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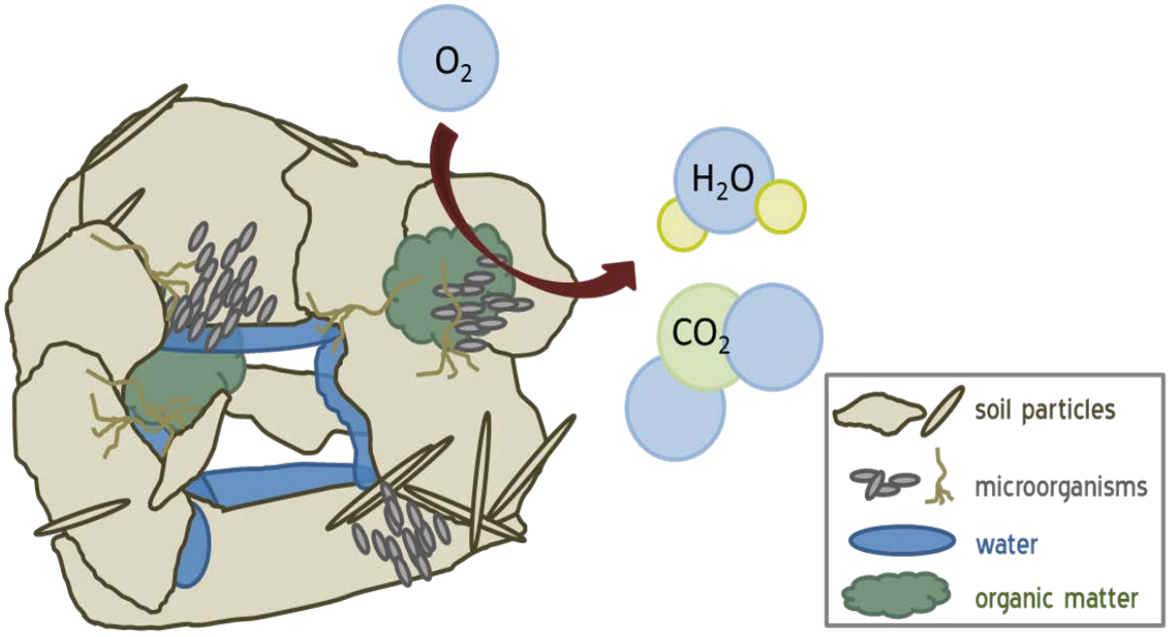
Soil Temperature and Moisture Effects on Soil Respiration and Microbial Community Abundance

Robyn A. Barbato, Karen L. Foley, and Charles M. Reynolds

April 2015



Conceptual model of a soil pore, emphasizing soil microorganisms' role in heterotrophic respiration.

Cold Regions Research and Engineering Laboratory

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Abstract

Soil biological processes are influenced by dynamic soil descriptors, such as water potential and temperature, and more stable factors, including organic matter content and particle size distribution. To better understand how soil temperature and soil water potential influence microbial activity, we measured soil respiration in laboratory incubations of four different soils. Though three of the soils had the same soil texture, they varied considerably by pH and soil nutrient concentrations. We found that the soils varied in how their native soil microbes responded to a range of soil water potential and temperature values, with soil activity being highest at approximately 30°C and −33 kPa. Further, the peak respiration rate for the soil with the highest measured organic matter content was 329.8 mg C-CO_2 m^{-2} day^{-1} and the rate for the soil with the lowest measured organic matter content was 14.7 mg C-CO_2 m^{-2} day^{-1}. Those soils with elevated organic matter content also contained the highest abundance of bacteria and archaea. Across all soils, if the moisture content was optimal but the temperature was around 5°C, the respiration rate was reduced. Therefore, microbial activity may depend more on temperature though moisture clearly had an effect on activity.

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Preface

This study was conducted for the U.S. Army Engineer Research and Development Center (ERDC) 6.2 Geospatial Research and Engineering (GRE) Program under Army Terrestrial-Environmental Modeling and Intelligence System (ARTEMIS), "Temporal Spatial Predictions of Soil Activities." The technical monitor was John Eylander, ERDC Cold Regions Research and Engineering Laboratory (CRREL).

The work was performed by Dr. Robyn Barbato, Karen Foley, and Dr. Charles Reynolds (Biogeochemical Sciences Branch, Dr. Justin Berman, Chief), ERDC-CRREL. At the time of publication, Dr. Loren Wehmeyer was Chief of the Research and Engineering Division. The Deputy Director of ERDC-CRREL was Dr. Lance Hansen, and the Director was Dr. Robert Davis.

LTC John Tucker was Acting Commander of ERDC, and Dr. Jeffery P. Holland was the Director.

Acronyms and Abbreviations

Ψ_m	Matric Potential
ANOVA	Analysis of Variance
ARTEMIS	Army Terrestrial-Environmental Modeling and Intelligence System
ATCC	American Type Culture Collection
Ca	Calcium
CEC	Cation Exchange Capacity
CO_2	Carbon Dioxide
CRREL	Cold Regions Research and Engineering Laboratory
Cu	Copper
ERDC	U.S. Army Engineer Research and Development Center
GRE	Geospatial Research and Engineering
GWC	Gravimetric Water Content
K	Potassium
L	Loam
L-OM	Loam with Low Organic Matter Content
LOI	Loss on Ignition
Mg	Magnesium
N	Nitrogen
ND	Not Detected
OM	Organic Matter
P	Phosphorous

Q_{10}	Temperature Coefficient
qPCR	Quantitative Polymerase Chain Reaction
S	Sulfur
SL	Non-Amended Sandy Loam
SL+OM	Sandy Loam Amended with Organic Matter
SL-OM	Sandy Loam with Low Organic Matter Content
TSP-SA	Temporal Spatial Predictions of Soil Activities
Zn	Zinc

1 Introduction

Soil microbiomes are inherently complex, with changes in microbial community structure and activity occurring in response to environmental factors such as pH, organic matter content, temperature, and moisture. In general, soils with a diverse microbiome are also functionally diverse; and these microorganisms have the potential to conduct many reactions, from chemical degradation to carbon mineralization. Though techniques have been developed to assess microbial community structure and function in soils, models to predict soil function are lacking.

When choosing environmental properties as input to a model, two criteria should be met: (1) the properties should be accessed through remote methods, and (2) the properties should influence soil activity. Given these criteria, we selected to study soil temperature and moisture because they would serve as inputs to our future model, which will be based on readily available weather and terrain predictions. In fact, many studies have demonstrated how soil temperature and moisture independently influence microbial community activity (Schlentner and Van Cleve 1985; Brockett et al. 2012; Wood et al. 2013; Streit et al. 2014). However, the combined effect of temperature and moisture on soil activity is still the subject of active debate (Moyano et al. 2013), especially because the largest disagreement between models is at the extremes of temperature and moisture (Sierra et al. 2015). In particular, datasets where temperature and moisture change simultaneously are lacking (Sierra et al. 2015). Other soil properties, such as pH (Lauber et al. 2009) and soil texture (Girvan et al. 2003) have been shown to impact soil community structure. However, these properties were not included in our study because they do not meet the above criteria.

General soil activity is typically measured by the flux of carbon dioxide (CO_2) out of a soil, termed soil respiration. Commonly expressed as a rate, soil respiration provides an indication of how much carbon is leaving the soil and entering the atmosphere. Soil activity could be assessed using the Q_{10} temperature coefficient, which is a measure of the rate of change in a biological system when the temperature is raised in 10°C increments. However, Wang et al. (2010) showed that the seasonally derived values of Q_{10} overestimate microbial activity in soil because seasonal variation in

plant activity influences Q_{10} values. Therefore, in the context of our study, we will be using CO_2 efflux rates to describe heterotrophic respiration, which occurs when soil organisms oxidize organic matter and release CO_2. On average, heterotrophic respiration contributes to approximately 54% of the total respiration in soils (Hanson et al. 2000).

1.1 Soil temperature

Previous studies have demonstrated that soil temperature affects microbial growth rates (Schlentner and Van Cleve 1985; Lloyd and Taylor 1994; Hanson et al. 2000; Ma et al. 2014). To determine temperature and climate impacts on soil activity, studies have investigated microbial activity in a range of ecotones and climates, from deserts (Cable et al. 2011) to palm-dominated forests in Puerto Rico (Wood et al. 2013), to aspen-birch forests in interior Alaska (Schlentner and Van Cleve 1985). As expected, in each of these locations, peak activity occurred at different temperatures, with the highest respiration rates observed at 25°C in the forests in Puerto Rico and at 30°C in cold and warm deserts across the world (Cable et al. 2011; Wood et al. 2013). Peak respiration was the lowest at 17°C in forested interior Alaska (Schlentner and Van Cleve 1985). Studies have also shown soil respiration to increase with a rise in temperature, as demonstrated when a forest soil in Switzerland was subjected to a range of temperatures (Streit et al. 2014).

1.2 Soil moisture

As mentioned above, soil moisture influences soil microbial activity. Moisture expressed as matric potential (Ψ_m) is the water available to soil microorganisms. It is negative because water attracted to the soil matrix has an energy state lower than that of pure water. At 0 kPa, a soil is at complete saturation; and at –1500 kPa, a soil is at a permanent wilting point, the lower limit of water availability to plants. In a meta-analysis, Manzoni et al. (2012) showed the decline in heterotrophic respiration with decreasing soil moisture across various biomes and climates and demonstrated that, at low matric potentials, solute diffusion becomes a limiting factor to the soil biological community. Oppositely, declines in respiration occur at high matric potentials because of limitations to oxygen diffusion to microorganisms. In between the dry and wet ends of the curve exists optimal matric potential, where microbial activity is highest due to the most favorable water content in the soil, where solute and oxygen diffusion both occur. Furthermore, low matric potential has a stronger negative effect on

microbial activity than low osmotic potential, which are two important drivers of soil activity in dry and hot climates (Chowdhury et al. 2011).

Though both soil temperature and moisture fluctuations influence microbial activity in soils, few studies have provided widely applicable respiration rates. Therefore, to elucidate the combined role that soil temperature and moisture have on soil microbial activity, our objectives were to (1) evaluate diurnal and seasonal variations in soil temperature and moisture and (2) investigate changes in microbial activity as a function of these soil properties. Our ultimate goal was to obtain an empirical dataset to predict soil microbial activity under varying environmental conditions.

2 Methods

2.1 Soil collection and soil water potential

In April 2012, we obtained samples from four discrete soils at the Cold Regions Research and Engineering Laboratory (CRREL) field site (Hanover, NH). The soils were originally imported from Lebanon, NH; Burlington, VT; and Hanover, NH. The soils were a sandy loam amended with organic matter (SL+OM), a non-amended sandy loam (SL), a loam with low organic matter content (L-OM), and a sandy loam with low organic matter content (SL-OM). After soil collection, plant materials were discarded and the soils were air dried, sieved to less than 2 mm, and stored in the dark at 23°C until the experiments commenced.

We used two methods to establish the water release curves from the dry and wet ends of the curve. To obtain measurements from the wet end of the curve (–10 to –150 kPa), we used a 1600 Pressure Plate Extractor (Soil Moisture Equipment Corp, Santa Barbara, CA). In brief, 600 g of each soil was saturated with water and placed into rings on porous plates for 18 hours. After holding a low pressure for 24 hours in the extractor vessel, we removed three replicate soil samples and determined their gravimetric moisture content. We increased the pressure in the kettle and repeated the procedure for a total of four to six pressure settings. To obtain measurements from the dry end of the curve (–200 to –5000 kPa), a Decagon WP-4 dewpoint potentiometer (Decagon Devices, Inc., Pullman, WA) was used. In brief, water was incrementally added to 100 g of each soil tested. After equilibration overnight, the moisture potential was recorded in triplicate using the potentiometer. For soil samples from both methods, we calculated the gravimetric water content (GWC) by comparing wet mass to dry mass following drying in a convection oven at 105°C for 24 hours.

2.2 Incubation conditions

Prior to setting up respiration experiments of the soils, each soil was held at approximately 4% moisture content to revive the native soil microorganisms. After 48 hours, each soil was rehydrated to five different moisture contents corresponding to matric potentials of approximately –1000, –200, –50, –20, and –10 kPa and mixed thoroughly. We prepared quadruplicate samples containing 140 g dry soil in jars that were packed to a

bulk density of approximately 1.3 g cm^{-3}. Each jar was sealed and connected to the Micro-Oxymax Respirometer (Columbus Instruments, Columbus, OH) and incubated the at a constant temperature of 5°C, 15°C, 25°C, or 30°C. In all, we obtained respiration rates for each soil under the ending soil temperature and moisture conditions tested, as the soils dried slightly during the experiment.

2.3 Soil properties

Before the incubation, triplicate samples from each soil were well mixed and analyzed by the Agricultural Analytical Services Laboratory at the Pennsylvania State University College of Agricultural Sciences (University Park, PA) for many soil properties. In brief, a portion of each sample was analyzed for pH (1:1 soil:water) (Eckert and Sims 2009) and particle size analysis for soil textural class by using the hydrometer method (Gee and Bauder 1986). Additionally, concentrations of phosphorus, potassium, magnesium, and calcium were measured using the Mehlich 3 protocol (Wolf and Beegle 2011). Cation exchange capacity (CEC) was measured with the summation method (Ross and Ketterings 2011), and soluble salts were measured using the electrical conductivity method (Gartley 2011). Ammonium-nitrogen and nitrate-nitrogen were determined using the specific ion electrode method (Griffin et al. 2011; Mulvaney 1996), and total nitrogen and carbon were measured by combustion (Bremner 1996). Finally, organic matter (OM) content in the samples was measured through the loss on ignition (LOI) method (Schulte and Hoskins 2011).

2.4 Soil heterotrophic respiration

We measured soil heterotrophic respiration by measuring the concentration of CO_2 released from the soils using the respirometer. The system was calibrated with a standard gas mix from Air Liquide (Houston, TX). The concentration of CO_2 in each sample jar's headspace was automatically measured every four hours without removing the samples from the incubator. Using conversion factors and the surface area of each sample, CO_2 efflux was converted to mg C-CO_2 m^{-2} day^{-1} given a surface area of 69.8 cm^2 for the incubation vessels. Once instantaneous CO_2 efflux rates stabilized, the soils were destructively sampled to determine the gravimetric water content and were stored at −20°C for molecular analysis.

2.5 Soil community abundance

Genomic DNA was extracted from approximately 0.25 g of soil by using the MoBio PowerSoil DNA extraction kit (Carlsbad, CA). DNA concentrations were quantified using the NanoDrop 2000 UV-Vis Spectrophotometer (Thermo Scientific, Wilmington, DE). DNA was diluted with sterile, DNA-free water to achieve 20 ng per quantitative polymerase chain reaction (qPCR).

We amplified the bacterial 16S rRNA genes by using primers 331F and 797R and probe BacTaq (Nadkarni et al. 2002) and amplified archaeal 16S rRNA genes by using primers Arch 349F and Arch 806R and probe TM Arch 516F (Takai and Horkoshi 2000). All qPCR reactions were conducted in duplicate on the Lightcycler 480 System (Roche Molecular Systems, Inc., Indianapolis, IN). The 20 µL reaction volumes included 20 ng DNA, 10 µM of primers, 5 µM of probe, and 10 µL of Lightcycler TaqMan Master Mix (Roche Molecular Systems, Inc., Indianapolis, IN). We prepared standards for bacterial and archaeal qPCR by using genomic DNA from *Pseudomonas fluorescens* and *Halobacterium salinarum*, respectively. Both were obtained from the American Type Culture Collection (ATCC, Manassas, VA) and grown according to ATCC's recommended protocols. Once the cultures reached log phase growth, we conducted plate counts and isolated DNA from the cultures by using the Microbial DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA). Genomic DNA was quantified using the NanoDrop 2000 UV-Vis Spectrophotometer (Thermo Fisher Scientific, Inc., Wilmington, DE) with the assumption of one and six copies of the 16S rRNA gene per genome for *H. salinarum* and *P. fluorescens*, respectively (Fogel et al. 1999; Bodilis et al. 2012). We optimized the cycling parameters to include both genes in the same experimental run with the following conditions: 95°C for 600 s followed by 45 cycles of 95°C for 30 s, 57°C for 60 s, and 72°C for 25 s with final extension at 40°C for 30 s.

2.6 Statistical analysis

For each soil, the experiment was complete once instantaneous respiration rates stabilized with a slope less than 2.5×10^{-4} mg CO_2-C m^{-2} min^{-1}. Contour plots were created in Surfer 8 software (Golden Software, Golden, CO) by taking the quadratic polynomial regression of the mean respiration rate from four replicates from each temperature and moisture experiment. Absolute values for matric potential were log-transformed prior to creating the contour plots. A similar approach was used to create contour plots of

the bacterial and archaeal abundance data, with the difference that the mean of the log-transformed gene copy numbers were used to create the plots.

The differences in bacterial and archaeal copy numbers between treatments were assessed by analysis of variance (ANOVA) using JMP 11 software (SAS, Cary, NC). Gene copy numbers were log-transformed prior to ANOVA to account for unequal variances between treatments.

3 Results

3.1 Soil properties

Three of the four soils were greater than 65% sand, designating them as sandy loam (SL) texture (Table 1). The L-OM soil had a higher percentage of silt and was designated as a loam (L) (Table 1). The physical and chemical properties from these soils ranged in meaningful ways. For instance, OM content varied significantly between soils, with the SL+OM soil containing a significantly higher amount of OM than the three other soils (Table 1). Though pH was significantly different between the soils, it only varied from 6.6 in the SL soil to 8.1 in the L-OM soil (Table 1). The CEC was highest in the L-OM soil and lowest in the SL soil (Table 1). Nitrogen content was highest in the SL+OM and L-OM soils, and lowest in the SL and SL-OM soils (Table 1). The SL+OM soil had significantly higher concentrations of phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) whereas the L-OM soil had a significantly higher concentration of Ca than the other soils (Table 2). Finally, the SL soil had the highest concentrations of the micronutrients zinc (Zn) and copper (Cu), and the SL-OM soil had a significantly lower concentration of sulfur (S) (Table 2).

Table 1. Physical soil properties, including particle size distribution, pH, cation exchange capacity (CEC), organic matter content (OM), and nitrogen (N) constituents. Values in the table are reported as mean ± standard error (n = 3). ND indicates not detected. *Different letters* represent significantly different means (p < 0.05) based on one-way ANOVA.

Soil	Sand (%)	Silt (%)	Clay (%)	pH	CEC (meq/100g)	OM (%) LOI	N (%)	NH_4^+-N (mg/kg)	NO_3^--N (mg/kg)
SL+OM	67.2 ± 0.57[a]	26.3 ± 0.44[a]	6.47 ± 0.19[a]	7.0 ± 0.07[a]	10.9 ± 0.09[a]	3.3 ± 0.09[a]	0.20 ± 0.006[a]	0.98 ± 0.01[a]	23.4 ± 0.80[a]
SL	66.4 ± 0.21[a]	26.9 ± 0.57[a]	7.7 ± 0.50[a]	6.6 ± 0.03[b]	8.6 ± 0.07[b]	2.6 ± 0.00[b]	0.02 ± 0.003[b]	1.39 ± 0.02[b]	48.4 ± 0.63[b]
L-OM	47.6 ± 0.92[b]	40.8 ± 0.84[b]	11.5 ± 0.46[b]	8.1 ± 0.09[c]	14.0 ± 0.52[c]	N.D.	0.17 ± 0.003[c]	0.73 ± 0.03[c]	13.1 ± 0.48[c]
SL-OM	65.6 ± 0.77[a]	24.1 ± 0.60[a]	10.2 ± 0.24[b]	7.7 ± 0.0[d]	11.6 ± 0.15[a]	0.9 ± 0.15[c]	0.09 ± 0.003[d]	1.06 ± 0.06[a]	5.9 ± 0.57[d]
F	197.4	152.4	38.1	117.5	66.9	605.3	406.8	55.21	868.64
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

meq = milliequivalents

Table 2. Concentrations of soil macro- and micronutrients. Values are reported as mean ± standard error (n = 3). *Different letters* represent significantly different means (p < 0.05) based on one-way ANOVA.

Soil	P (mg/kg)	S (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	Zn (mg/kg)	Cu (mg/kg)
SL+OM	142.3 ± 3.2[a]	43.4 ± 0.9[a]	105.3 ± 0.9[a]	1666.3 ± 9.7[a]	274.3 ± 2.9[a]	8.6 ± 0.2[a]	4.7 ± 0.03[a]
SL	33.0 ± 0.6[b]	27.0 ± 0.4[ab]	38.7 ± 0.9[b]	1125.3 ± 12.9[b]	96.7 ± 1.3[b]	10.1 ± 0.1[b]	7.6 ± 0.03[b]
L-OM	2.7 ± 0.3[c]	41.5 ± 8.9[a]	39.0 ± 0.6[b]	2620.3 ± 80.7[c]	102.7 ± 12.8[b]	0.9 ± 0.0[c]	2.0 ± 0.23[c]
SL-OM	35.0 ± 2.3[b]	9.1 ± 0.8[b]	51.7 ± 1.8[c]	2163.3 ± 32.1[d]	78.0 ± 4.4[b]	2.3 ± 0.1[d]	3.4 ± 0.03[d]
F	943.02	12.58	803.61	212.30	172.81	1343.36	317.89
P	<0.0001	0.0021	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

3.2 Soil respiration rates

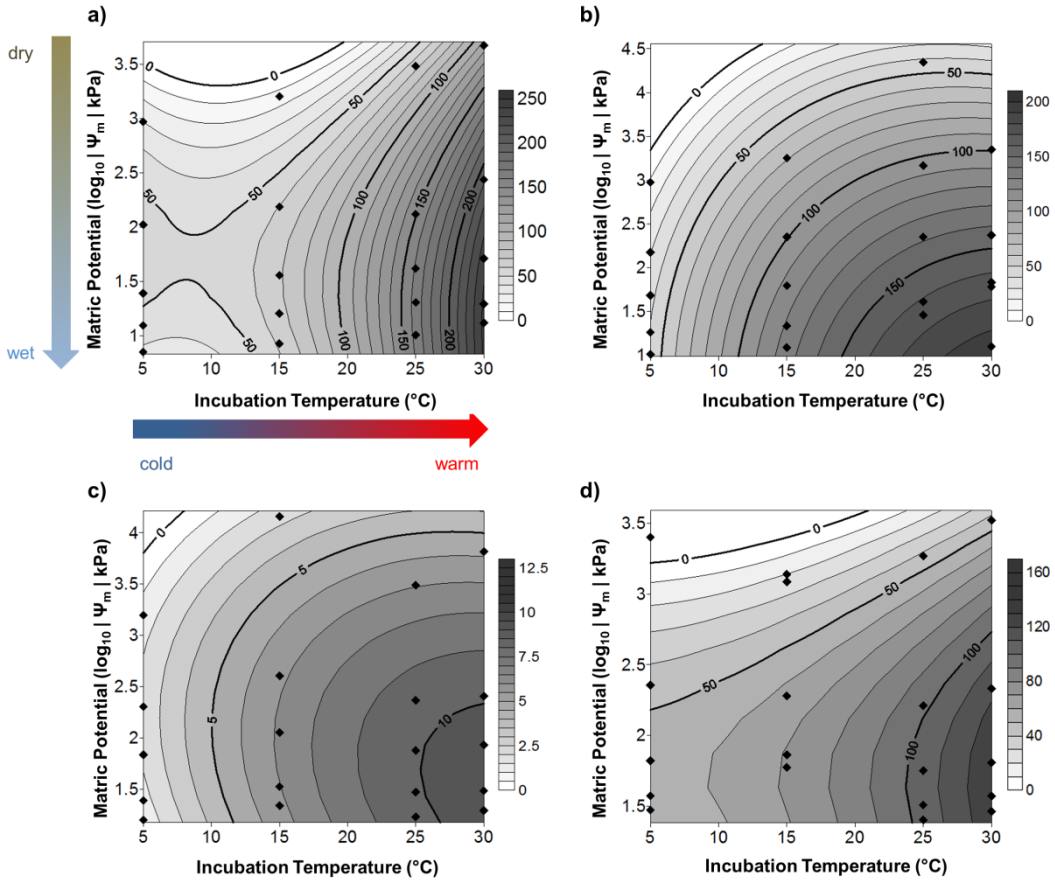
Soil respiration rates were expressed as response surfaces to determine how soil activity changed as a function of both soil temperature and moisture. The observed maximum respiration rate of each soil varied, from 329.8 mg C-CO_2 m^{-2} day^{-1} in the SL+OM soil (Figure 1a) to 14.7 mg C-CO_2 m^{-2} day^{-1} in the L-OM soil (Figure 1c). Another attribute that varied significantly between these two soils was OM content, with the SL+OM containing higher OM content (Table 1).

In all of the soils, maximum respiration rates occurred at an optimal temperature and moisture content and then declined steadily (Figure 1). We observed the highest average respiration rates at 25°C or 30°C, depending on the soil tested, while we observed the lowest respiration rates typically at 5°C (Figure 1). Additionally, the highest respiration rates were observed at a matric potential between −19 and −75 kPa and declined under dry conditions (Figure 1).

For the SL+OM soil, the average respiration rate peaked at 329.8 C-CO_2 m^{-2} day^{-1} for samples incubating at 30°C under −20 kPa moisture tension, and it was the lowest at 22.8 mg CO_2-C m^{-2} day^{-1} at 5°C under −932 kPa moisture tension (Figure 1a). For the SL soil, the average respiration rate was highest at 290.8 mg C-CO_2 m^{-2} day^{-1} for samples incubating at 25°C under −41 kPa moisture tension; and it was the lowest at 25.4 C-CO_2 m^{-2} day^{-1} at 5°C under −943 kPa (Figure 1b). The average respiration rate for the L-OM soil was the highest at 14.7 mg CO_2-C m^{-2} day^{-1} under the conditions of 25°C and −75 kPa and lowest at 1.7 mg CO_2-C m^{-2} day^{-1} under the conditions of 5°C and −25 kPa (Figure 1c). For the SL-OM soil, the average respiration rate was the highest at 191.9 mg CO_2-C m^{-2} day^{-1} under the

conditions of 30°C and −64 kPa and lowest at 5.4 mg CO_2-C m^{-2} day^{-1} under the conditions of 5°C and −2548 kPa (Figure 1d).

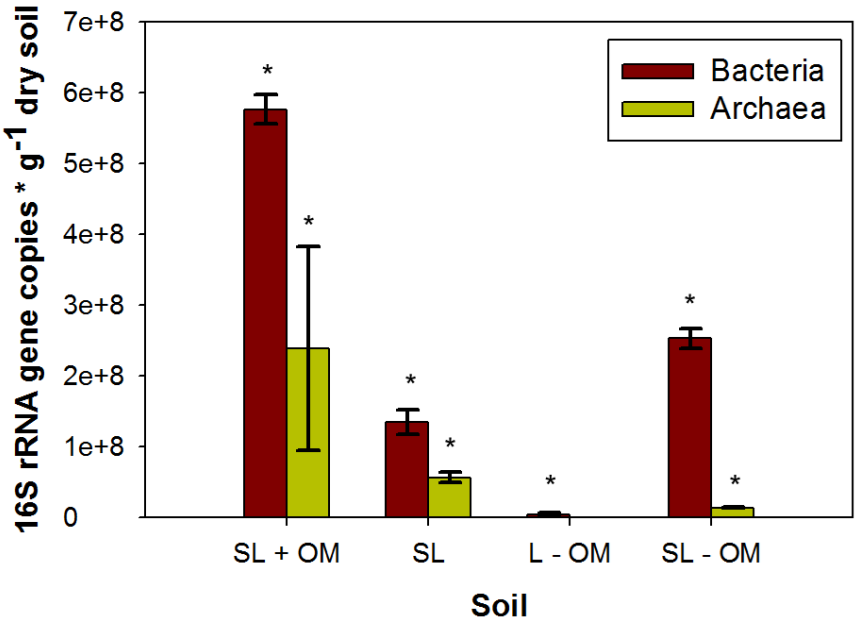
Figure 1. Contour plots of mean soil respiration rates (mg C-CO_2 m^{-2} day^{-1}) as a function of incubation temperatures and matric potentials for (*a*) SL+OM, (*b*) SL, (*c*) L–OM, and (*d*) SL–OM soils. The vertical bars to the right of each graph indicate the corresponding respiration values.



3.3 Abundance of soil bacteria and archaea

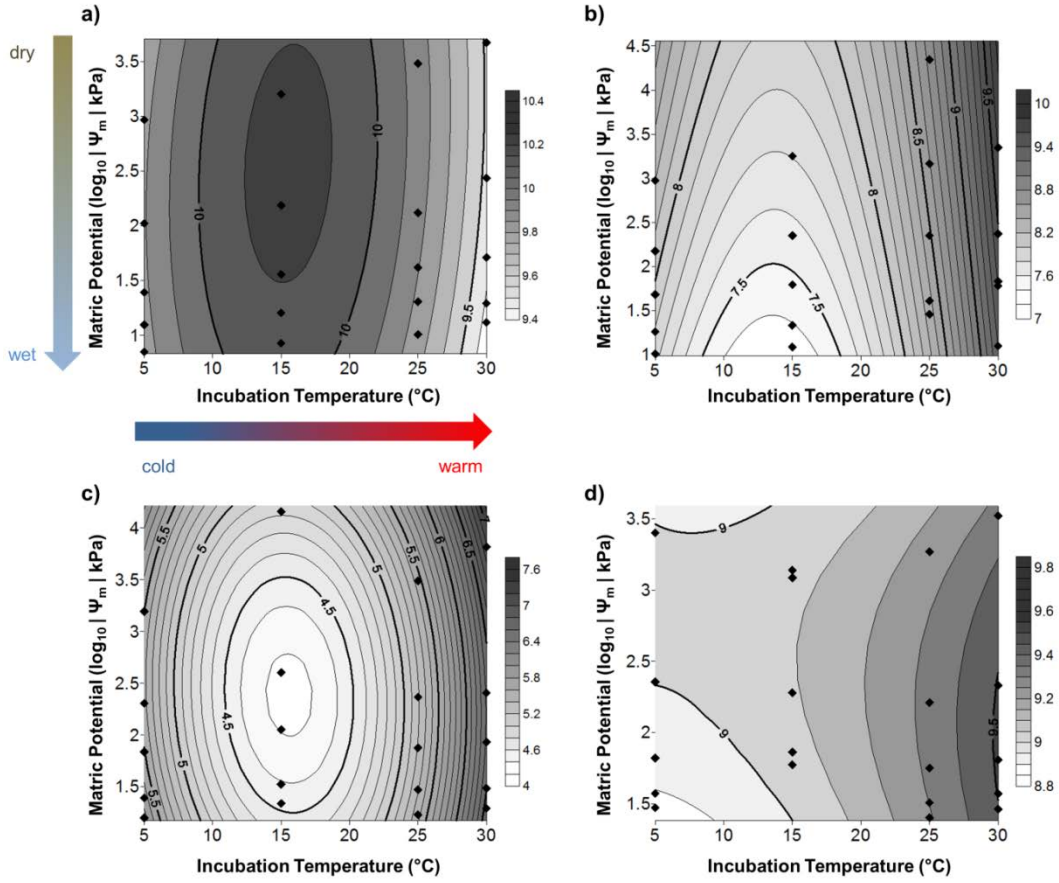
For the SL+OM, SL, and SL-OM soils, bacteria were more abundant than archaea ($p < 0.01$) (Figure 2). Bacterial and archaeal copy numbers were significantly higher in the SL+OM soil as compared to the other soils tested, indicating that soil type influenced both bacterial and archaeal 16S rRNA gene abundance. Interestingly, there was a higher abundance of bacteria in the SL-OM soil when compared to the SL soil even though the organic matter content was higher in the SL soil (Table 1). Archaea were not detected in the L-OM soil.

Figure 2. Influence of soil type on bacterial and archaeal 16S rRNA gene abundance. Asterisks indicate a significant difference in copy numbers for that gene between each soil tested ($p < 0.01$).



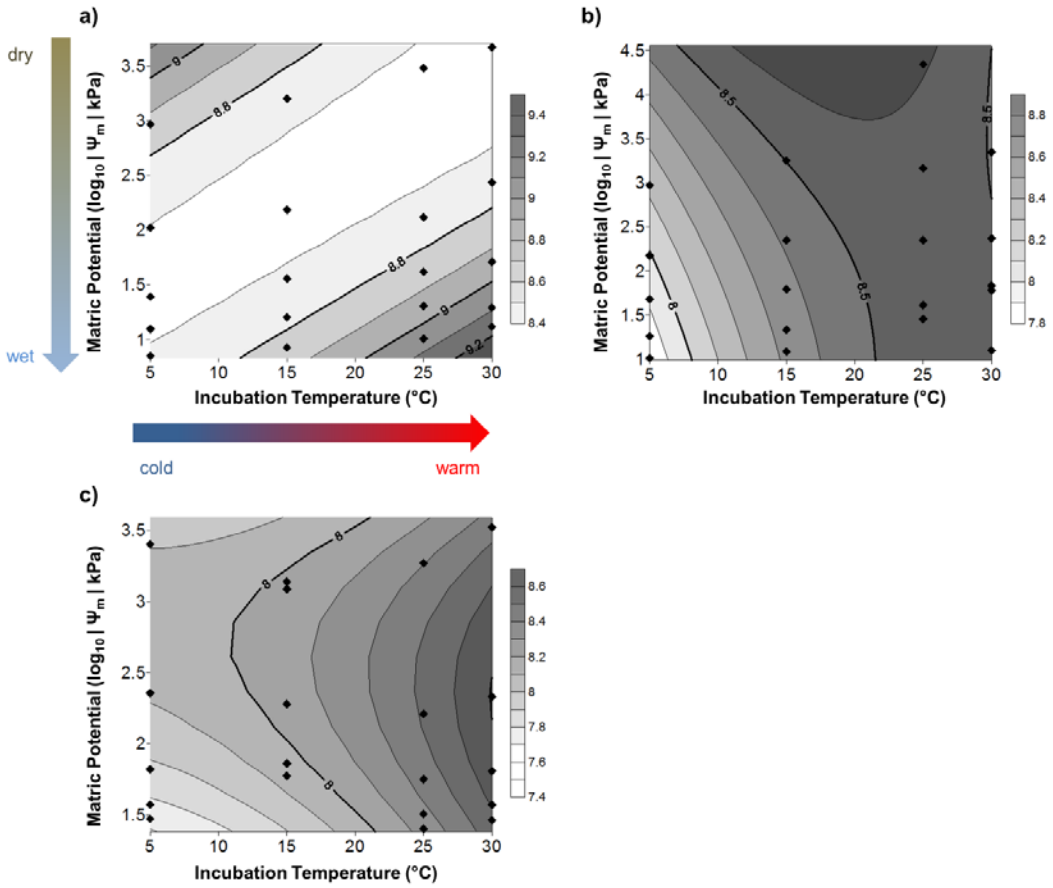
In these for soils, soil temperature and matric potential also influenced the abundance of bacteria and archaea. Specifically, there were 1.32×10^{10} bacterial copies g^{-1} dry soil in the SL+OM soil at 25°C and −132 kPa whereas there were only 1.44 bacterial copies g^{-1} dry soil at 30°C and −52 kPa (Figure 3a). In the SL soil, bacterial copy numbers were the highest (2.03×10^{9} bacterial copies g^{-1} dry soil) at 30°C and −60 kPa; and the copy numbers were the lowest (6.16×10^{6} bacterial copies g^{-1} dry soil) at 15°C and −12 kPa (Figure 3b). For the L-OM soil, bacterial abundance peaked at 1.06×10^{8} bacterial copy numbers g^{-1} dry soil at 30°C and −20 kPa and were four orders of magnitude lower (1.94×10^{4} bacterial copies g^{-1} dry soil) at 25°C and −30 kPa (Figure 3c). The bacterial abundance in the SL-OM soil was 6.05×10^{9} bacterial copies g^{-1} dry soil at 30°C and −37 kPa and was lowest (7.38×10^{8} bacterial copies g^{-1} dry soil) at 5°C and −2548 kPa (Figure 3d).

Figure 3. Respiration surfaces showing the log of the mean bacterial abundances according to incubation temperature and log of the matric potential for (*a*) SL+OM, (*b*) SL, (*c*) L-OM, and (*d*) SL-OM soils. The vertical bars to the right of each graph indicate the corresponding log-transformed bacterial gene copy numbers.



Soil archaeal abundance was also characterized using response surfaces created by polynomial regression analysis. Similar to the bacterial results, archaeal abundance was highest in the SL+OM soil (Figure 4). Specifically, under 30°C and –13 kPa, the archaeal abundance was 1.51×10^{10} archaeal copies g^{-1} dry soil (Figure 4a). In the SL+OM soil, archaeal abundance was lowest (2.84×10^{8} archaeal copies g^{-1} dry soil) at 30°C and –4712 kPa (Figure 4a). There were 6.64×10^{8} archaeal copies g^{-1} dry soil at 25°C and –23121 kPa, and only 6.09×10^{7} archaeal copies g^{-1} dry soil at 5°C and –10 kPa (Figure 4b). In the SL-OM soil, there were 3.55×10^{8} archaeal copies g^{-1} dry soil at 25°C and –162 kPa and 4.81×10^{7} archaeal copies g^{-1} dry soil at 5°C and –30 kPa (Figure 4c).

Figure 4. Contour plots of the log of the mean archaeal abundances according to incubation temperature and log of the matric potential for (*a*) SL+OM, (*b*) SL, and (*c*) SL–OM. Archaea were not detected in the L-OM soil. The vertical bars to the right of each graph indicate the corresponding log-transformed archaeal gene copy numbers.



4 Discussion

Modeling microbial activity in soils requires robust measurements to develop functions that estimate respiration rates as a function of edaphic properties. Predicting nutrient cycling processes is critical to better understand how these processes will change under a variety of environmental conditions. Currently, empirical data similar to what we collected from widely representative soils is lacking. To fill in this gap, we modeled soil respiration as a function of soil temperature and moisture in four distinct soils to broadly characterize microbial activity under these environmental regimes. Our goal was to use these observations to obtain predictions of microbial activities that could be used in larger models (e.g., climate change models).

It is well known that temperature drives microbial growth; however, the extent that this occurs over a large temperature and moisture gradient in soil is not well known. The results from our study indicated that, together, soil temperature and soil moisture impacted respiration in four different soils. Between soils, there were some similarities in the curvature of the response surfaces, though the peak respiration differed, especially when comparing the L-OM soil to the rest of the soils.

Hanson et al. (2000) showed that, taken separate from moisture, temperature influences soil respiration in most ecosystems, with elevated respiration rates observed in soils with higher temperatures in biomes from pine forests in Japan to peatlands in Finland to tall grass prairies in the United States (Lloyd and Taylor 1994). Our findings showed that the highest respiration rates occurred between 25°C and 30°C, suggesting that the soil microbial communities were adapted to warmer temperatures. We also observed the lowest respiration rates at 5°C, which was the lowest temperature that we tested. An increase in respiration at lower temperatures could occur in some soils, possibly due to the lysis of cells and subsequent release of carbon (Brooks et al. 2005; Schimel et al. 2007). In cold-climate ecosystems, such as Alaskan and Chinese soils, soil respiration peaked between 15°C and 18°C (Schlentner and Van Cleve 1985; Ma et al. 2014), suggesting that the microbial communities in these soils were adapted to grow under a slightly lower temperature regime than the microorganisms in our soils. In fact, recent studies demonstrated that winter respiration

occurred at meaningful rates and should be included when estimating carbon flux from soils (Aanderud et al. 2013). Along with winter respiration, respiration in thawing permafrost should also be included in estimates of carbon flux as the incidence of oxic microhabitats will increase in areas of thawing permafrost (Goulden et al. 1998). Our understanding of soil respiration at low temperatures could enhance these models by improving our understanding of soil microbial activity in cold climates.

Similar to temperature, soil moisture, expressed as matric potential, influences microbial activity in soils. In our study, respiration rates peaked when the matric potential was between −19 and −75 kPa, with declines in respiration rates under dry conditions. However, respiration rates did not decline as dramatically with increasing moisture in the SL+OM, SL, and SL-OM soils, as observed by Xu et al. (2004) in California grassland, savannas, and oak woodland soils. In our study, peak respiration rates were near −33 kPa, which is the optimal matric potential for plant and microbial activity (Brady and Weil 2002). Similarly, Chowdhury et al. (2011) observed high soil activity at −30 and −100 kPa in South Australian sandy and sandy loam soils. Alternatively, Curtin et al. (2012) found that optimal matric potential for mineralization may be as high as −5 kPa in agricultural soils from New Zealand.

Similar to our findings, respiration rates have also been shown to decline under dry conditions, specifically in subtropical forest soils in the Guangdong Province in China (Zhou et al. 2014) and in a tropical forest in Puerto Rico (Wood et al. 2013). When soils dry, the water around soil aggregates becomes thinner, resulting in a more negative matric potential (Illstedt et al. 2000). Under these conditions, the soil microorganisms are limited by substrate diffusion, resulting in a reduction in soil activity. In these dry conditions, Stark and Firestone (1995) showed that cells of nitrifying bacteria dehydrate below −600 kPa, indicating the important role that moisture has on populations of soil microbes.

Respiration captures the soil microorganisms that are active in soils though it does not give an indication of the types of microbes in the soils. Therefore, to better understand the role of bacteria and archaea under certain conditions, we assessed their abundance. Commonly, the response of ammonia oxidizers (Avrahami and Bohannan 2007), nitrifiers, and denitrifiers (Stres et al. 2008; Szukics et al. 2010) has been tested under

varying temperature and moisture regimes, though testing the response of bacteria and archaea was not as common.

Similar to our respiration results, the bacterial and archaeal abundance was significantly higher in the SL+OM soils, likely because this soil contained the highest organic matter content and concentrations of nutrients. Generally, bacterial and archaeal abundance was highest between 25°C and 35°C and in the drier soils. Curtin et al. (2012) observed a similar trend in microbial biomass measurements by noting that temperature affects the size of the microbial biomass and subsequently soil organic matter mineralization, especially with declines in biomass at 5°C and 25°C. Stres et al. (2008) showed the dynamic response of archaeal community structure to temperature but did not observe changes in bacterial community structure in a drained fen grassland soil. We found both domains to be heavily influenced by changes in both soil temperature and moisture.

Furthermore, factors such as soil texture and OM content strongly influenced soil respiration and microbial abundance in these soils. These relationships fit with previous work that has shown soil texture (Girvan et al. 2003) and OM content (Howard and Howard 1993; Riveros-Iregui et al. 2007) to be key drivers of microbial activity in soils. Community changes might occur at higher temperatures above optimal growth as the higher temperatures result in cell death, enabling colonization by other organisms adapted to growth at higher temperatures (Bárcenas-Moreno et al. 2009).

In our study, we did not investigate fungal abundance. Generally, fungi and Actinomycetes are more active under dry conditions (Zenova et al. 2007; Williams and Hallsworth 2009); yet arid ecosystems generally have lower fungal to bacterial ratios (Fierer et al. 2007). Also, fungi are favored at lower temperatures (Ley and Schmidt 2002; Pietikäinen et al. 2005). Perhaps at low temperatures and dry matric potentials, bacteria may not be the dominant contributor to soil respiration. Further research on fungal abundance would be necessary to elucidate the above statement.

When taken together, temperature and moisture have meaningful impacts on soil activity. In our study, when the matric potential was optimal but the temperature was low, the respiration rate was reduced, indicating that microbial activity may depend more on temperature than moisture. Both Wood et al. (2013) and Raich and Schlesinger (1992) agree that elevated

respiration rates are more influenced by temperature as long as soil moisture is not a limiting factor. This occurs because when moisture is held at a more negative matric potential, substrate diffusion is limited, thus limiting microbial activity. In fact, Raich and Schlesinger (1992) noted that temperature was the best predictor of soil respiration, and precipitation enhanced the predictive power of the model. Clearly in our study, matric potential affected soil activity, with declines in respiration under extremely wet or dry conditions. Further, when the soils were incubated at higher matric potentials, respiration rates increased across all temperatures for all four soils tested. Future work should include evaluating changes in microbial community composition as a function of soil temperature and moisture. Advances in remote sensing techniques to reveal better predictions of soil temperature and moisture across the landscape also help to improve soil activity models. For instance, Zhang et al. (2014) has begun to improve remote sensing data of soil moisture by using multiple sensors in a given region. Weather models will also improve our understanding of soil temperature and moisture across the landscape.

5 Conclusion

Our study showed how soils with high OM content also exhibited elevated respiration rates and contained a higher abundance of bacteria and archaea. In all four soils tested, soil temperature and moisture impacted microbial activity. When matric potential was optimal (−33 kPa) but soil temperature was low, soil respiration rates were reduced. Therefore, microbial activity may depend more on temperature though soil moisture clearly affected activity. Microbial abundance showed a similar trend as respiration rates, with the exception of the SL and SL-OM soils. These findings will inform predictions as climate change progresses.

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14. ABSTRACT

Soil biological processes are influenced by dynamic soil descriptors, such as water potential and temperature, and more stable factors, including organic matter content and particle size distribution. To better understand how soil temperature and soil water potential influence microbial activity, we measured soil respiration in laboratory incubations of four different soils. Though three of the soils had the same soil texture, they varied considerably by pH and soil nutrient concentrations. We found that the soils varied in how their native soil microbes responded to a range of soil water potential and temperature values, with soil activity being highest at approximately 30°C and −33 kPa. Further, the peak respiration rate for the soil with the highest measured organic matter content was 329.8 mg $C\text{-}CO_2$ m^{-2} day^{-1} and the rate for the soil with the lowest measured organic matter content was 14.7 mg $C\text{-}CO_2$ m^{-2} day^{-1}. Those soils with elevated organic matter content also contained the highest abundance of bacteria and archaea. Across all soils, if the moisture content was optimal but the temperature was around 5°C, the respiration rate was reduced. Therefore, microbial activity may depend more on temperature though moisture clearly had an effect on activity.

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