AIMS Geosciences, 5(4): 886–898.
DOI: 10.3934/geosci.2019.4.886
Received: 05 May 2019
Accepted: 08 October 2019
Published: 15 October 2019

http://www.aimspress.com/journal/geosciences

Communication

Experimental test of temperature and moisture controls on the rate of microbial decomposition of soil organic matter: preliminary results

Corey A. Palmer[1], Katherine P. Markstein[2], Lawrence H. Tanner[2,*]

[1] Department of Geosciences, University of Massachusetts, Amherst, MA, USA
[2] Department of Biological and Environmental Sciences, Le Moyne College, Syracuse, NY, USA

*** Correspondence:** Email: TannerLH@Lemoyne.edu; Tel: +13154454537.

Abstract: Soil organic matter (SOM) is a major reservoir of carbon derived from the biosphere that is returned to the atmosphere largely via microbial decomposition. The potential for feedbacks between climate change and SOM decomposition makes a full understanding of the controls on SOM decomposition rates essential to modeling future climate changes. We measured soil CO_2 flux in a laboratory setting using pots containing a uniform mix of soil in which we varied both temperature and moisture. Following initial desiccation, a strong CO_2 pulse was measured within two hours of rewetting and a return to equilibrium conditions obtained within 168 hours, with the magnitude of the initial pulse varying by soil temperature and moisture addition. At equilibrium conditions, no correlation was found between CO_2 flux and temperature across all moisture levels, although a weak positive correlation (r^2 = 0.1 to 0.2) was seen at moderate to high moisture levels. A much stronger correlation (r^2 > 0.4) was found between CO_2 flux and soil moisture across the full range of temperatures and at both low and high temperatures. Thus, we conclude that when all other variables were constrained, soil moisture fluctuations appeared to have greater impact than temperature variations on the rate of microbial decomposition of SOM. These preliminary results suggest directions for future research examining the relationships between soil moisture, temperature and CO_2 flux for soils in which clay mineral and/or SOM composition are varied.

Keywords: soil CO_2 flux; soil organic matter; soil respiration; microbial heterotrophs

Abbreviations: MAT: Mean Annual Temperature; NPP: Net Primary Productivity; SOM: Soil Organic Matter; WFPS: Water-Filled Pore Space

1. Introduction

Modeling the anthropogenic climate change anticipated in the coming decades requires a thorough understanding of carbon cycle dynamics, in particular the exchange of carbon between the atmosphere, biosphere and soil reservoirs on time scales of years to decades. At the current measure of pCO_2 (partial pressure of atmospheric CO_2), the atmospheric reservoir of carbon is ca. 850 Gt (as elemental C), but the global reservoir of carbon in the soils (as SOM) is at least twice, possibly three times that of the atmosphere [1,2], with potentially 50% of the soil reservoir stored in the upper 30 cm [3,4], facilitating its ability to exchange with the atmosphere.

Changes in global temperature and moisture patterns forced by climate change are likely to impact the rate at which microbial organisms in soil break down SOM and release CO_2 back to the atmosphere, providing potential feedbacks. However, any feedbacks driven by climate change will depend on the balance between changes to net primary productivity (NPP) and terrestrial ecosystem respiration, including respiration by both autotrophs and heterotrophs. Development of accurate climate models for the future will need to quantify these relationships. Indeed, it has become increasingly essential that we establish the circumstances under which soil respiration will provide either positive or negative feedbacks for the purposes of modeling the climate system of the future. In particular, there is a need to better understand the response of SOM decomposition to climate change.

Numerous studies have concluded that increased mean annual temperature (MAT) will drive an increased rate of microbial respiration that will likely overwhelm the carbon drawdown from rising NPP and result in a positive feedback to the climate system [5–13]. The review by Conant et al. [14] produced a synthesis of the current knowledge (in 2011) that concluded that future temperature changes are likely to cause long-term increases in soil respiration. The emphasis on the effect of temperature on soil also extends to modeling studies. Rustad et al. [2] commented specifically in 2000 that the then-current carbon models focused almost exclusively on the role of temperature in driving soil carbon changes, despite evidence that multiple other factors are involved. As an example, Cox et al. [15] used a coupled 3-D carbon-climate model to demonstrate that an increased positive feedback resulting from increased respiration due to warming will accelerate climate change.

In fact, the responses of soil respiration to climate change are more complex. One example is the sometimes dissimilar respiratory responses of autotrophs (via plant roots) and heterotrophs, including both microbial and fungal decomposers; conditions that favor the increased rate of activities of one may be inhibitory for the other. Respiration by roots and microbial decomposers often varies seasonally, although usually asynchronously, so that the relative proportions of their contributions to the atmosphere will vary greatly [16]. O'Connell et al. [17], for example, found that soil CO_2 flux in tropical forest soils increased during drought conditions and suggested that the increase reflected increased autotrophic respiration under drought stress conditions that simultaneously decreased microbial heterotroph activity. This complexity was well-stated by Subke and Bahn [18], "…it is impossible to measure *actual* temperature response of (soil respiration), and that a range of confounding effects creates the observed *apparent* temperature relations reported in the literature." This complexity continues to produce large uncertainties as models attempt to project future soil-carbon dynamics using more refined input assumptions [19].

Our study is a preliminary attempt to refine our understanding of the relative importance of temperature and moisture on microbial respiration in soils by eliminating all other variables. Notably,

most of the previous studies have been conducted in field settings with methodologies that commonly allowed for a number of unconstrained variables (i.e., root respiration, soil fauna, additional SOM input) to persist. The study presented herein examines the roles of both temperature and moisture in a laboratory setting where temperature and moisture were controlled and all confounding factors were eliminated. The results that follow suggest directions for additional research.

2. Methods and materials

The rate of SOM decomposition presented herein is measured as soil CO_2 flux. All measurements were made on pots filled from a single lot of commercial topsoil enriched with humus to provide a source of labile SOM for heterotrophic respiration. Soil aggregates were crushed and the soil was sieved with a 2-mm screen to remove rocks and woody fragments; all macrofauna (primarily arthropods) were removed manually. Visual inspection confirmed the absence of plant roots and fungal hyphae. Soil invertebrate extractions using Berlese funnels failed to produce any microfauna (e.g. nematodes). Sieve and settling tube analysis determined that the soil consisted of sand (ca. 78%) and silt and clay (ca. 11% each); therefore the soil is sandy loam. Powder X-ray diffraction (using a Bruker D2 Phaser X-ray diffractometer) of clay separates determined that the clay fraction consists of a mixture of illitic and chloritic components. The organic carbon content of the soil was measured by combustion analysis (using a Leco TruSpec CN analyzer) at 11%.

The soil mixture was loaded in terracotta pots to a depth of 10 cm, with a resulting soil volume of 4.75 L. The pots were housed in a greenhouse with an ambient temperature of ca. 20 °C, but subject to fluctuations of up to 5 °C. One set of four pots remained at ambient temperature, another set of four rested on seedling heating mats to create an elevated soil temperature, and a third set was placed on the heating mats but with an intervening layer of foam insulation that created an intermediate temperature level between the other two sets. The temperature differences between the ambient and intermediate sets and between the intermediate and highest temperature sets were each consistently 4 to 5 °C. Soil temperature was measured at the time of flux measurements with a handheld soil temperature probe (manufactured by Hanna Instruments) inserted to the midpoint of the soil (5 cm depth).

All pots initially were allowed to dry for four weeks to establish baseline moisture and flux conditions. Moisture was then increased through weekly addition of 400 mL water to two pots at each of the three temperature levels, and 800 mL water to a second set of two pots at each of the three temperature levels. The higher addition rate was chosen as it corresponds approximately to the mean weekly precipitation for the central New York region. Thus, there were six combinations of temperature and moisture, each with two replicates for a total of 12 pots. Soil CO_2 flux was measured with a Li-Cor 8100A® soil CO_2 chamber system using a 17 cm diameter soil collar with 8 cm soil offset, and a 90 second measurement duration following a 45 second purge cycle. Soil CO_2 flux was calculated in units of μmol CO_2 m^{-2} s^{-1} through an exponential curve-fitting algorithm analysis of the changes in CO_2 within the chamber across the measurement interval. Soil moisture was measured at the time of flux measurement by a ML2x type Theta soil probe (manufactured by Delta Devices) connected to the Li-Cor unit. The measurements are presented here as percent water filled pore space (WFPS).

Watering and flux measurement time protocols were determined following measurements of the dynamics of CO_2 pulses following wetting. A separate set of six pots, using the same three temperature and two wetting protocols, was dedicated to measuring responses to watering at intervals of 2, 4, 7, 17, 24, 48, 72, 96, 120, 144 and 168 hours to determine the time required for pots to reach equilibrium flux conditions following watering. The results of these measurements (discussed below) confirmed that the pots recovered from an initial flux pulse and were at equilibrium within 168 hours of wetting, Soil CO_2 flux was measured on the "steady-state" (i.e., equilibrium) pots one week following each wetting, with the next wetting immediately following measurement. Each flux measurement was conducted in triplicate and tested against the coefficient of variance of flux during the measurement interval. Measurements with an excessively high coefficient of variance were eliminated from the sample set, and the remaining measurements averaged.

The significance of the relationship between the resulting mean flux measurements (i.e., the means of the triplicate measurements) and both temperature and soil moisture was evaluated by both single linear regression and multiple regression analysis with analysis of variance. The analysis was performed using software by SigmaStat® (version 4.5).

3. Results

3.1. Pulse measurement

As described above, six pots were dedicated to measuring the timing and magnitude of the CO_2 flux pulse following wetting at the three temperature controls and addition of water at the two levels (six pots total) described above. All pots exhibited a strong CO_2 pulse (compared to initial conditions) at 2 hours, however the magnitude of the pulse varied greatly (Figure 1). The two pots at ambient temperature (20.5 to 20.9 °C) plus one pot at elevated temperature (26.4 °C) with elevated moisture peaked at flux values between 7.8 and 11.0 μmol m^{-2} s^{-1}. The three remaining pots, all at higher temperatures (26.4 to 31 °C) and including both low and high-water addition (400 mL and 800 mL) experienced CO_2 pulses of 16.4 to 28.8 μmol m^{-2} s^{-1}. In all pots, the initial pulse declined only slightly by 4 hours. By 17 hours, the flux from most pots declined by ca. 30% to 50%. The flux continued to decline more gradually for the remainder of the measurement period, returning to very near the starting conditions by 168 hours.

3.2. Steady-state measurement

Following the initial desiccation interval, the 12 pots representing the six temperature-moisture combinations were monitored over a period of 11 months, with over 1000 individual flux measurements collected. Across the entire range of temperatures (19.5 to 44.1 °C) and moistures (ca. 1 to 56% WFPS), CO_2 flux ranged from 0 to 19.9 μmol m^{-2} s^{-1}. The full data set was tested by multiple linear regression analysis which demonstrated a correlation of significance between the flux values and the corresponding soil moisture measurements ($p < 0.001$; t = 7.033), but not between the flux values and the corresponding temperature measurements ($p = 0.790$; t = 0.267). The r^2 of the regression line is 0.196 (adjusted $r^2 = 0.188$). Analysis of variance of the regression produced values of f = 24.843 and $p < 0.001$. When tested separately by single linear regression, the CO_2 flux values display no correlation with temperature when examined across all moisture levels ($r^2 = 0.002$; Figure

2A). When the data are filtered by moisture level, CO_2 flux again exhibits no correlation to temperature at low soil moisture (WFPS < 20%; Figure 2B), but weak positive correlations are shown at intermediate soil moisture (WFPS = 20 to 30%; r^2 = 0.231; Figure 2C) and high soil moisture (WFPS > 30%; r^2 = 0.105; Figure 2D). We note, however, the lack of flux measurements for higher soil moistures (WFPS > 20%; Figures 2C, D) at temperatures above 30 °C; high evaporative rates at higher temperatures consistently lowered the soil moisture during the 168 hour interval between wetting and flux measurement. Much stronger positive correlations are observed in comparisons of CO_2 flux against soil moisture across all temperatures (r^2 = 0.401; Figure 3A) and when filtered for both low temperature (T < 30 °C; r^2 = 0.439) and high temperature (T > 30 °C; r^2 = 0.44; Figures 3B,C).

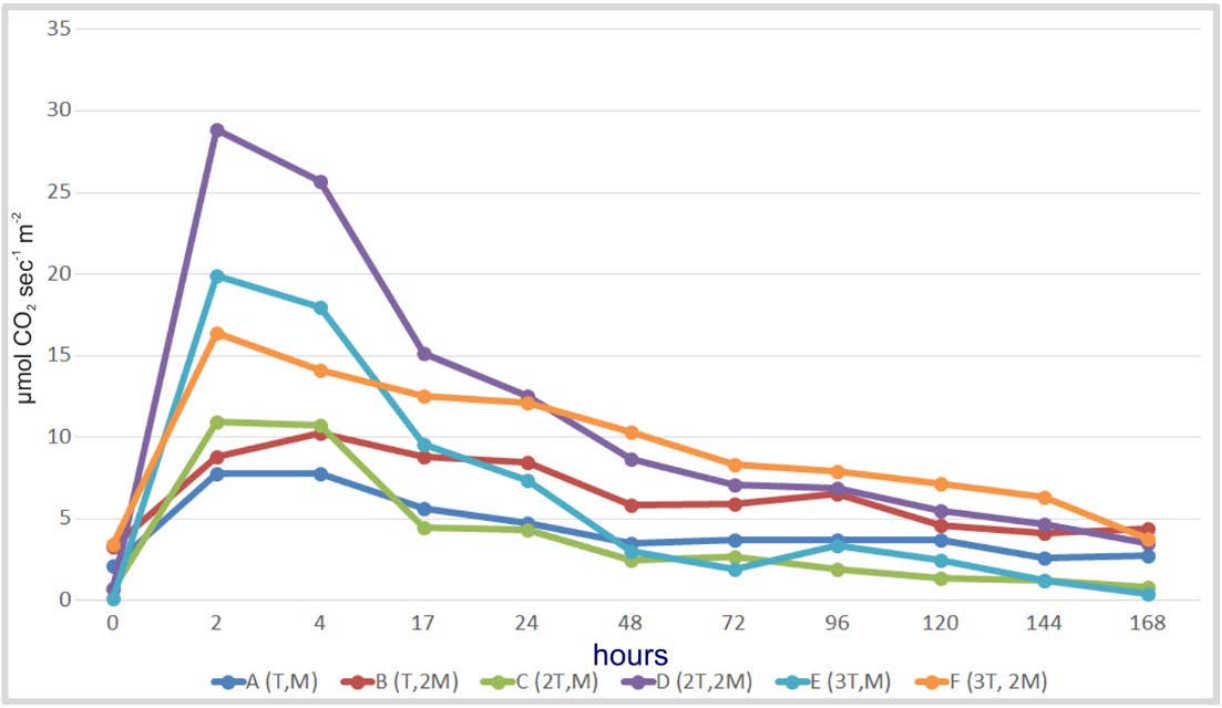

Figure 1. Results of pulse effect measurements of flux vs. time following wetting. Environmental factors: T = ambient temperature; 2T = intermediate elevated temperature; 3T = highest temperature; M = 400 mL water addition; 2M = 800 mL water addition.

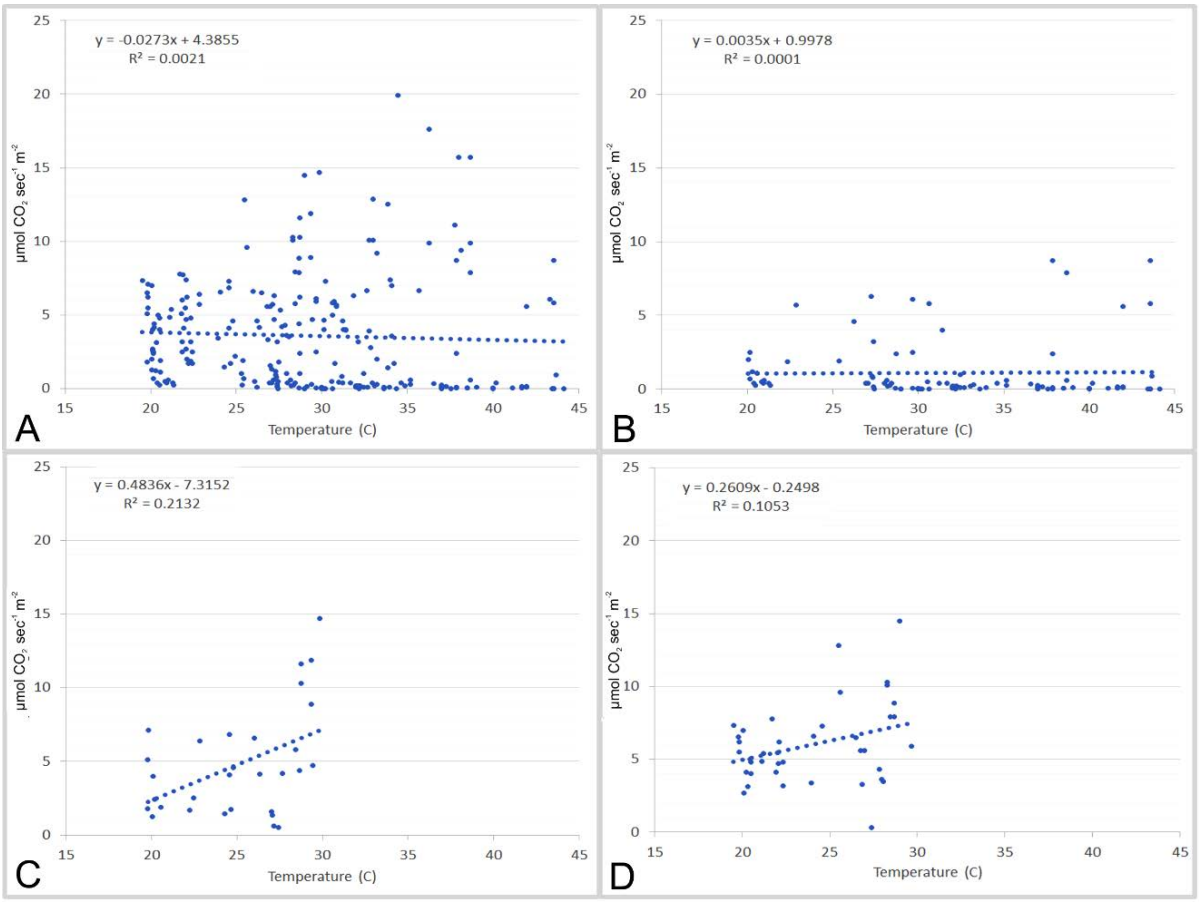

Figure 2. Single linear regressions of CO_2 flux data as a function of temperature with regression equations and calculated r^2. Each data point represents the average of three CO_2 flux trials for a given pot when measured. A) Regression for flux vs. temperature data at all moisture levels. B) Regression of flux data filtered for low soil moisture (WFPS < 20%). C) Regression of flux data vs temperature for intermediate soil moisture (WFPS 20–30%). D) Regression of flux data vs. temperature for high soil moisture (WFPS > 30%).

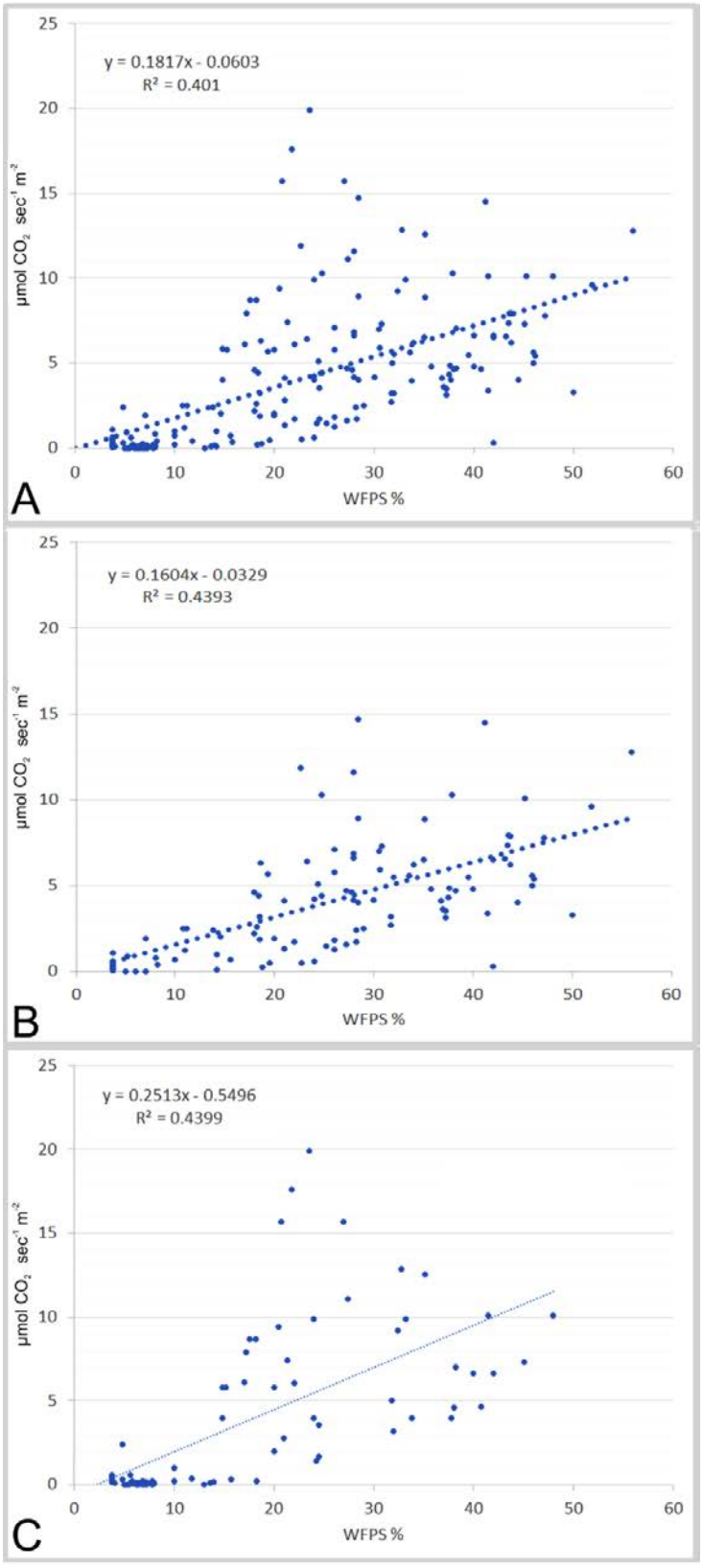

Figure 3. Single linear regressions of CO_2 flux vs. soil moisture with regression equations and calculated r^2. A) Flux vs. moisture across all temperatures. B) Flux vs. moisture data filtered for T < 30 °C. C) Flux vs. moisture data filtered for T ≥ 30 °C.

4. Discussion

As discussed previously, there are numerous confounding factors that complicate the relationships between temperature, moisture and SOM decomposition rate. By using a uniformly prepared soil, we ensured consistent soil properties in all pots, i.e., mineralogy, SOM content and composition, pH, density, porosity and field capacity, all properties that have the capacity to affect the microbial biomass growth and metabolic activity rates [4,20–22]. Additionally, in the laboratory setting there was no additional input of organic matter, hence there was no "priming" of microbial decomposition activity [23–25]. Finally, the lack of roots or observable macro- or microfauna provides confidence that the CO_2 flux is the product solely of microbial respiration and that microbial activity was not stimulated by root exudates.

4.1. Pulse effect

The Birch effect is a well-known response of soils in producing a short-lived CO_2 pulse on wetting, with the magnitude of the response typically related inversely to prior soil moisture [26–29]. The source of the CO_2 pulse is not universally agreed upon but is most typically attributed to the resuscitation and return to metabolic activity of a microbial community that is dormant during periods of low soil moisture [30], with the magnitude of the pulse related to the size of the wetting event [29]. Placella et al. [30] examined the relationship between the pulse response of dry soils upon rewetting and the phylogenetics of the microbial community and found that the latter comprise three distinct groups based on the timing of the pulse: rapid responders that produced a distinct pulse within an hour of rewetting; intermediate responders for which the pulse occurred three to 24 hour following rewetting; and delayed responders that did not produce a significant response until 24 to 72 hours following rewetting. All pulse dynamic pots in our study demonstrated a strong response at two hours with the response continuing at approximately the same rate at four hours and declining by 17 hours. Although the phylogeny of the decomposers in our pots was not examined, they responded quickly to rewetting, with the magnitude of the response depending on both soil temperature and moisture input. Overall, higher temperatures and moistures resulted in higher magnitude pulses, but the relationship is not completely clear from our results. As expected, the smallest pulse was measured in the pot at ambient temperature and lower moisture input. Rather than observing the highest pulse in the high temperature/high moisture pot, however, the largest pulse was measured in an intermediate temperature/high moisture pot, and the second largest pulse was observed in the pot with high temperature/low moisture, contrary to expectations. Because all pots were filled from a single, uniform soil batch, we assume that the soil structure and microbial communities in each pot are similar. We have no explanation for this discrepancy at this time other than speculating that higher moisture levels may have some inhibitory effect on microbial respiration at elevated temperature.

4.2. Steady-state measurements

As described above, the steady-state pots underwent an initial period of desiccation at the ambient temperature of the greenhouse for four weeks prior to the initiation of watering protocols during which soil moisture declined to minimal values (<3% WFPS). Microbial respiration was at or

near zero prior to the initiation of watering, suggesting near complete dormancy of the microbial heterotrophic population. The resumption of respiration following wetting in all pots in this study demonstrates that the microbial population survived the initial interval of desiccation. Potts [20] observed that prokaryotes are more likely to survive desiccation when dried slowly, although this trend may be species dependent. The study design by which our pots were heated from the base and not exposed to direct sunlight may have enhanced the survival of the microbial population.

Both multiple and single linear regression analyses of the full data set demonstrated a much stronger correlation between flux and moisture than between flux and temperature under our experimental protocols (Figures 2 and 3). This differs from the primary finding of many previous studies, although some of these noted a potentially important role for moisture in combination with temperature in controlling respiration. Davidson and Janssens [8], for example, concluded that while rates of soil respiration (combined root and microbial decomposition) are temperature dependent, soil moisture is a limiting factor. Several recent studies have focused specifically on the role of moisture on soil respiration. Gabriel and Kellman [31], for example, found that moisture can play a more important role than temperature, but only at very low or very high soil moisture levels. Lu et al. [32], in their examination of the importance of throughfall precipitation on temperate forest soils, found little to no effect from reduced precipitation on total soil respiration, heterotrophic respiration or autotrophic respiration until soil moisture dropped below a threshold of 10% (soil volume). These findings are consistent with the results presented herein. The lack of correlation between temperature and flux at low soil moisture (<20% WFPS; Figure 2B), in which most of the flux measurements were <1 μmol m^{-2} s^{-1}, likely reflects dormancy of most of the microbial population, superseding the role of soil temperature.

Gabriel and Kellman [31] found that flux correlated with temperature when soil moisture remained constant (in shallow soil cores), but also found that flux correlated with moisture up to 60% WFPS, beyond which moisture impeded aerobic activity. We saw no inhibitory effect of high soil moisture on steady-state flux in our study, although we note that moisture did not exceed 60% WFPS for any measurements in our study. For example, a more clay-rich soil with a higher water-retention capacity might produce different results. We note further that the peak flux values in our study, of 15 to 20 μmol m^{-2} s^{-1}, were measured at temperatures above 30 °C at soil moisture levels of 20 to 30% WFPS (Figure 3C). This suggests that there is an optimal set of conditions for microbial respiration combining elevated temperature but moderate moisture. However, we anticipate that these conditions vary among soils by soil structure (pore space geometry), microbial phylogeny, soil mineralogy and composition of the SOM.

As stated by Bond-Lamberty et al. [33], the sensitivity of respiration by microbial heterotrophs to future changes in temperature, precipitation and organic matter input remains very uncertain. The meta-analysis by Moyano et al. [34] suggested that moisture is an important control of heterotrophic soil respiration, but that this relationship is controlled by other soil properties, such as the density, porosity and composition of mineral soils. Wang et al. [35] addressed the question of how CO_2 growth rate (CGR) will respond to changes in temperature and precipitation and found the stronger correlations with soil moisture variations. However, they also noted that modeling favors dominance of NPP over heterotrophic respiration in driving CGR. Jung et al. [36] similarly concluded that moisture availability largely controls the balance between primary productivity and respiration. Given the range of NPP responses to moisture changes by various plant communities, however,

accurately modeling soil-carbon feedbacks resulting from climate change is likely to remain a challenge for the foreseeable future.

4.3. Future directions

It is well-established that factors other than moisture come into play in controlling the response of soil respiration to temperature. In particular, the response of heterotrophic respiration to rising temperature has been found to vary with the composition of the SOM. Craine et al. [37] concluded that SOM that is more biochemically recalcitrant, i.e., is more resistant to decomposition and produces lower rates of respiration, responds more strongly to temperature increases. Conversely, more labile SOM can be expected to produce a weaker response to increased temperature. The data presented here, in particular the weak response to temperature at constant moisture level, suggests that the humus in our soils contained abundant labile SOM. Repetition of this experiment with identical protocols but a different source of SOM might yield a very different result and should be investigated.

Other work has questioned the importance of the chemical recalcitrance of SOM compared to other soil properties, such as grain size, minerology and soil structure, e.g., aggregates [38]. Specifically, some studies have suggested that SOM is stabilized on the surfaces of the clay-sized (<2 μm) fraction of soil minerals (extensively reviewed by [39]. We note that although numerous experiments have studied organic matter adsorption and stabilization by various clay minerals, few have examined these effects on soil respiration, with field studies by Doetterl et al. [21,22] being an exception. Here again, we suggest experiments testing different clay concentrations and mineralogies as potential avenues of future research.

5. Conclusions

This study is a pilot examination of the relative effectiveness of varying temperature and soil moisture on controlling rates of microbial decomposition of SOM. The measurements were made in a laboratory setting where all other factors were held constant. The experimental soil pots demonstrated a very pronounced and rapid CO_2 flux pulse on rewetting of dry soil, as expected, with the magnitude of the pulse shown to increase with increases in both temperature and water input, although the relationship between these factors is not completely clear. Steady-state measurements over a wide range of soil moistures and temperatures demonstrates a stronger response to changes in moisture than to temperature. A positive correlation was found between CO_2 flux and moisture across all temperature levels. Conversely, no correlation was found between CO_2 flux and temperature when examined across all moisture levels, and at low soil moisture levels. Only weak positive correlations were observed at intermediate and higher moisture.

We believe the results presented herein validate our experimental design as a method of studying the rate of decomposition of SOM. We note that the soil used for this study was a uniform mixture with a low clay content and potentially labile SOM. Therefore, future studies could examine soils with different proportions of clay, varied clay mineralogies and/or different SOM compositions.

Acknowledgments

This work was supported by awards made to CAP and KPM by the McDevitt Center for Excellence and the Student Research Committee at Le Moyne College. This manuscript was improved by thoughtful reviews from two anonymous reviewers.

The data generated in this study are available from the corresponding author on request.

Conflicts of interest

All authors declare that they have no conflicts of interest regarding the publication of this paper.

References

1. Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10: 423–436.
2. Rustad LE, Hungtington TG, Boone RD (2000) Controls on soil respiration: implications for climate change. *Biogeochem* 48: 1–6.
3. Balesdent J, Basile-Doelsch I, Chadoeuf J, et al. (2018) Atmosphere–soil carbon transfer as a function of soil depth. *Nature* 559: 599–602.
4. Malik AA, Puissant J, Buckeridge KM, et al. (2018) Land use driven change in soil pH affects microbial carbon cycling processes. *Nat Commun* 9: 3591.
5. Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272: 393–396.
6. Cao MK, Woodward FI (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* 393: 249–252.
7. Knorr W, Prentice IC, House JI, et al. (2005) Long-term sensitivity of soil carbon turnover to warming. *Nature* 433: 298–301.
8. Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440: 165–173.
9. Crowther TW, Todd-Brown KEO, Rowe CW, et al. (2016) Quantifying global soil carbon losses in response to warming. *Nature* 540: 104–108.
10. Teramoto M, Liang N, Takagi M, et al. (2016) Sustained acceleration of soil carbon decomposition observed in a 6-year warming experiment in a warm-temperate forest in southern Japan. *Sci Rep* 6: 35563.
11. Hicks Pries CE, Castanha C, Porras RC, et al. (2017) The whole-soil carbon flux in response to warming. *Science* 355: 1420–1423.
12. Melillo JM, Frey SD, DeAngelis KM, et al. (2017) Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* 358: 101–105.
13. Nottingham AT, Whitaker J, Ostle NJ, et al. (2019) Microbial responses to warming enhance soil carbon loss following translocation across a tropical forest elevation gradient. *Ecol Lett*.
14. Conant RT, Ryan MJ, Ågren GI, et al. (2011) Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. *Glob Change Biol* 17: 3392–3404.

15. Cox PM, Betts RA, Jones CD, et al. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408: 184–187.
16. Hanson PJ, Edwards NT, Garten CT, et al. (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochem* 48: 115–146.
17. O'Connell CS, Ruan L, Silver WL (2018) Drought drives rapid shifts in tropical rainforest soil biogeochemistry and greenhouse gas emissions. *Nat Comm* 9: 1348.
18. Subke JA, Bahn M (2010) On the 'temperature sensitivity' of soil respiration: can we use the immeasurable to predict the unknown? *Soil Biol Biochem* 42: 1653–1656.
19. Shi Z, Crowell S, Luo Y, et al. (2018) Model structures amplify uncertainty in predicted soil carbon responses to climate change. *Nat Comm* 9: 2171.
20. Potts M (1994) Desiccation tolerance for prokaryotes. *Microbiol Mol Biol Rev* 58: 755–805.
21. Doetterl S, Stevens A, Six J, et al. (2015) Soil carbon storage controlled by interactions between geochemistry and climate. *Nat Geosci* 8: 780–783.
22. Doetterl S, Behre AA, Arnold C, et al. (2018) Links among warming, carbon and microbial dynamics mediated by soil mineral weathering. *Nat Geosci* 11: 589–593.
23. Kuzyakov Y (2010) Priming effects: interactions between living and dead organic matter. *Soil Biol Biochem* 42: 1363–1371.
24. Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biol Biochem* 32: 1485–1498.
25. Liang J, Zhou Z, Huo C, et al. (2018) More replenishment than priming loss of soil organic carbon with additional carbon input. *Nat Comm* 9: 3175.
26. Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen. *Plant Soil* 10: 9–31.
27. Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88: 1386–1394.
28. Wang L, Manzoni S, Ravi S, et al. (2015) Dynamic interactions of ecohydrological and biogeochemical processes in water-limited systems. *Ecosphere* 6: 133.
29. Waring BG, Powers JS (2016) Unraveling the mechanisms underlying pulse dynamics of soil respiration in tropical dry forests. *Environ Res Lett* 11: 105005.
30. Placella SA, Brodie EL, Firestone MK (2012) Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. *Proc Nat Acad Sci* 109: 10931–10936.
31. Gabriel C, Kellman L (2014) Investigating the role of moisture as an environmental constraint in the decomposition of shallow and deep mineral soil organic matter of a temperate coniferous soil. *Soil Biol Biochem* 68: 373–384.
32. Lu H, Liu S, Wang H, et al. (2017) Experimental throughfall reduction barely affects soil carbon dynamics in a warm-temperate oak forest, central China. *Sci Rep* 7: 15099.
33. Bond-Lamberty B, Bailey VL, Chen M, et al. (2018) Globally rising soil heterotrophic respiration over recent decades. *Nature* 560: 80–83.
34. Moyano FE, Vasilyeva NA, Bouckaert L, et al. (2012) The moisture response of soil heterotrophic respiration: interaction with soil properties. *Biogeosciences* 9: 1173–1182.
35. Wang Q, He T, Liu J (2016) Litter input decreased the response of soil organic matter decomposition to warming in two subtropical forest soils. *Sci Rep* 6: 33814.

36. Jung M, Reichstein M, Schwalm CR, et al. (2017) Compensatory water effects link yearly global land CO_2 sink changes to temperature. *Nature* 541: 516–520.
37. Craine JM, Fierer N, McLauchlan KK (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nat Geosci* 3: 854–857.
38. Schmidt MWI, Torn MS, Abiven S, et al. (2011) Persistence of soil organic matter as an ecosystem property. *Nature* 478: 49–56.
39. Barré P, Fernandez-Ugalde O, Virto I, et al. (2014) Impact of phyllosilicate mineralogy on organic carbon stabilization in soils: incomplete knowledge and exciting prospects. *Geoderma* 235–236: 382–395.