Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Soil Biology & Biochemistry 42 (2010) 373-375

Contents lists available at ScienceDirect

# Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio



## Short communication

# Landscape-level variation in temperature sensitivity of soil organic carbon decomposition

## Joseph Craine<sup>a,\*</sup>, Rebecca Spurr<sup>a</sup>, Kendra McLauchlan<sup>b</sup>, Noah Fierer<sup>c</sup>

<sup>a</sup> Division of Biology, Kansas State University, Manhattan, KS 66506, USA

<sup>b</sup> Department of Geography, Kansas State University, Manhattan, KS 66506, USA

<sup>c</sup> Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

#### ARTICLE INFO

Article history: Received 14 September 2009 Received in revised form 22 October 2009 Accepted 27 October 2009 Available online 10 November 2009

Kevwords: Soil organic carbon Warming Grassland Microbial respiration Temperature sensitivity

### ABSTRACT

We examined landscape-level variation in temperature sensitivity of labile SOC across 71 sites at a central North American grassland. The observed range in activation energy of decomposition  $(E_a)$ , an index of temperature sensitivity, was as great at the landscape scale as has been observed at the continental scale.  $E_{\rm a}$  was lower for soils with more labile C, consistent with the 'Carbon qualitytemperature' hypothesis. Soil pH explained 67% of the variation in  $E_a$ . Although there are strong environmental correlates with the  $E_a$  of SOC decomposition at landscape scales, the amount of variation within landscapes could confound regional- to global-scale predictions of the response of soil C to warming.

© 2009 Elsevier Ltd. All rights reserved.

The fate of soil organic carbon (SOC) in a warmer world is one of the largest uncertainties in predicting future climate and terrestrial ecosystem function (Holland et al., 2000; Jones et al., 2003; Lenton and Huntingford, 2003). Although the 'Carbon quality-temperature' (CQT) hypothesis (Bosatta and Ågren, 1999; Fierer et al., 2005; Davidson and Janssens, 2006) predicts that the temperature sensitivity of organic matter decomposition increases with biochemical recalcitrance and it has been tested on a variety of substrates and scales (Fierer et al., 2005, 2006b), we know little about landscape-level variation in SOC temperature sensitivity and whether the CQT hypothesis explains a significant proportion of the observed variation in it.

To better understand the landscape-level variation in temperature sensitivity of SOC decomposition, we collected surface soils (0-20 cm) across 71 sites at Konza Prairie Biological Station, KS, USA in June, 2009. Sites were all located within 5.3 km of one another and distributed among 11 watersheds, each of which differed in the frequency at which they experience fire (annual, biennial, or greater than every 20 years). In 9 watersheds, soils were acquired from a grassland topographic sequence that spanned uplands, slopes, and lowlands. Soils from an additional 9 sites were acquired from riparian areas, defined as having tree cover adjacent

to permanent or intermittent streams. After collection, soils were passed through a 4-mm sieve. For each soil, we measured texture via the hydrometer method (Gee and Bauder, 1979), C and N concentrations on a Leco CHN analyzer, water holding capacity (WHC) (Elliott et al., 1999), and pH in a 1:1 mixture of soil and water (Robertson et al., 1999).

After adjusting the soil moisture of each soil to 35% WHC, 7 replicates of each soil were incubated at 20 °C. At two time points during this incubation, individual replicates of each soil were moved to different temperatures (10, 15, 20, 25, 30 °C) for approximately 24 h with the last two replicates maintained at 20 °C. Average date since acquisition for the first set of respiration measurements was 13.3 d and 35.7 d for second set. From these incubations for each soil, we used the Arrhenius equation to calculate the apparent activation energy of the chemical reactions that contributed to respiration  $(E_a)$  where the rate of respiration relative to total SOC (k) is described by:

$$k = A e^{-\frac{E_a}{RT}} \tag{1}$$

where T is temperature in Kelvin, R is the gas constant and A is the frequency factor that is specific to each reaction. The relative respiration rates of the two additional replicates incubated at 20 °C (R<sub>20</sub>) were used as an index of lability, and were independent from the samples used to calculate  $E_a$ .



Corresponding author. Tel.: +1 785 532 3062; fax: +1 785 532 6653. E-mail address: jcraine@ksu.edu (J. Craine).

<sup>0038-0717/\$ -</sup> see front matter © 2009 Elsevier Ltd. All rights reserved. doi:10.1016/j.soilbio.2009.10.024

The increases in respiration with temperature closely followed the Arrhenius equation. The average coefficient of determination across all soils and both time points was 0.970  $\pm$  0.003 using the Arrhenius equation (n = 142).  $E_a$  for first and second measurement periods were correlated (r = 0.88, P < 0.001) with no differences in means (93.9 and 93.1 kJ mol<sup>-1</sup>, P = 0.46). Respiration rates were also correlated between the first and second measurement periods (r = 0.89, P < 0.001) although respiration rates were 38% higher for the second period than the first (7.46 vs. 5.41  $\mu$ g g<sup>-1</sup> d<sup>-1</sup>, respectively; *P* < 0.001). Thirty-four percent of the variation in the difference between R<sub>20</sub> at the second period vs. the first was explained by the fraction of soil that was clay. Low clay (high sand) soils showed greater increases between the second and first periods than high clay (low sand) soils  $(dR_{20} = 8.07 - 0.22^{*})$ Clay,  $r^{2} = 0.34$ , P < 0.001;  $dR_{20} = -3.79 + 0.15^{*})$ Sand,  $r^2 = 0.32$ , P < 0.001). As  $E_a$  and  $R_{20}$  measurements for the soils were strongly correlated between time periods, we averaged  $E_a$  and  $R_{20}$  between the two time points for subsequent analyses.

Among the 71 soils,  $E_a$  averaged 93.5 kJ mol<sup>-1</sup> and ranged from 69.0 to 146.8 kJ mol<sup>-1</sup>. These are the equivalents of Q<sub>10</sub> values (change in rates between 20 and 30 °C) of 3.55 and 2.54–7.34 respectively. High C soils had SOM with higher  $E_a$  ( $E_a$  = 65.33 + 0.59\* [C],  $r^2$  = 0.20, P < 0.001), but lower R<sub>20</sub> (ln(R<sub>20</sub>) = 2.73–0.025\*[C],  $r^2$  = 0.15, P < 0.001), while neither were affected by soil N content (P > 0.2). There were no strong relationships between soil texture and  $E_a$  (data not shown), while high clay soils had lower R<sub>20</sub> (ln (R<sub>20</sub>) = 2.74–0.043\*%Clay,  $r^2$  = 0.16, P < 0.001).

At the continental scale for North America (Fierer et al., 2006b),  $E_a$  of labile SOM, which we recalculated from the original data, ranged from 56.8 to 108.5 kJ mol<sup>-1</sup>. Not only was the range of  $E_a$  greater within Konza than at the continental scale (77.8 vs. 56.8 kJ mol<sup>-1</sup>), but maximum  $E_a$  within Konza exceeded those observed at the continental scale by 38.3 kJ mol<sup>-1</sup> (146.8 vs. 108.5 kJ mol<sup>-1</sup>, respectively).

 $E_a$  declined with increasing  $R_{20}$  ( $E_a = 118.9-16.34^*\ln(R_{20})$ ;  $r^2 = 0.61$ , P < 0.001). (Fig. 1), supporting the CQT hypothesis. Soils with more labile C being decomposed, as evidenced by higher relative respiration rates, were less sensitive to changes in temperature than soils with more recalcitrant C. Surprisingly,  $E_a$  increased with soil pH (Fig. 1), which explained an even higher proportion of the variation in  $E_a$  than  $R_{20}$  ( $E_a = -65.24 + 23.78^*$ pH;  $r^2 = 0.67$ , P < 0.001). Konza soils are derived from limestone, shale, or loess, and the relative contribution of each is likely a main driver of surface soil pH. Konza uplands on average had lower soil pH than lowlands (6.2 vs. 6.8, P < 0.001), and soil pH increased with soil C ( $r^2 = 0.16$ , P < 0.001), which in total explain 33% of the variation in pH. Although

#### Table 1

Regression model results for activation energy ( $E_a$ ) and relative respiration rate of SOC at 20 °C ( $R_{20}$ ) as predicted by landscape position, fire frequency, and bison grazing.

	Ea		R <sub>20</sub>	
	SS	Р	SS	Р
Position	2838	0.02	240	0.008
Lowland	$97.8\pm4.2$	2 <sup>a</sup>	$4.82 \pm 1.12^a$	
Riparian	$98.8\pm 6.0^a$		$4.76\pm1.62^a$	
Slope	$101.6 \pm 3.3$	3 <sup>a</sup>	$4.99\pm0.88^a$	
Upland	$85.8 \pm 3.9$	Э <sub>р</sub>	$9.14 \pm 1.06^{\text{b}}$	
Fire frequency	830	0.08	15	0.67
Grazing	1229	0.10	198	0.002
Ungrazed	$92.5\pm2.9$	9 <sup>a</sup>	$7.63\pm0.78^a$	
Grazed	$99.5\pm3.3$	3 <sup>a</sup>	$4.22\pm0.88^{b}$	

Included are least squares means for  $E_a$  (kJ mol<sup>-1</sup>) and R<sub>20</sub> (µg C g C<sup>-1</sup> d<sup>-1</sup>). Superscripts denote significant differences in  $E_a$  and R<sub>20</sub> among position and grazing categories. For both regressions, n = 71;  $r^2 = 0.23$  for  $E_a$  and 0.28 for R<sub>20</sub>.

soil pH is a strong correlate with microbial community structure (Fierer and Jackson, 2006a), there is no underlying principle that would cause soil pH to directly affect the temperature sensitivity of decomposition. At the continental scale, soil pH was not a correlate of  $E_{a}$ , even over the same pH range as observed at Konza (5.4–7.6; data not shown). We hypothesize that at Konza, soil pH must indirectly be associated with factors that affect SOC biochemical recalcitrance, such as plant productivity or microbial utilization of soil C. That said, little is known at this time about the patterns of soil pH at Konza, no less why it would be associated with  $E_a$ .

 $E_a$  did not differ among soils acquired from slope, lowland, and riparian landscape positions (P = 0.81), while  $E_a$  was 14% lower in upland positions than other landscape positions 82.9  $\pm$  3.8 vs. 97.0  $\pm$  2.2 kJ mol<sup>-1</sup> (P = 0.002; Table 1). Bison grazing and fire frequency had no influence on  $E_a$  (P = 0.10, 0.12 respectively; Table 1). R<sub>20</sub> was lower in areas grazed by bison (7.6 vs. 4.2, P = 0.004), which suggests that the intense grazing of bison leads to smaller labile pools of SOC. In part, this is likely due to inputs of carbon in grazed areas, as belowground production and soil CO<sub>2</sub> flux is lower in bison-grazed areas of Konza (Johnson and Matchett, 2001), but could also be associated with changes in the quality of organic matter inputs. R<sub>20</sub> was not affected by fire treatment (Table 1).

Overall, this survey for a single grassland landscape reveals the necessity of improving our understanding of landscape-level variation in the temperature sensitivity of SOC decomposition when attempting to refine predictions of the effect of warming on SOC pools. Not only might it be difficult to stratify predictions within



Fig. 1. Relationships between the apparent activation energy of the reactions that determine respiration (*E*<sub>a</sub>) and soil pH (a) and the relative respiration of SOC at 20 °C (*R*<sub>20</sub>) (b).

a landscape, the similar range of  $E_a$  observed at the landscape level as at continental scales could preclude large-scale generalizations of SOC temperature sensitivity if other landscapes are similarly diverse in SOC composition.

#### Acknowledgments

Research was supported by an NSF grant (DEB-0816629) and a Research Experience for Undergraduates supplement. Konza Prairie Biological Station assisted in logistics of sampling and Adam Skibbe assisted in georeferencing sampling points. The KSU Agronomy Soil Testing Lab performed the CN analyses.

### Appendix. Supplementary information

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2009.10.024.

#### References

- Bosatta, E., Ågren, G.I., 1999. Soil organic matter quality interpreted thermodynamically. Soil Biology & Biochemistry 31, 1889–1891.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

- Elliott, E.T., Heil, J.W., Kelly, E.F., Monger, H.C., 1999. Soil structural and other physical properties. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-term Ecological Research. Oxford University Press, Oxford.
- Fierer, N., Jackson, R.B., 2006a. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the United States of America 103, 626–631.
- Fierer, N., Craine, J., McLauchlan, K., Schimel, J., 2005. Litter quality and the temperature sensitivity of decomposition. Ecology 85, 320–326.
- Fierer, N., Colman, B.P., Schimel, J.P., Jackson, R.B., 2006b. Predicting the temperature dependence of microbial respiration in soil: a continental-scale analysis. Global Biogeochemical Cycles 20.
- Biogeochemical Cycles 20.
  Gee, G.W., Bauder, J.W., 1979. Particle-size analysis by hydrometer simplified method for routine textural analysis and a sensitivity test of measurement parameters. Soil Science Society of America Journal 43, 1004–1007.
- Holland, E., Neff, J., Townsend, A., McKeown, B., 2000. Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: implications for models. Global Biogeochemical Cycles 14, 1137–1151.
- Johnson, L.C., Matchett, J.R., 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82, 3377–3389.Jones, C.D., Cox, P., Huntingford, C., 2003. Uncertainty in climate-carbon-cycle
- Jones, C.D., Cox, P., Huntingford, C., 2003. Uncertainty in climate-carbon-cycle projections associated with the sensitivity of soil respiration to temperature. Tellus Series B-Chemical & Physical Meteorology 55, 642–648.
- Lenton, T., Huntingford, C., 2003. Global terrestrial carbon storage and uncertainities in its temperature sensitivity examined with a simple model. Global Change Biology 9, 1333–1352.
- Robertson, G.P., Sollins, P., Ellis, B.G., Lajtha, K., 1999. Exchangeable ions, pH, and cation exchange capacity. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-term Ecological Research. Oxford University Press, Oxford, pp. 106–114.