sediment beds in a freshwater wave-dominated environment. Limnol Oceanogr 52:577–589
Evans SE, Wallenstein MD (2014) Climate change alters ecological strategies of soil bacteria. Ecol Lett 17:155–164. https://doi.org/10.1111/ele.12206
Favis-Mortlock DT, Boardman J (1995) Nonlinear responses of soil-erosion to climate change: a modeling study on the UK South Downs. Catena 25:365–387
Feng X, Simpson MJ (2009) Temperature and substrate controls on microbial phospholipid fatty acid composition during incubation of grassland soils contrasting in organic matter quality. Soil Biol Biochem 41:804–812. https://doi.org/10.1016/j.soilbio.2009.01.020
Franzluebbers AJ (1999) Microbial activity in response to water-filled pore space of variably eroded southern Piedmont soils. Appl Soil Ecol 11:91–101. https://doi.org/10.1016/S0929-1393(98)00128-0
Frostegård Å, Bååth E (1994) The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. Biol Fertil Soils 22:59–65. https://doi.org/10.1007/BF00384433
Frostegård Å, Bååth E, Tunlid A (1993) Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis. Soil Biol Biochem 25:723–730
Frostegård Å, Tunlid A, Bååth E (2011) Use and misuse of PLFA measurements in soils. Soil Biol Biochem 43:1621–1625. https://doi.org/10.1016/j.soilbio.2010.11.021
Grabowski RC, Droppo IG, Wharton G (2011) Erodibility of cohesive sediment: the importance of sediment properties. Earth-Science Rev 105:101–120. https://doi.org/10.1016/j.earscirev.2011.01.008
Grabowski RC, Wharton G, Davies GR, Droppo IG (2012) Spatial and temporal variations in the erosion threshold of fine riverbed sediments. J Soils Sediments 12:1174–1188. https://doi.org/10.1007/s11368-012-0534-9
Grangeon T, Droppo IG, Legout C, Esteves M (2014) From soil aggregates to riverine flocs: a laboratory experiment assessing the respective effects of soil type and flow shear stress on particles characteristics. Hydrol Process 28:4141–4155. https://doi.org/10.1002/hyp.9929
Jeffery S, Harris JA, Rickson RJ, Ritz K (2010) Effects of soil-surface microbial community phenotype upon physical and hydrological properties of an arable soil: a microcosm study. Eur J Soil Sci 61:493–503. https://doi.org/10.1111/j.1365-2389.2010.01249.x
Jenkinson DS (1976) The effects of biocidal treatments on metabolism in soil - IV. The decomposition of fumigated organisms in soil. Soil Biol Biochem 8:203–208
Jennings DH (1987) Translocation of solutes in fungi. Biol Rev 62:215–243
Kelishadi H, Mosaddeghi MR, Ayoubi S, Mamedov AI (2018) Effect of temperature on soil structural stability as characterized by high energy moisture characteristic method. Catena 170:290–304. https://doi.org/10.1016/j.catena.2018.06.015
Kemper WD, Koch EJ (1966) Aggregate stability of soils from western United States and Canada. United States Department of Agriculture, U.S. Dept. Agric. Tech. Bull. No. 1355. http://ageconsearch.umn.edu/bitstream/171386/2/tb1355.pdf
Knapen A, Poesen J, Galindo-Morales P et al (2007) Effects of microbiotic crusts under cropland in temperate environments on soil erodibility during concentrated flow. Earth Surf Process Landforms 32:1884–1901. https://doi.org/10.1002/esp.1504
König S, Vogel H-J, Harms H, Worrich A (2020) Physical, chemical and biological effects on soil bacterial dynamics in microscale models. Front Ecol Evol 8:. https://doi.org/10.3389/fevo.2020.00053
Lavee H, Sarah P, Imeson AC (1996) Aggregate stability dynamics as affected by soil temperature and moisture regimes. Geogr Ann 78:73–82
Le Bissonnais Y (1996) Aggregate stability and assessment of soil crustability and erodibility: 1. Theory and methodology. Eur J Soil Sci 47:425–437
Lehmann A, Rillig MC (2015) Understanding mechanisms of soil biota involvement in soil aggregation: a way forward with saprobic fungi? Soil Biol Biochem 88:298–302. https://doi.org/10.1016/j.soilbio.2015.06.006
Lehmann A, Zheng W, Ryo M et al (2020) Fungal traits important for soil aggregation. Front Microbiol 10:1–13. https://doi.org/10.3389/fmicb.2019.02904
Li C, Cao Z, Chang J et al (2017) Elevational gradient affect functional fractions of soil organic carbon and aggregates stability in a Tibetan alpine meadow. Catena 156:139–148. https://doi.org/10.1016/j.catena.2017.04.007
Li J, Wang G, Mayes MA et al (2019) Reduced carbon use efficiency and increased microbial turnover with soil warming. Glob Chang Biol 25:900–910. https://doi.org/10.1111/gcb.14517
Liss SN, Droppo IG, Flannigan DT, Leppard GG (1996) Floc architecture in wastewater and natural riverine systems. Environ Sci Technol 30:680–686
Moyano FE, Manzoni S, Chenu C (2013) Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biol Biochem 59:72–85. https://doi.org/10.1016/j.soilbio.2013.01.002
Mullan D (2013) Soil erosion under the impacts of future climate change: assessing the statistical significance of future changes and the potential on-site and off-site problems. Catena 109:234–246. https://doi.org/10.1016/j.catena.2013.03.007
Nazih N, Finlay-Moore O, Hartel PG, Fuhrmann JJ (2001) Whole soil fatty acid methyl ester (FAME) profiles of early soybean rhizosphere as affected by temperature and matric water potential. Soil Biol Biochem 33:693–696. https://doi.org/10.1016/S0038-0717(00)00197-8
Nearing MA (2001) Potential changes in rainfall erosivity in the U.S. with climate change during the 21st century. J Soil Water Conserv 56:229–232
Nearing MA, Pruski FFF, O'Neal MRR (2004) Expected climate change impacts on soil erosion rates: a review. J Soil Water Conserv 59:43–50

NERC (1975) Flood studies report: volume 2: Meteorological and map annex. London

Nunan N (2017) Game changer in soil science: the microbial habitat in soil: scale, heterogeneity and functional consequences. Zeitschrift fur Pflanzenernahrung und Bodenkd 180:425–429. https://doi.org/10.1002/jpln.201700184

Or D, Phutane S, Dechesne A (2007a) Extracellular polymeric substances affecting pore-scale hydrologic conditions for bacterial activity in unsaturated soils. Vadose Zo J 6:298. https://doi.org/10.2136/vzj2006.0080

Or D, Smets BF, Wraith JM et al (2007b) Physical constraints affecting bacterial habitats and activity in unsaturated porous media – a review. Adv Water Resour 30:1505–1527. https://doi.org/10.1016/j.advwatres.2006.05.025

Peng X, Horn R (2005) Modeling soil shrinkage curve across a wide range of soil types. Soil Sci Soc Am J 69:584–592. https://doi.org/10.2136/sssaj2004.0146

Plum RL, Esrig MI (1969) Some temperature effects on soil compressibility and pore water pressures. Highw Res Board Spec Rep 103:231–242

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Regelink IC, Stoof CR, Rousseva S et al (2015) Linkages between aggregate formation, porosity and soil chemical properties. Geoderma 247–248:24–37. https://doi.org/10.1016/j.geoderma.2015.01.022

Ritz K, Black HIJ, Campbell CD et al (2009) Selecting biological indicators for monitoring soils: a framework for balancing scientific and technical opinion to assist policy development. Ecol Indic 9:1212–1221. https://doi.org/10.1016/j.ecolind.2009.02.009

Ritz K, Harris JA, Pawlett M, Stone D (2006) Catabolic profiles as an indicator of soil microbial functional diversity. Environment Agency SC040063/SR, Bristol

Ritz K, Young IM (2004) Interactions between soil structure and fungi. Mycologist 18:52–59. https://doi.org/10.1017/S0269915XO4002010

Roberson EB, Firestone MK (1992) Relationship between desiccation and exopolysaccharide production in a soil *Pseudomonas* sp. Appl Environ Microbiol 58:1284–1291

Ruess L, Chamberlain PM (2010) The fat that matters: soil food web analysis using fatty acids and their carbon stable isotope signature. Soil Biol Biochem 42:1898–1910. https://doi.org/10.1016/j.soilbio.2010.07.020

Salvador Sanchis MP, Torri D, Borselli L, Poesen J (2008) Climate effects on soil erodibility. Earth Surf Process Landforms 33:1082–1097. https://doi.org/10.1002/esp.1604

Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. Ecology 88:1386–1394. https://doi.org/10.1890/06-0219

Schloter M, Dilly O, Munch JC (2003) Indicators for evaluating soil quality. Agric Ecosyst Environ 98:255–262. https://doi.org/10.1016/S0167-8809(03)00085-9

Six J, Bossuyt H, Degryze S, Denef K (2004) A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil Tillage Res 79:7–31. https://doi.org/10.1016/j.still.2004.03.008

Skopp J, Jawson MD, Doran JW (1990) Steady-state aerobic microbial activity as a function of soil water content. Soil Sci Soc Am J 54:1619. https://doi.org/10.2136/sssaj1990.03615995005400060018x

Supramaniam Y, Chong C-W, Silvaraj S, Tan IK-P (2016) Effect of short term variation in temperature and water content on the bacterial community in a tropical soil. Appl Soil Ecol 107:279–289. https://doi.org/10.1016/j.apsoil.2016.07.003

Tang J, Mo Y, Zhang J, Zhang R (2011) Influence of biological aggregating agents associated with microbial population on soil aggregate stability. Appl Soil Ecol 47:153–159. https://doi.org/10.1016/j.apsoil.2011.01.001

Tisdall JM, Oades JM (1982) Organic matter and water-stable aggregates in soils. J Soil Sci 33:141–163. https://doi.org/10.1111/j.1365-2389.1982.tb01755.x

Truu M, Juhanson J, Truu J (2009) Microbial biomass, activity and community composition in constructed wetlands. Sci Total Environ 407:3958–3971. https://doi.org/10.1016/j.scitotenv.2008.11.036

Uhlířová E, Elhottová D, Tříska J, Šantrůčková H (2005) Physiology and microbial community structure in soil at extreme water content. Folia Microbiol (Praha) 50:161–166. https://doi.org/10.1007/BF02931466

Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. Soil Biol Biochem 19:703–707. https://doi.org/10.1016/0038-0717(87)90052-6

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th editio. Springer, New York

Walker TWN, Kaiser C, Strasser F et al (2018) Microbial temperature sensitivity and biomass change explain soil carbon loss with warming. Nat Clim Chang 8:885+. https://doi.org/10.1038/s41558-018-0259-x

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York

Zelles L (1999) Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil : a review. Biol Fertil Soils 29:111–129