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The responses of soil and rhizosphere respiration to simulated climatic changes vary by season

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Abstract. Responses of soil respiration (R_s) to anthropogenic climate change will affect terrestrial carbon storage and, thus, feed back to warming. To provide insight into how warming and changes in precipitation regimes affect the rate and temperature sensitivity of R_s and rhizosphere respiration (R_r) across the year, we subjected a New England old-field ecosystem to four levels of warming and three levels of precipitation (ambient, drought, and wet treatments). We measured R_s and heterotrophic respiration (R_h) monthly (in areas of the plots with and without plants, respectively) and estimated R_r by calculating the difference in respiration between R_s and R_h . Even in this mesic ecosystem, R_s and R_r responded strongly to the precipitation treatments. Drought reduced R_s and R_r , both annually and during the growing season. Annual cumulative R_s responded nonlinearly to precipitation treatments; both drought and supplemental precipitation suppressed R_s compared to the ambient treatment. Warming increased R_s and R_r in spring and winter when soil moisture was optimal but decreased these rates in summer when moisture was limiting. Cumulative winter R_r increased by about 200% in the high warming ($\sim 3.5^\circ\text{C}$) treatment. The effect of climate treatments on the temperature sensitivity of R_s depended on the season. In the fall, the drought treatment decreased apparent Q_{10} relative to the other precipitation treatments. The responses of R_s to warming and altered precipitation were largely driven by changes in R_r . We emphasize the importance of incorporating realistic soil moisture responses into simulations of soil carbon fluxes; the long-term effects of warming on carbon–climate feedback will depend on future precipitation regimes. Our results highlight the nonlinear responses of soil respiration to soil moisture and, to our knowledge, quantify for the first time the loss of carbon through winter rhizosphere respiration due to warming. While this additional loss is small relative to the cumulative annual flux in this system, such increases in rhizosphere respiration during the non-growing season could have greater consequences in ecosystems where they offset or reduce subsequent warming-induced gains in plant growth.

Key words: microbial respiration; precipitation; root respiration; temperature sensitivity; warming; winter respiration.

INTRODUCTION

The rate of terrestrial carbon (C) storage depends on the balance between C fixed by photosynthesis and released to the atmosphere through plant and heterotrophic respiration (Friedlingstein et al. 2006). Thus, if climate change alters rates of soil respiration without offsetting changes in plant productivity, it will affect the C budget. Although temperature and moisture are clearly major drivers of R_s (Luo and Zhou 2006), the seasonal responses of the two components of soil respiration (heterotrophic [R_h] and rhizosphere [R_r] respiration) to combined effects of warming and altered precipitation are poorly understood (Reichstein and

Beer 2008). Wintertime processes have received the least attention; few experimental studies have included winter measurements of soil respiration, and we are not aware of any studies that have quantified winter rhizosphere respiration to warming. A recent warming and nitrogen addition experiment at Harvard Forest reported a winter flux of 2–17% of annual C and nitrogen flux, emphasizing the importance of winter measurements for predicting winter biogeochemical processes (Contosta et al. 2011). Rhizosphere respiration during the non-growing season is mostly for maintenance of roots, and a majority of the C used for winter maintenance respiration is derived from stored resources (Regier et al. 2010, Kuptz et al. 2011). C reserves can help plants, especially mature trees, to survive through environmental stresses such as droughts, fires, or pest outbreaks (Chapin et al. 1990). Increases in winter temperatures due to climate change could deplete plant C reserves by enhancing maintenance respiration. This could subsequently reduce reemergence or new root growth and

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productivity of plants in the spring, reducing C uptake and offsetting positive effects of warmer spring temperatures on growth. Previous studies evaluating the effect of warming on R_r have focused on the snow-free season (Scott-Denton et al. 2006, Schindlbacher et al. 2009), and have not considered the effects of warming on winter rhizosphere respiration and in turn on plant carbon use efficiency (CUE; ratio of NPP to production plus autotrophic respiration [Ryan et al. 1997]) and ecosystem C balance.

Untangling the effects of multiple factors of climate change on terrestrial C stocks is complex due to the differential responses of R_h and R_r . R_h results from the microbial decomposition of a range of substrates, including soil organic matter and plant litter with varying ages and complexities (Trumbore 2006). R_r not only includes root and associated mycorrhizal respiration, but also the decomposition of labile root exudates by microorganisms in the root (Kuzayakov and Larionova 2005). Although several studies have reported similar responses of R_r and R_h to warming (Schindlbacher et al. 2009), many other experiments have reported a greater response of R_r than R_h (Boone et al. 1998, Lavigne et al. 2003). Our lack of understanding of the relative sensitivities of these responses limits our ability to predict soil C loss in future climate scenarios.

Although R_s is often modeled as a function of temperature, changes in soil moisture, photosynthesis, and substrate availability may modify this temperature response function (Davidson et al. 1998). Temperature sensitivity of R_s derived from annual patterns may not be accurate, due to seasonal changes in plant phenology and belowground C allocation (Yuste et al. 2004). Hence, representing R_s and R_r as exponential functions of temperature could over- or underestimate respiration, reducing the realism of C budget projections under future climate scenarios.

To date, most studies with multiple climate factors such as warming and altered precipitation have been conducted in semiarid ecosystems where soil water availability is critical to many ecosystem processes (Liu et al. 2009). Mesic systems are thought to be less responsive to changes in soil water. However, Suseela et al. (2012) found that soil heterotrophic respiration responded more strongly to manipulations of soil moisture than manipulations of temperature in a mesic old field. Whereas Suseela et al. (2012) explored the response of heterotrophic respiration (R_h) alone, the present study, using the same plots at the Boston-Area Climate Experiment (BACE), seeks to address the following questions: (1) How do soil and rhizosphere respiration (R_r) respond to gradients of warming and precipitation at different temporal scales? and (2) What are the roles of warming and precipitation in driving the temperature sensitivities of R_s and R_r at different temporal scales? We hypothesized that the rate and temperature sensitivity of R_s to warming would strongly depend on soil moisture. During dry periods in the

growing season, we expected warming to dry the soil, and thus suppress R_s by limiting substrate availability. We also hypothesized that the response of R_r to warming and altered precipitation would depend on the season. More specifically, we expected that warming would increase R_r in winter.

MATERIALS AND METHODS

Site description

Measurements were taken from March 2009 to March 2010 at the Boston-Area Climate Experiment (BACE) located in Waltham, Massachusetts, USA (42°23.1' N, 71°12.9' W). The study site was an old-field dominated by grasses and forbs (~40 species; Hoepfner and Dukes 2012). We also planted seedlings of four tree species: *Acer rubrum*, *Quercus rubra*, *Betula lenta*, and *Pinus strobus*. Nearby, the city of Boston, Massachusetts has a mean annual temperature of 9.5°C and mean annual precipitation of 1194 mm (NOAA National Climatic Data Center Cooperative station ID 190535, years 1960–2008). The soil at the site is a Mesic Typic Dystrudept with a loamy topsoil (45% sand, 46% silt, 9% clay; gravel content 7%) and a gravelly sandy loam subsoil.

Experimental design

The BACE employs a factorial design, with precipitation treatments applied to main plots and warming treatments applied to subplots across three experimental blocks (36 plots in total; Tharayil et al. 2011). The four warming treatments included unwarmed controls, and low, medium, and high warming levels, which warmed the plant canopy by a maximum of ~1°, ~2.7°, and 4°C, respectively. For each 2 × 2 m plot, warming was achieved using four ceramic infrared heaters, which were mounted 1 m above the corners of each subplot. Heaters of different wattages were used in the low (200 W), medium (600 W), and high warming (1000 W) treatments. Each precipitation plot contained four subplots that were arranged linearly, with one subplot assigned to each of the four warming treatments. Within each main plot, canopy temperatures of the control and high warming subplots were measured every 10 s using infrared radiometers. Feedback control of all four subplots was achieved by programming control software (Labview, National Instruments, Austin, Texas, USA) to limit the temperature difference between the unwarmed and high subplots to a maximum of 4°C, and by controlling all heaters within each precipitation plot on the same circuit. Main plots experienced either ambient precipitation, a “drought” treatment, or a “wet” treatment. Drought treatments were located under rainout shelters with polycarbonate slats (15 cm wide) that excluded 50% of the rainfall. During the non-freezing months, this water was diverted to storage tanks and immediately applied to the wet section of the block using overhead sprinklers. The wet treatment thus

received 150% of ambient rainfall during the growing season. By July 2008, all treatments were operational.

Soil responses

We measured soil and heterotrophic respiration monthly, between 10:00 and 16:00 (local time), using a LiCor 6400 attached to a 6400-09 soil CO₂ flux chamber (Li-Cor, Lincoln, Nebraska, USA). In each plot, measurements of R_s were taken inside two replicate PVC rings that were 10 cm in diameter and 5 cm in height, inserted to a depth of 2–3 cm in the ground; these measurements captured respiration from plant roots and microbes (shoots were removed from within the rings). Measurements of R_h were taken in each plot using a similar PVC ring (10 cm diameter and 5 cm height) installed inside a larger (25 cm diameter, 30 cm deep) PVC “plant exclusion collar” that excluded plant roots and organic matter inputs (Suseela et al. 2012). The CO₂ efflux from this collar was mainly due to the microbial decomposition of soil organic matter (Suseela et al. 2012). Most of the root growth at our site occurred in the top 10 cm and few roots grew beyond 30 cm; thus, we could rule out the possibility of meaningful amounts of root respiration coming from the plant exclusion collar. Along with respiration measurements, we simultaneously measured soil temperature (5 cm depth) in each ring using a thermocouple attached to the LiCor 6400. We also measured volumetric soil moisture in the top 10 cm of the soil column in all main plots and plant exclusion collars using time domain reflectometry (TDR).

Rhizosphere respiration (R_r) was estimated as the difference in soil CO₂ efflux between R_s and corrected R_h . Because soils inside the plant exclusion collars were wetter than those in the surrounding plot, we corrected R_h values for the difference in soil moisture. A best-fit quadratic equation was obtained relating R_h to soil moisture in the plant exclusion collar. This function was then used to “correct” measured R_h values, based on differences in moisture between soil inside and outside of each plant exclusion collar. Soil temperatures also differed slightly ($P < 0.05$) between the R_h and R_s collars on four of the measurement dates; soils were 0.7°C warmer in the plant exclusion collars in March and May, and 0.6–0.8°C cooler in August and September. Because these temperature differences were slight (<1°C) and transient, we did not correct for them. Soil respiration and its temperature sensitivity in the low warming treatment (which consistently warmed plots by ~1°C) were statistically similar to the unwarmed treatment, suggesting that temperature correction was unnecessary.

We periodically measured diel respiration (measurements every 2 hours over 24-hour cycles) in both the main plots and plant exclusion collars. We made diel measurements only in the unwarmed and high warming treatments, due to time constraints. The diel measurements were used to calculate the annual, growing

season (April–September), non-growing season (October to March), and winter season (December to February) cumulative R_s and R_r . We followed the method of Bremer et al. (1998) for calculating cumulative values. Briefly, respiration measured at the BACE during the daytime was assumed to be the daily maximum soil CO₂ efflux. We used diel measurements to calculate the daily minimum efflux as a percentage of maximum efflux. The daily minimum and maximum efflux were used to calculate the average daily efflux. We estimated cumulative flux as the product of average daily flux and the number of days between each measurement.

Data analysis

In the main plots, R_s measurements from the two replicate rings were averaged by plot for statistical analysis. To test the main and interactive effects of warming and altered precipitation on climate variables (soil temperature and soil moisture) and on respiration, both annually and seasonally, we used mixed model restricted maximum likelihood estimation with repeated measures (PROC MIXED; SAS version 9.2; SAS Institute 2008). Warming and precipitation treatments were assigned as fixed factors and block as a random factor. We used Tukey’s HSD multiple comparison test to identify differences among treatments.

We used an exponential function (Eq. 1; Zhou et al. 2007) to calculate the temperature sensitivity of R_s and R_r :

$$R_x = ae^{bT} \quad (1)$$

where R_x is the soil CO₂ efflux ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), T is the soil temperature (°C) at 5 cm depth, a is the basal respiration, and b is the temperature sensitivity of soil CO₂ efflux. The respiratory quotient (Q_{10}) is calculated as $Q_{10} = e^{10b}$.

To assess the effect of moisture on R_s we fitted R_s and volumetric soil moisture using a quadratic function (Eq. 2; Wan and Luo 2003):

$$R_s = y_0 + ax + bx^2 \quad (2)$$

where x is the volumetric moisture content (V/V) in the top 10 cm of soil, and y_0 , a , and b are constants. To evaluate the effect of both soil temperature and soil moisture on R_s , we fitted R_s using a combined exponential and quadratic function (Eq. 3; Mielnick and Dugas 2000):

$$R_s = (ae^{bT})[2.12(\theta v - \min \theta v)(\max \theta v - \theta v)^c] \quad (3)$$

where θv is the volumetric moisture content (the minimum volumetric water content of our data set was 0.3% and the maximum was 36.8%) and c is the coefficient for soil moisture. We used Sigmaplot (version 12; Systat Software, San Jose, California, USA) for all curve-fitting.

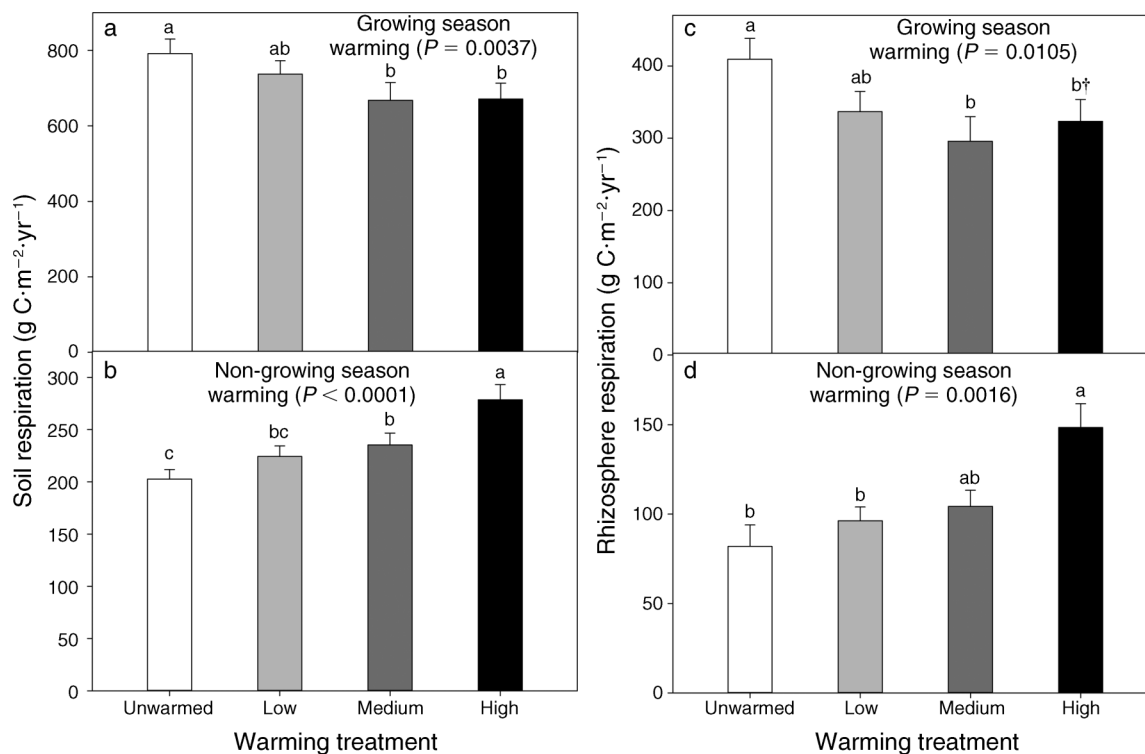


FIG. 1. Cumulative growing-season (April–September) and non-growing-season (a, b) soil respiration and (c, d) rhizosphere respiration. Bars represent means \pm SE ($n=9$ samples). The dagger (†) in panel (c) marks the high-warming treatment, which only marginally decreased R_r compared to the unwarmed treatment (see *Results: Soil and rhizosphere respiration: cumulative measures*).

RESULTS

Soil microclimate

Soil temperature at 5 cm depth varied seasonally from an average minimum of $0.29^\circ \pm 0.5^\circ\text{C}$ (mean \pm SE) in January to a maximum of $26.4^\circ \pm 0.6^\circ\text{C}$ in August in the unwarmed, ambient-precipitation treatment (Appendix A: Fig. A1a). Warming treatments consistently altered soil temperature throughout the summer and fall ($P < 0.0001$; Appendix A: Table A1). However, the effect of warming varied by month during spring ($P = 0.0137$) and winter ($P < 0.0001$). Warming increased soil temperature by an annual average of 0.76° , 2.3° , and 3.1°C in the low, medium, and high warming treatments, respectively, relative to the unwarmed treatment ($P < 0.0001$). From July to September, drought treatment plots were warmer than the ambient (by 2°C) and wet plots (by 2.6°C ; $P < 0.05$).

Soil moisture fluctuated dramatically throughout the year, corresponding to rain events (Appendix A: Fig. A1b). The drought treatment had lower soil moisture from April to October (except for June) compared to both ambient and wet treatments ($P < 0.05$; Appendix A: Table A2). The reduction in soil moisture in the drought treatment varied from 19% (in April compared to ambient treatment) to 80% (in August compared to ambient treatment). High warming ($\sim 4^\circ\text{C}$) reduced soil moisture compared to the unwarmed treatment

from April to October and compared to the low ($\sim 1^\circ\text{C}$) warming treatment during May, September, and October (Appendix A: Fig. A2). In May, medium ($\sim 2.7^\circ\text{C}$) warming reduced soil moisture relative to the unwarmed and the low warming treatments.

Soil and rhizosphere respiration: cumulative measures

The annual cumulative R_s for the 12 treatments ranged from 717 – $1103 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Although warming did not affect the annual cumulative R_s , warming had opposing effects on cumulative R_s during the growing ($P = 0.0037$) and non-growing seasons ($P < 0.0001$). During the growing season, both medium ($P = 0.0072$) and high warming ($P = 0.0117$; Fig. 1a) suppressed R_s by 17% and 16%, respectively, compared to the unwarmed treatment. This trend was reversed during the non-growing season, when medium and high warming increased R_s by 16% and 37% respectively, compared to the unwarmed treatment ($P < 0.0001$; Fig. 1b). Over this period, high warming also increased cumulative respiration compared to the low ($P = 0.0028$; +24%) and medium ($P = 0.0196$; +18%) warming treatments. Drought reduced annual cumulative R_s ($806 \pm 32 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) compared to ambient ($1061 \pm 21 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; $P < 0.0001$) and wet treatments ($975 \pm 24 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; $P = 0.0001$; Appendix A: Table A3). During the growing season, drought reduced cumulative R_s by 28% and 23% compared to the ambient ($P <$

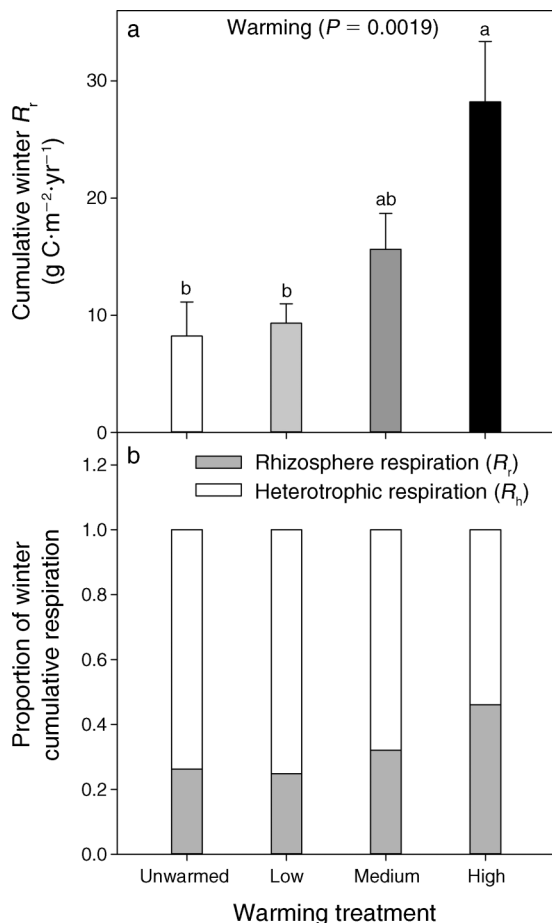


FIG. 2. (a) Cumulative winter (December–February) rhizosphere respiration R_r and (b) proportion of cumulative respiration attributable to rhizosphere and heterotrophic respiration. Values represent means ($n = 9$ samples); +SE is shown in panel (a).

0.0001) and wet ($P < 0.0001$) treatments, respectively. The wet treatment showed a trend of decreasing annual cumulative R_s in comparison with the ambient treatment ($P = 0.08$; -8%) from April 2009 to March 2010. We also calculated cumulative R_s from December 2008 to November 2009 to check whether the above pattern was consistent over time. During this period, supplemental precipitation suppressed cumulative R_s by 10% compared to ambient ($P = 0.046$).

Annual cumulative R_r varied with precipitation treatments; drought reduced estimated annual R_r relative to the ambient (-29% ; $P = 0.0002$) and wet precipitation treatments (-20% ; $P = 0.0094$; Appendix A: Table A4). Growing season cumulative R_r responded similarly; drought decreased R_r compared to ambient (-34% ; $P < 0.0001$) and supplemental precipitation treatments (-29% ; $P = 0.0008$). During the growing season medium warming decreased R_r compared to unwarmed plots ($P = 0.0067$) and high warming marginally decreased R_r compared to the unwarmed treatment ($P = 0.07$; Fig.

1c). During the non-growing season, high warming increased cumulative R_r compared to low ($+54\%$; $P = 0.0349$) and unwarmed ($+81\%$; $P = 0.0008$) treatments (Fig. 1d). When winter months were analyzed separately, the high warming treatment increased cumulative R_r by 243% and 202% compared to no warming ($P = 0.0027$) and low warming treatments ($P = 0.0044$), respectively (Fig. 2a). Rhizosphere respiration also contributed a higher proportion of cumulative winter R_s in the high warming treatment (Fig. 2b).

Soil respiration (R_s) and rhizosphere respiration (R_r): temporal dynamics

Across the year, soil respiration generally tracked soil temperature, with the maximum efflux during summer and the minimum in winter (Appendix A: Fig. A3a). However, seasonal variability in precipitation modified the soil respiration pattern (Appendix A: Fig. A3b, c). The effect of warming and precipitation treatments on R_s over the year (April 2009–March 2010) varied by month (Table 1; Appendix A: Table A5; $P < 0.0001$). During early and late winter, high warming increased respiration (Fig. 3; Appendix A: Table A6). However, during summer (June and August) warming decreased R_s (Fig. 3a; Appendix A: Table A6). During summer and fall, precipitation treatments altered R_s (Appendix A: Fig. A4). The diel pattern of soil respiration did not closely follow the diel patterns of soil temperature in either August 2009 (Appendix A: Fig. A5) or April 2010 (Appendix A: Fig. A6).

Rhizosphere respiration was higher from April to September, which coincided with the period of maximum plant activity. Rhizosphere respiration of the unwarmed, ambient treatment varied from 3.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in July to no detectable respiration on measurement dates in January and February. The effects of warming ($P < 0.0001$; Table 2) and precipitation on R_r varied by month ($P < 0.0001$; Fig. 4; Appendix A: Table A7). Drought decreased R_r in August (61%; $P = 0.0142$; Fig. 4b) and had a marginal effect in June (48%; $P = 0.06$) compared to ambient precipitation. During September, drought decreased R_r compared to both ambient (49%) and wet (55%) treatments ($P < 0.0001$).

Soil respiration (R_s) and rhizosphere respiration (R_r): temperature sensitivity

When we modeled R_s using the exponential temperature function (Eq. 1), temperature at 5 cm depth

TABLE 1. Decrease in soil respiration (R_s) in drought compared to ambient and wet precipitation treatments during different months.

Month	Drought vs. ambient (%)	Drought vs. wet (%)	P
June	33	36	<0.05
August	46	44	<0.05
September	26	18	<0.05

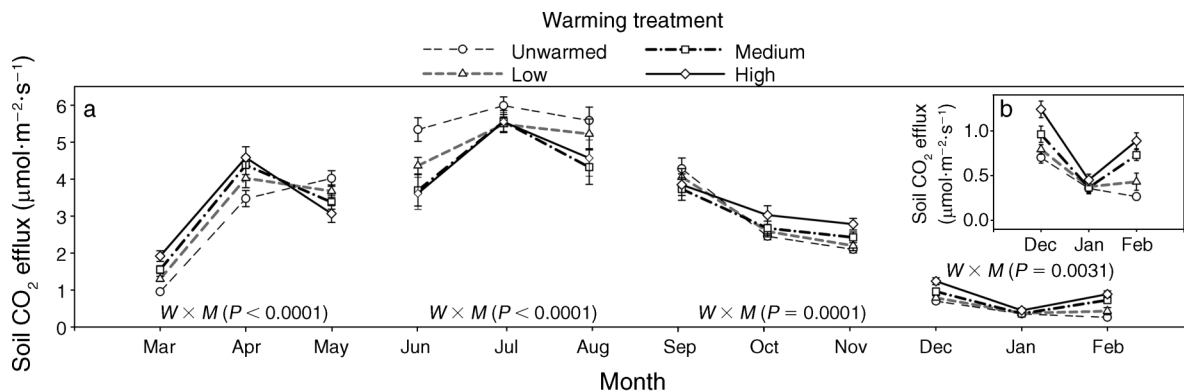


FIG. 3. Seasonal variation in soil respiration R_s averaged by warming treatment ($n = 9$ samples) in (a) spring, summer, fall, winter and (b) winter alone from March 2009 to February 2010. Values represent means \pm SE. Key: W , warming; M , month.

explained more than 50% of the variation in R_s in the ambient and wet precipitation treatments (Fig. 5, Table 3). However, the correlation of R_s with temperature decreased to about 25% in the high and medium warming, drought treatments. The annual Q_{10} of R_s varied from 1.29 in the high warming, drought treatment to 2.07 in the unwarmed, wet treatment.

Mixed model analysis of annual apparent Q_{10} revealed that warming and altered precipitation both affected the apparent Q_{10} of R_s (Appendix A: Table A8) and R_r (Appendix A: Table A9 and Appendix B). The high and medium warming treatments decreased apparent Q_{10} and coefficient b of R_s and R_r compared to the low and unwarmed treatments ($P < 0.05$). Drought decreased apparent Q_{10} and coefficient b of R_s ($P < 0.05$) and R_r ($P = 0.05$ and $P = 0.036$, respectively) relative to the wet treatment. Basal respiration (coefficient a) was not affected by either warming or precipitation. Apparent Q_{10} of R_s ranged from 1.4–2.8 in the spring, but plummeted to about 1.0 during the summer drought (Fig. 6). In the fall, the apparent Q_{10} ranged from 1.2 to 2.4. The effect of climatic treatments on apparent Q_{10} and the coefficients varied with seasons (Appendix B).

Soil respiration: characterizing sensitivity to moisture and temperature

Most of the annual variability in R_s was explained by soil temperature at 5 cm (Eq. 1; Appendix C: Table C1). During spring, the combined moisture and temperature (Melnick-Dugas) model provided the best fit to data from the high warming treatments across all precipitation treatments. In the other treatments, the exponential temperature model explained most of the variation. The soil moisture function (Eq. 3) performed best in summer and the temperature function alone provided the best fit in the fall.

DISCUSSION

Many studies have examined the effects of warming on R_r during the growing season, but to our knowledge,

this is the first study to examine the response of winter R_r to warming. We speculate that the increased R_r we observed in winter, presumably maintenance respiration (R_m), may not only deplete stored plant C, but also reduce productivity in the following season. If increases in non-growing-season R_m such as this were a general phenomenon, they could alter ecosystem C budgets, particularly in high latitude ecosystems with a long cold season. Here, in a mesic ecosystem where water availability might not be expected to drive ecosystem processes, the effect of warming on R_s and R_r nonetheless depended on precipitation. Seasonal variability in soil moisture strongly influenced temperature sensitivity of R_s , and cumulative annual R_s responded nonlinearly to precipitation inputs.

Response of soil (R_s) and rhizosphere (R_r) respiration to warming and altered precipitation

Many single-factor climate change experiments have reported increases in soil respiration with warming (Rustad et al. 2001, Mellillo et al. 2002). In contrast, we found that the effect of warming on R_s and R_r varied by season in the BACE, with warming decreasing R_s (Appendix A: Fig. A7) and R_r during summer, but increasing them during spring and winter. These contrasting effects of warming in different seasons are most likely a consequence of differences in soil moisture content. Drought also decreased annual cumulative R_s

TABLE 2. Increase in rhizosphere respiration (R_r) in high warming compared to low and unwarmed treatments during different measurement periods.

Period	High vs. low warming (%)	High vs. unwarmed (%)	P
March	104	210	<0.05
June		60	<0.05
November		66	<0.05
December–February	197	194	<0.05

Note: Empty cells indicate that there was no significant difference in rhizosphere respiration between high and low warming in June and November.

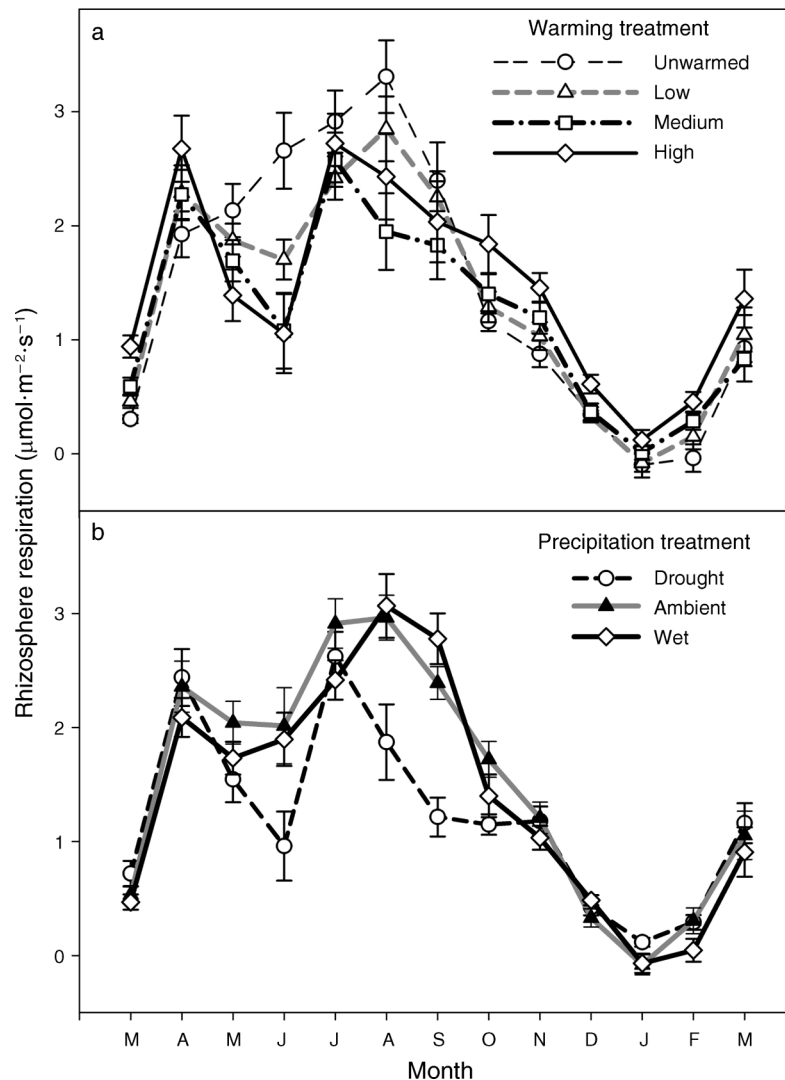


FIG. 4. Seasonal variation in R_r from March 2009 to March 2010 averaged by (a) warming treatment ($n = 9$ samples) and (b) precipitation treatment ($n = 12$ samples). Symbols represent means \pm SE.

and R_r , likely due to the soil moisture stress experienced by plants and microbes (Shen et al. 2008). Dry soils reduce the movement of substrates in the soil, lowering the activity of root microbes, and stressing plants, leading to reduced photosynthesis and belowground C allocation. Drought also reduces the coupling between plant photosynthesis and belowground processes by reducing the movement of photosynthates to phloem loading sites and also by impairing the phloem loading itself, which potentially affects substrate availability and hence C cycling (Ruehr et al. 2009). During winter and spring, when more water was available for root and microbial activity, warming increased R_s . However, warming exacerbated soil moisture limitation of plant and microbial activity during summer, further reducing R_s .

Response of non-growing season rhizosphere respiration (R_r) to warming

Although many studies evaluating the effects of warming on rhizosphere respiration have omitted the winter months, information on temperature sensitivity during these months can contribute to useful benchmarks for ecosystem models. Ecosystem autotrophic respiration in the dormant season (mostly R_m) can constitute $>25\%$ of the annual C budget in forest systems (Ryan et al. 1997), and model representations of the warming response of respiration can strongly influence projected climate feedbacks (Piao et al. 2010). In the BACE, warming treatments increased R_r during the non-growing season (October to March). The pattern of increase in R_r during winter in the high warming treatment was consistent over four years

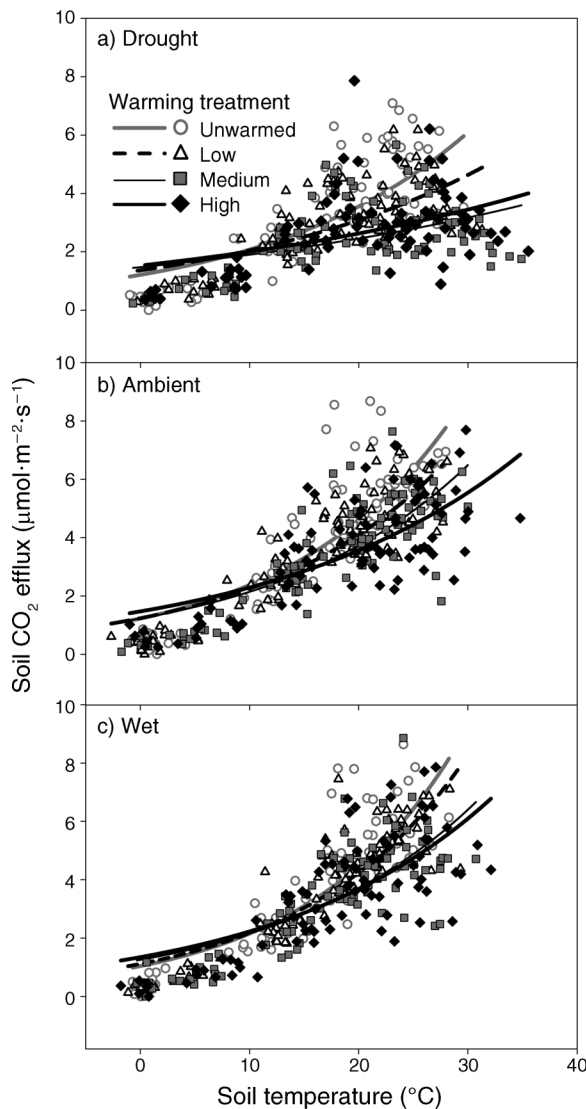


FIG. 5. Exponential relationship between R_s and soil temperature (April 2009–March 2010) in (a) drought, (b) ambient, and (c) wet precipitation treatments. Details are in Table 3.

(2008–2012) of treatment application (V. Suseela and J. S. Dukes, *unpublished data*). The energy expended in this process, presumably as R_m , would have reduced carbohydrate reserves. We speculate that this C loss

could affect emergence and reduce growth of perennial species the following year (Ogren et al. 1997, Regier et al. 2010). Differences among treatments in cumulative non-growing season R_r suggest that the high ($\sim 4^\circ\text{C}$) warming treatment would sustain an ecologically meaningful loss of C by increasing R_r in the non-growing season (Fig. 1). During the growing season, warming could offset this C loss through increases in production due to the lengthening of the growing season or increased nutrient availability (Melillo et al. 2011). However, such increases are not universal (Zhao and Running 2010) and can depend on precipitation regimes (Berdanier and Klein 2011, Hoeppepner and Dukes 2012). Further research to characterize the implications of increased R_r in the non-growing season for subsequent growth and productivity could help to refine ecosystem process models.

Nonlinear response of cumulative soil respiration to altered precipitation

Drought and wet treatments both decreased cumulative R_s . The decrease in cumulative R_s in the wet treatment resulted from equal reductions in R_r and R_h . The reduction in microbial activity and respiration could have resulted from limited diffusion of oxygen, as previously discussed (Suseela et al. 2012). Unstudied changes in microbial community structure could have also affected respiration; a mechanistic understanding of how these communities respond to warming and changes in precipitation would help to better predict the microbially mediated carbon-climate feedback (Davidson et al. 2012, Zhou et al. 2012).

The reduction in R_r in the wet treatment could have resulted from a nutrient feedback. Aboveground tree biomass was higher in the wet than the drought treatments (S. S. Hoeppepner and J. S. Dukes, *unpublished data*), suggesting that more water and nutrients were available for plant production. Increased nitrogen availability has been found to decrease soil respiration by reducing belowground C allocation, as plants need not provide more C to symbionts to obtain nutrients (Janssens et al. 2010). Increased nutrient availability has also been shown to decrease fine root biomass and soil respiration (Haynes and Gower 1995, Jimenez et al. 2009). Reduced C allocation below ground may consequently have reduced the associated mycorrhizal and rhizosphere microbial respiration.

TABLE 3. Exponential relationship between R_s and soil temperature T ($^\circ\text{C}$; April 2009–March 2010) and apparent Q_{10} values.

Warming treatment	Drought			Ambient			Wet		
	R_s	r^2	Q_{10}	R_s	r^2	Q_{10}	R_s	r^2	Q_{10}
Unwarmed	$1.21e^{0.05T}$	0.58	1.71	$1.23e^{0.07T}$	0.71	1.93	$1.04e^{0.07T}$	0.76	2.07
Low	$1.37e^{0.04T}$	0.48	1.50	$1.24e^{0.06T}$	0.73	1.82	$1.12e^{0.06T}$	0.79	1.95
Medium	$1.47e^{0.03T}$	0.25	1.29	$1.23e^{0.06T}$	0.67	1.74	$1.25e^{0.05T}$	0.59	1.72
High	$1.53e^{0.03T}$	0.24	1.31	$1.47e^{0.04T}$	0.52	1.56	$1.35e^{0.05T}$	0.52	1.65

Effects of climate treatments on temperature sensitivity of R_s and R_r : implications for climate-carbon feedbacks

The uncertainty in climate-carbon feedback projections could be reduced by more accurately representing the sensitivity of soil respiration to warming (Jones et al. 2003, Friedlingstein et al. 2006, Luo 2007). Many global scale models represent the relationship between respiratory processes and temperature using a constant Q_{10} value of 2 (Friedlingstein et al. 2006, Mahecha et al. 2010). However, as soil respiration involves heterotrophic and autotrophic (rhizosphere) components controlled by plant and climatic factors, the differential responses of R_h and R_r to warming and precipitation changes may alter the exponential relationship between soil respiration and temperature. Temperature sensitivity can be influenced by changes in environmental constraints to decomposition such as soil moisture and substrate availability (Davidson and Janssens 2006). Warming and drought can also cause physiological stress to plants, slowing photosynthesis and below-ground C allocation. In our system, the annual apparent Q_{10} of both R_s and R_r behaved similarly, suggesting that R_r drove the response of the apparent temperature sensitivity of soil respiration to warming and altered precipitation. Heterotrophic respiration at the BACE (Suseela et al. 2012) was less sensitive to warming than R_s and R_r , a pattern previously observed in other systems (Boone et al. 1998, Zhou et al. 2007). The annual apparent Q_{10} of R_s and R_r decreased with warming and drought. Warming has also decreased the temperature sensitivity of R_s in other systems (Luo et al. 2001, Zhou et al. 2006, 2012).

The apparent Q_{10} of R_s responded differently to warming and altered precipitation in different seasons and was greater in spring and fall than in summer (Fig. 6). Greater substrate availability in spring (due to freeze thaw cycles; Schimel and Clein 1996) and fall (due to litter inputs) could contribute to the higher Q_{10} values. Also, a severe soil moisture limitation in the summer resulted in a sharp decline in apparent Q_{10} across all precipitation treatments and eliminated treatment differences due to both warming and precipitation. This underscores the strong dependence of R_s on moisture, even in mesic systems. The trees in the old field at the BACE were relatively small during this study. Nonetheless, in a soil warming experiment with mature hardwood trees in the same region, Contosta et al. (2011) reported similar seasonal differences in the effect of warming on R_s , with the greatest effects in spring and fall.

Our results suggest that the apparent temperature sensitivity of R_s varies with season mainly due to changes in soil moisture and seasonal variability in substrate availability. This has important implications for climate-carbon modeling, as mean annual temperature and mean annual precipitation may not explain the temperature sensitivity of R_s and R_r (Wang et al. 2010). Rather, our results suggest that, at least in this system,

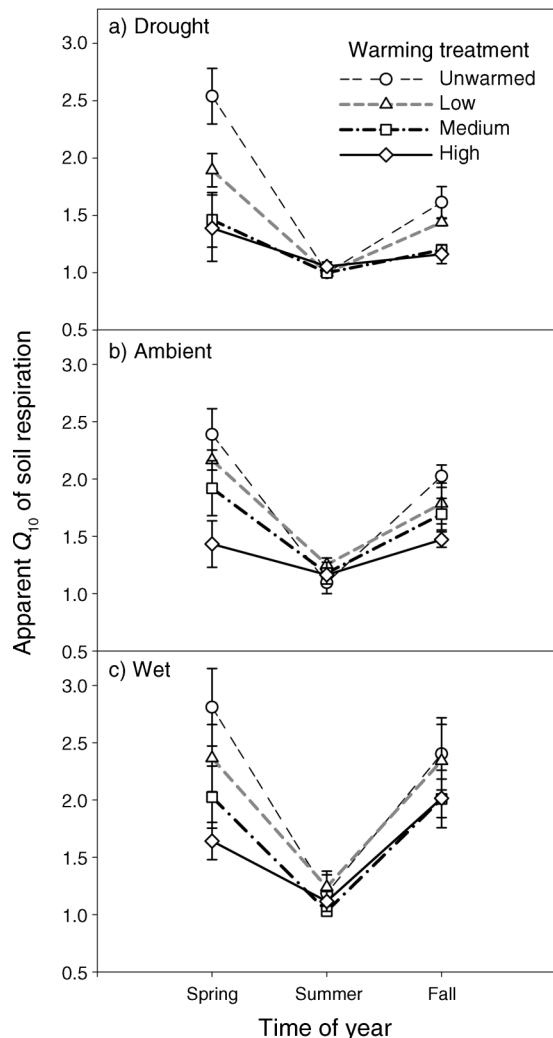


FIG. 6. Seasonal apparent Q_{10} values of (a) drought, (b) ambient, and (c) wet precipitation treatments for each warming treatment. Values represent means \pm SE ($n = 3$).

intra-annual variation in precipitation and subsequent changes in substrate availability modulate the apparent Q_{10} of R_s and R_r . Although many studies have used Arrhenius kinetics to represent temperature sensitivity, their application might be limited under conditions of varying substrate availability (Reichstein and Janssens 2009). Underlying assumptions of the Q_{10} concept, such as abundant substrate and stable enzyme quantities, may not be met under future global change scenarios (and may not be met currently; Ise and Moorcroft 2006). Thus, representing R_s (or its components R_h and R_r) as exponential functions of temperature without incorporating other potentially limiting factors could overestimate the C cycle feedback to climate change.

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SUPPLEMENTAL MATERIAL

Appendix A

Seven figures depicting seasonal variation in soil temperature and moisture and response to precipitation and temperature treatments, as well as nine tables showing results from mixed-model REML analysis of response to warming and precipitation treatments ([Ecological Archives E094-034-A1](#)).

Appendix B

Detailed results of the seasonal variation in apparent Q_{10} and coefficients of R_s and R_r ([Ecological Archives E094-034-A2](#)).

Appendix C

A table of the correlation of soil respiration with different environmental variables predicted using temperature, moisture, and combined exponential and quadratic (Mielnick-Dugas) functions ([Ecological Archives E094-034-A3](#)).