

Acclimatization of soil respiration to warming in a tall grass prairie

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The latest report by the Intergovernmental Panel on Climate Change (IPCC) predicts a 1.4–5.8 °C average increase in the global surface temperature over the period 1990 to 2100 (ref. 1). These estimates of future warming are greater than earlier projections, which is partly due to incorporation of a positive feedback. This feedback results from further release of greenhouse gases from terrestrial ecosystems in response to climatic warming^{2–4}. The feedback mechanism is usually based on the assumption that observed sensitivity of soil respiration to temperature under current climate conditions would hold in a warmer climate⁵. However, this assumption has not been carefully examined. We have therefore conducted an experiment in a tall grass prairie ecosystem in the US Great Plains to study the response of soil respiration (the sum of root and heterotrophic respiration) to artificial warming of about 2 °C. Our observations indicate that the temperature sensitivity of soil respiration decreases—or acclimatizes—under warming and that the acclimatization is greater at high temperatures. This acclimatization of soil respiration to warming may therefore weaken the positive feedback between the terrestrial carbon cycle and climate.

The third IPCC assessment on climate change has made a great advance in predicting future global climate with, among other improvements, coupled climate and carbon cycle models. Such coupled models are essential to examine biotic feedbacks into the climatic system. Climatic warming, on one hand, potentially stimulates nutrient mineralization and lengthens growing seasons, which consequently increases plant growth and carbon sequestration⁶ (Fig. 1). On the other hand, warming can accelerate biospheric metabolism, resulting in the greater release of heat-trapping gases to the atmosphere^{7–9}, which in return reinforces anthropogenic warming. Indeed, a coupled climate–carbon cycle model by Cox *et al.* (ref. 2) predicts 8.0 °C of global terrestrial warming by the year 2100 rather than the 5.5 °C predicted without the climate–carbon cycle connection. A major uncertainty associated with such a prediction is the assumption that the observed sensitivity of soil respiration to temperature under the current climate—approximately, a doubling of respiration for every 10 °C increase, that is, the temperature quotient $Q_{10} = 2$ —would hold in a future warmed climate⁵. Here we provide experimental evidence that this assumption may be unwarranted.

We have conducted a field warming experiment in a tall grass prairie in central Oklahoma, USA (34° 59' N, 97° 31' W) since 21 November 1999 to study respiratory sensitivity to climate change. We also used clipping to mimic hay harvesting, which is extensively practised in the US Great Plains, in an attempt to examine the interaction of global warming and land-use change. Experimental warming, on average, increased the daily mean air temperature by 1.1 °C, and daily mean soil temperature by 2.0 °C and 2.6 °C in the unclipped and clipped subplots, respectively (Fig. 2a and b).

With a fixed Q_{10} of 2, an increase of 2.0–2.6 °C in soil temperature should cause soil respiration to increase by 15–20%. However, our data showed that experimental warming generally caused no significant changes in soil respiration (Fig. 2e and f). Soil respiration in the warmed plots decreased by, on average, 5% in comparison to that in unwarmed plots without clipping and increased by 0.2% with clipping. This result is supported by long-term field studies in lowland tundra¹⁰ and Finnish soils¹¹, showing that measured soil

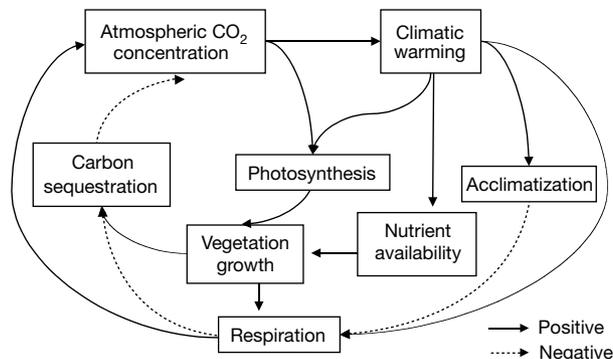


Figure 1 Schematic diagram of major feedbacks in a coupled climate–carbon cycle system. Climatic warming could trigger both a negative feedback through stimulation of nutrient mineralization, plant growth and carbon sequestration on one hand and a positive feedback via an increase in ecosystem respiration to release additional CO₂ on the other hand. Our study provides experimental evidence that acclimatization of soil respiration to warming could potentially weaken the positive feedback through the warming–respiration–atmospheric CO₂ connection. Those mechanisms of climate–carbon cycle coupling may operate at different timescales²⁸.

respiration is not significantly different between two or more temperature regimes. Initial increases in soil respiration under warming in other experiments^{12–14} declined over time^{15,16}. It was also observed that experimental warming reduced soil respiration in an alpine meadow study¹⁷.

To examine the temperature sensitivity of soil respiration, we conducted regression analyses (Fig. 3) using $R_s = ae^{bT}$, where R_s is soil respiration, T is soil temperature, coefficient a is the intercept of soil respiration when temperature is zero, and coefficient b represents the temperature sensitivity of soil respiration. In order to reduce variation in this analysis, we used the soil temperature that was measured at a depth of 5 cm at the time when soil respiration was measured. Four data points of soil respiration per treatment during the summer drought period (Fig. 2c and d) were excluded when soil moisture was below 7% (grams of water per 100 grams of soil, above which soil respiration was not significantly regulated by soil moisture (X. Liu, S.W., B. Su, D.H. & Y.L., unpublished work). Analysis of data from the four treatments (unwarmed, unclipped; warmed, unclipped; unwarmed, clipped; and warmed, clipped) indicates that warming did not significantly affect coefficient a with either clipping regime but did alter the temperature sensitivity coefficient b (Table 1). We merged two a values between unwarmed and warmed plots and then re-estimated the temperature sensitivity coefficient b . The difference in the re-estimated b values between warmed and unwarmed plots was found to be statistically significant with either clipping treatment (Table 1). The b values were used to calculate a respiration quotient $Q_{10} (= e^{10b})$, which decreased from 2.70 in the unwarmed, unclipped plots to 2.43 in the warmed, unclipped plots. The Q_{10} value decreased from 2.25 in the unwarmed, clipped plots to 2.10 in the warmed, clipped plots.

The decrease in temperature sensitivity of soil respiration under warming could result from several mechanisms, including concurrent reduction in plant production leading to less root respiration¹⁷, soil drying reducing root and microbial activity¹⁴, and substrate limitation^{13,16,18}. We measured aboveground live biomass on 28 April, 18 May and 18 November 2000, which was significantly higher (18.3% on average) in the warmed plots than in the unwarmed plots. Increased plant biomass growth presumably enhances root respiration, thus contributing to soil respiration, rather than reducing it.

Measured soil moisture was, on average, 6.4% lower in the warmed plots than in the unwarmed plots over the entire experimental period. To discern the effects of moisture from temperature

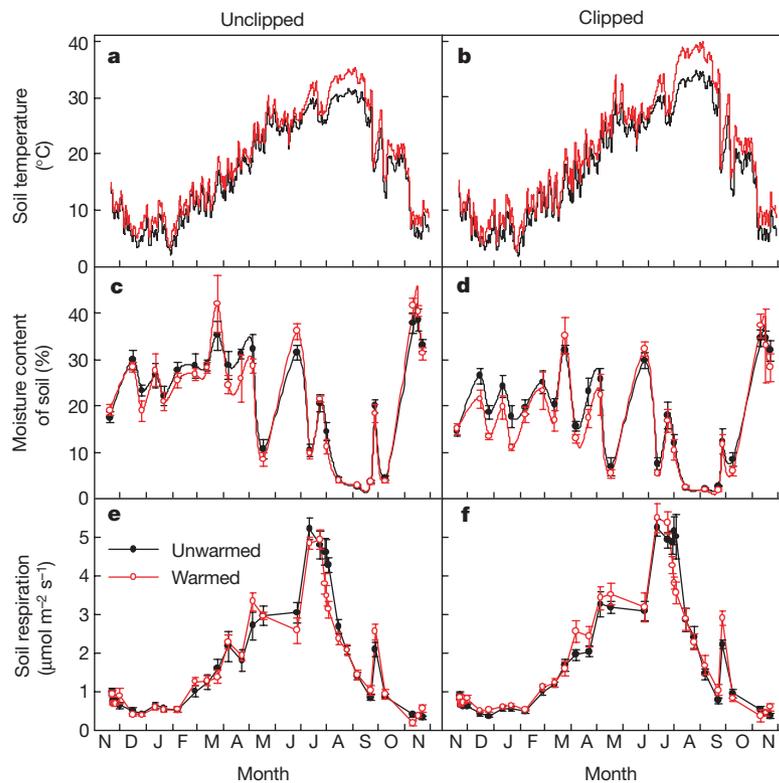


Figure 2 Time courses of measured soil temperature, soil moisture content, and soil respiration from November 1999 to November 2000. **a, b**, Soil temperature; **c, d**, soil moisture content; **e, f**, soil respiration. Data from unwarmed (black lines) and warmed (red lines) plots are shown without clipping (left column) and with clipping (right column). Soil moisture content and respiration are displayed as mean \pm standard error with the sample

size $n = 5$. The sharp decreases in soil respiration in August and September were caused by severe summer drought. The slight increase under warming from April to July with clipping (**f**) was correlated with increased biomass growth. Overall, warming treatment did not significantly change soil respiration either with or without clipping.

on soil respiration, we used the Chi-square (χ^2) test of independence to examine whether effects of warming on soil respiration were correlated with warming-induced changes in soil moisture. We developed three contingency tables for unclipped plots, clipped plots and merged data from unclipped and clipped plots, respectively. The χ^2 tests indicate that the effects of warming on soil respiration are independent of warming-induced changes in soil moisture ($P = 0.31\text{--}0.84$; see the Supplementary Information). Thus, decreased temperature sensitivity of soil respiration to warming was unlikely to be caused by soil drying.

Substrate quality and quantity regulate responses of soil respiration to temperature^{13,18,19}, potentially resulting in acclimatization²⁰. That is, the temperature sensitivity of the soil ensemble decreases when exposed to a warmed environment. Respiratory acclimatization possibly results from changes in the composition of the microbial community²¹, reduced respiratory capacity in soil and/

or other physiological and ecological adjustments²² in response to a limited substrate supply. In our experimental site, soil carbon content is 1.42% on a mass basis, which is relatively low in comparison to other warming experimental sites¹⁵. Soil with low carbon content may be prone to acclimatization.

To evaluate the degree of acclimatization of soil respiration to experimental warming, we define a theoretical isocline of full acclimatization by $R_w = R_u$ at T_w , where R_w is the soil respiration in the warmed plots, R_u in the unwarmed plots, and T_w is the soil temperature in the warmed plots. Comparison of the temperature sensitivity curve in the warmed plots with the isocline indicates that soil respiration was less than fully acclimatized to warming when the temperature was lower than 13.9 °C and more than fully acclimatized when the temperature is higher than 13.9 °C in the unclipped subplots (Fig. 3a). When plants were clipped, soil respiration was less than fully acclimatized at temperatures lower than 20.8 °C and

Table 1 Statistical analysis of temperature relationships of soil respiration

Treatment		<i>a</i>	<i>b</i>	<i>r</i> ²	<i>t</i> _a	<i>t</i> _b	<i>Q</i> ₁₀
Unclipped	Unwarmed	0.267 \pm 0.033	0.104 \pm 0.005	0.967	-1.195	2.859*	-
Unclipped	Warmed	0.332 \pm 0.070	0.085 \pm 0.008	0.870			-
Clipped	Unwarmed	0.333 \pm 0.058	0.086 \pm 0.006	0.923	-1.089	2.074	-
Clipped	Warmed	0.430 \pm 0.112	0.070 \pm 0.009	0.767			-
Pooled coefficient <i>a</i> between two warming treatments							
Unclipped	Unwarmed	0.300 \pm 0.033	0.099 \pm 0.001	0.966	-	7.824**	2.70
Unclipped	Warmed		0.089 \pm 0.002	0.868			2.43
Clipped	Unwarmed	0.381 \pm 0.065	0.081 \pm 0.001	0.921	-	4.164**	2.25
Clipped	Warmed		0.074 \pm 0.002	0.766			2.10

* indicates a statistical significance at $P < 0.01$; and ** at $P < 0.001$.

a and *b* are two coefficients in the regression line $R_s = ae^{bT}$, where R_s is soil respiration and T is soil temperature. r^2 is the determinant coefficient, t_a and t_b are the Student *t* values for testing statistical significance in coefficient *a* and *b* values, respectively, between unwarmed and warmed plots in each clipping regime. Coefficient *a* is not statistically different between the two warming levels, so we pooled a values together and then re-estimated *b* for each of the treatments. Q_{10} is the temperature quotient ($= e^{10a}$).

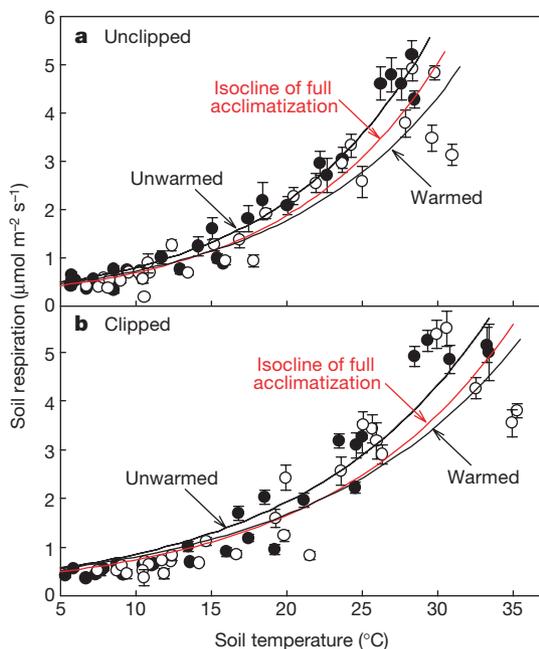


Figure 3 The relationships between soil respiration and temperature in unwarmed (filled circles) and warmed (open circles) treatments with standard errors. **a**, Unclipped subplots; **b**, clipped subplots. Response curves of soil respiration to temperature in the warmed treatment are below that in the unwarmed treatment, indicating that warming reduced temperature sensitivity. The theoretical isoclines of full acclimatization are defined as identical rates of respiration in the warmed plots to those in the unwarmed plots, at the temperature in the warmed plots. Soil temperature used in this analysis was measured at a depth of 5 cm at the time when soil respiration was measured. It was 1.5 °C and 1.9 °C higher in the warmed than the unwarmed plots without and with clipping, respectively.

more than fully acclimatized at temperatures higher than 20.8 °C (Fig. 3b).

This study, for the first time, to our knowledge, has quantified the degree of the acclimatization of soil respiration to warming that varies with temperature itself. Other lines of evidence^{16,23} also support our result that respiratory acclimatization is stronger in the high rather than in the low temperature range. If this relationship holds over larger spatial and temporal scales, ecosystems in warm regions might acclimatize to global warming more than ecosystems in cold regions. Ecosystems in a future, warmer climate might acclimatize more than the current ecosystems do. If acclimatization is indeed caused by limited substrate supply, ecosystems with low soil carbon content may acclimatize to global warming more than ecosystems with a high carbon supply. That means ecosystems in cold regions with high carbon storage may be more closely coupled with climate than ecosystems in warm regions with low carbon storage, as suggested by other studies²⁰. In general, the spatial and temporal variability in respiratory responses to warming not only highlights the limitations of the Q_{10} approach to global scaling but also emphasizes the need for research on the biosphere–atmosphere interactions.

Interactions between climatic change and the carbon cycle are likely to be complicated by land-use change^{24,25}. In this study, the unwarmed, unclipped subplots probably represent undisturbed prairie under the current climate. The warmed, clipped subplots presumably represent a land-use scenario in a future, warmed climate. Soil temperature differed by 3.2 °C between the two treatments, suggesting that clipping or grazing exacerbates the effects of climatic warming. Despite the large temperature difference, observed soil respiration between the two scenarios was similar, owing to a decrease in Q_{10} values from 2.7 to 2.1. Thus, strong acclimatization of soil respiration to temperature may mitigate the

effects of land use and global warming on the terrestrial carbon cycle.

Overall, acclimatization of soil respiration to global warming counteracts the positive feedback between the carbon cycle and climatic warming and may act as a short-term mechanism of homeostasis in the earth system (Fig. 1). As carbon released via soil respiration accounts for approximately 10% of the carbon in the atmospheric pool²⁵, most modelling studies demonstrate a major feedback of soil respiration to reinforce global warming^{2–4,7}. On the basis of temperature sensitivity with a fixed Q_{10} value (for example, 2.0) across the globe, global warming by 2 °C is predicted to increase additional carbon release from soil by more than 10 Pg (10^{15} g) of C per year. The additional carbon release to the atmosphere results in more greenhouse effects, aggravating anthropogenic warming^{2,3}. Acclimatization of soil respiration to global warming has the potential to offset, at least partially, the additional carbon release that would be stimulated by a temperature increase; it thus weakens the climate to carbon cycle coupling. □

Methods

The experimental site is at the Central Redbed Plains²⁶. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium*, *Sorghastrum nutans* and *Eragrostis* spp.) and C_3 forbs (*Ambrosia psilostachya* and *Xanthocephalum texanum*). Mean annual temperature is 16.3 °C with January being the coldest month (3.3 °C) and July the warmest (28.2 °C). Mean annual precipitation is 914 mm. The soil is part of the Nash–Lucien complex, which is characterized as having a low permeability rate, high available water capacity and a deep, moderately penetrable root zone²⁷.

The experiment used a paired, nested design with warming as a primary factor and clipping as a secondary factor. Five pairs of plots of 2 m × 2 m were established for warming and unwarmed control. Each plot was divided into four 1 m × 1 m subplots. Plants in two diagonal subplots were clipped at the height of 10 cm above the ground on 15 November 1999 and 28 July 2000 with the other two as unclipped control. An infrared radiator (Kalglo Electronics, Bethlehem, Pennsylvania) was used as the heating device, suspended 1.5 m above the ground. The device has been effectively used in other studies¹⁷.

Air temperature was monitored with sheltered thermocouples at the height of 25 cm in each plot. Soil temperature was measured at the depth of 2.5 cm in one clipped and one unclipped subplot in each plot. All the thermocouples were connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). Air and soil temperatures were measured every 10 minutes. Averages within one hour were stored in SM196 Storage Module. Soil respiration was measured between 10:00 and 15:00 twice a month with an infrared gas analyser Li-Cor 6400 with an attachment of soil chamber Li-Cor 6400-09 (Li-Cor, Lincoln, Nebraska). We collected soil samples at the depth of 0–5 cm in one unclipped and one clipped subplot in each plot to measure soil moisture gravimetrically at the time of measuring respiration.

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Supplementary information is available from Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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The earliest known fully quadrupedal sirenian

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Modern seacows (manatees and dugongs; Mammalia, Sirenia) are completely aquatic, with flipperlike forelimbs and no hindlimbs^{1,2}. Here I describe Eocene fossils from Jamaica that represent nearly the entire skeleton of a new genus and species of sirenian—the most primitive for which extensive postcranial remains are known. This animal was fully capable of locomotion on land, with four well-developed legs, a multivertebral sacrum, and a strong sacroiliac articulation that could support the weight of the body out of water as in land mammals. Aquatic adaptations show, however, that it probably spent most of its time in the water. Its intermediate form thus illustrates the evolutionary transition between terrestrial and aquatic life. Similar to contemporary primitive cetaceans³, it probably swam by spinal extension with simultaneous pelvic paddling, unlike later sirenians and cetaceans, which lost the hindlimbs and enlarged the tail to serve as the main propulsive organ. Together with fossils of later sirenians elsewhere in the world^{1,4–7}, these new specimens document one of the most marked examples of morphological evolution in the vertebrate fossil record.

Since 1990, abundant remains of sirenians, together with other marine taxa of early middle Eocene age (roughly 50 Myr ago), have been collected from Seven Rivers, Jamaica. The sediments (siltstones and sandstones) represent a lagoonal, estuarine or deltaic depositional environment. The age of the site was determined from molluscs (*Campanile*, *Eovasum*, *Paraseraphs*, *Velates*), and

corroborated by the presence of a primitive rhinoceros, *Hyrachyus* sp., of late early or early middle Eocene date⁸. The terrestrial fauna also includes an iguanian lizard⁹ and possibly a primate¹⁰. The sirenian fossils are found in five distinct bone-beds within a 5-m stratigraphic section referred to the Guys Hill Member of the Chapelton Formation, and occur as isolated bones and associated partial skeletons, with the remains of several individuals commingled. In the lower three bone-beds, all the sirenian remains appear to represent a single taxon (described here: Figs 1 and 2). These provide the first view of the overall anatomy and mode of locomotion of sirenians during their evolutionary transition from land-dwelling to obligatorily aquatic life.

Order Sirenia Illiger, 1811
 Family Prorastomidae Cope, 1889
Pezosiren portelli, gen. et sp. nov.

Etymology. Generic name from Greek *pezos* (on foot, walking) and *Seiren* (Latin *Siren*, f., siren). Specific epithet in honour of Roger W. Portell, discoverer and co-investigator of the site.

Locality and horizon. Known only from Seven Rivers (about 15 km south of Montego Bay), parish of St James, western Jamaica; Guys Hill Member, Chapelton Formation, Yellow Limestone Group (early middle Eocene).

Holotype. US National Museum of Natural History, Paleobiology collection (USNM), no. 511925 (Fig. 2a): pair of partial mandibles from Seven Rivers bone-bed II.

Referred material. Specimens illustrated here (Fig. 2b–h) comprise sacrum (associated with 7 thoracic, 4 lumbar and 1 caudal vertebrae), USNM 517463, bone-bed II; left and right innominates, USNM 517464, bone-bed II; left femur with separated distal epiphysis, USNM 517465, bone-bed II; left tibia, USNM 517466, bone-bed III; intermediate phalanx, USNM 517467, bone-bed II. The following description also draws on several hundred other cranial and postcranial elements from Seven Rivers bone-beds II–IV, not formally referred at this time, that remain to be catalogued in the USNM, University of the West Indies, and Florida Museum of Natural History collections.

Diagnosis. The diagnosis for the genus is the same as for the species until other species are described. *Pezosiren portelli* differs from *Prorastomus sirenoides*, the only other named member of the family, in having (1) a sagittal crest; (2) an auditory meatus that is about as wide anteroposteriorly as high; (3) a periotic that is not fused to the alisphenoid; (4) an unenlarged P₁; and (5) a horizontal mandibular ramus whose ventral border is turned down anteriorly. Character states 1 and 4 are primitive within the Sirenia; character states 2, 3 and 5 are considered derived¹¹.

Description. *Pezosiren* was a pig-sized quadruped (estimated total length 2.1 m) with a relatively short (but not extremely compressed) neck, a long, barrel-shaped trunk, short legs and a substantial (but not powerfully muscled) tail (Fig. 1). The skull (estimated condylobasal length 26.5 cm, zygomatic width 14.5 cm) is of clearly sirenian form, with a prominent although undeflected rostrum, large mesorostral fossa, large nasals, horizontally jutting supraorbital processes, and laterally projecting zygomatic arches. A weak sagittal crest is present; this appears to be absent in the holotype of *Prorastomus sirenoides* but may have been removed by erosion or preparation. The sphenopalatine region is primitively long, and lacks the enlarged, stout, ventrally projecting pterygoid processes characteristic of later sirenians. An alisphenoid canal is present, and the foramen ovale seems to be completely enclosed by bone.

The mandible (Fig. 2a) is long (19 cm) and slender, with its ventral border strongly turned down anteriorly; the symphysis is long, deep and mediolaterally compressed; the incisors and canines are arranged in parallel, parasagittal rows; several mental foramina are present; and the mandibular foramen is small, not exposing the dental capsule. The dental formula is uncertain (the toothrows are incomplete anteriorly) but was presumably 3.1.5.3 as in all other