LETTER

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Boreal and temperate trees show strong acclimation of respiration to warming

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Plant respiration results in an annual flux of carbon dioxide (CO_2) to the atmosphere that is six times as large as that due to the emissions from fossil fuel burning, so changes in either will impact future climate. As plant respiration responds positively to temperature, a warming world may result in additional respiratory CO_2 release, and hence further atmospheric warming[1,2]. Plant respiration can acclimate to altered temperatures, however, weakening the positive feedback of plant respiration to rising global air temperature[3–7], but a lack of evidence on long-term (weeks to years) acclimation to climate warming in field settings currently hinders realistic predictions of respiratory release of CO_2 under future climatic conditions. Here we demonstrate strong acclimation of leaf respiration to both experimental warming and seasonal temperature variation for juveniles of ten North American tree species growing for several years in forest conditions. Plants grown and measured at 3.4 °C above ambient temperature increased leaf respiration by an average of 5% compared to plants grown and measured at ambient temperature; without acclimation, these increases would have been 23%. Thus, acclimation eliminated 80% of the expected increase in leaf respiration of non-acclimated plants. Acclimation of leaf respiration per degree temperature change was similar for experimental warming and seasonal temperature variation. Moreover, the observed increase in leaf respiration per degree increase in temperature was less than half as large as the average reported for previous studies[4,7], which were conducted largely over shorter time scales in laboratory settings. If such dampening effects of leaf thermal acclimation occur generally, the increase in respiration rates of terrestrial plants in response to climate warming may be less than predicted, and thus may not raise atmospheric CO_2 concentrations as much as anticipated.

Rising global temperatures (of 1.1–6.4 °C by 2100) will probably result in a positive terrestrial feedback to the global carbon cycle, because respiratory flux to the atmosphere from soils and plants is anticipated to increase more with warming than is the rate of gross primary production (GPP)[5,6]. Respiration in terrestrial plants releases approximately 64 Gt of carbon each year to the atmosphere (~six times the amount of fossil fuel emissions), directly offsetting roughly half of the GPP of terrestrial ecosystems[5,6], so even a small fractional change in total plant respiration with climate warming could be important for both global net productivity and the carbon content of the atmosphere. If long-term net respiratory fluxes from terrestrial ecosystems follow the near-exponential short-term relationship of respiration to temperature[3], climate warming will trigger a sharp increase in ecosystem respiration. Such an increase in CO_2 release would probably be greater than the offsetting increase in GPP, because GPP tends to show a saturating, hump-shaped response to rising temperature. This would result in a heightened net CO_2 release from terrestrial ecosystems, and further atmospheric warming[1,2].

Plants, however, can dynamically adjust the response of respiration to temperature over the long term (weeks to years), even though plant respiration always shows an accelerating increase when subjected to a short-term (minutes to hours) increase in temperature. Typically, a plant that has experienced warmer temperatures will have a lower rate of respiration at a standardized measurement temperature than a plant that has experienced cooler temperatures (Extended Data Fig. 1). This process is labelled thermal acclimation[3,4,7]. The greater the thermal acclimation of respiration globally, the smaller the positive feedback between climate warming and ecosystem CO_2 release[3,7,8]. Thermal acclimation of plant respiration has been noted in most, but not all, cases studied[3,7–13], but the degree of acclimation is extremely uncertain[3,7–13], especially for plants in natural settings. Such information will be crucial for making better predictions of terrestrial feedbacks[14,15]. The need for ecologically realistic acclimation generalizations is clear, because current state-of-the-art models[16,17] predict acclimation based on a study of first-year seedlings grown for 2–3 months at constant 7, 14, 21 and 28 °C conditions in growth cabinets[4]. Hence, observations of acclimation of plants grown in more realistic field settings (for as long as 5 years), as presented here, should provide a meaningful advance.

High latitude boreal and temperate forests account for approximately one-third of Earth's total forest area, and have an important role in terrestrial carbon cycling[4,5,13–15]. To advance understanding of carbon cycling in a changing climate, we assessed the acclimation capacity of more than 1,200 individuals of 10 dominant North American tree species grown in ambient and warmed (+3.4 °C) plots in a free-air warming experiment[18,19]. We present the results of 1,620 leaf respiration–temperature response curves[3,20–22] made from 2009 to 2013 in both open and understory forest habitats at two sites (~150 km apart) at the boreal–temperate forest ecotone in Minnesota, USA. Species were measured in three ($n = 4$), four ($n = 2$) or all five ($n = 4$) years. Temperatures measured for each response curve ranged from 12 to 37 °C in 5-degree intervals (see Methods). Because the shape of the short-term temperature response curves did not vary with warming treatment for any of the species (see later), comparing the curves of plants from warmed and ambient treatments enables assessment of the magnitude of thermal acclimation in response to experimental warming. Additional information is gained by comparing the curves of plants measured at different times during the growing season; that is, assessing how much lower leaf respiration is at a given measurement temperature in a warm spell compared to a cold spell.

We focus on the magnitude of acclimation induced by experimental warming as well as the magnitude of acclimation comparing warmer to cooler time periods. For example, if a plant grown at 20 °C increased leaf respiration (R_{leaf}) by 40% after being moved to 25 °C for 30 min, but had the same rate after 3 weeks at 25 °C as initially when grown and measured at 20 °C, it would have completely (100%) acclimated

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(see Extended Data Fig. 1a, equivalent to homeostatic acclimation)[7]. If the rate after 3 weeks at 25 °C had increased, but by less than 40% compared to the plant grown and measured at 20 °C, this would represent partial acclimation (Extended Data Fig. 1b). Thus, an acclimated plant will eliminate some or all of the increase in R_{leaf} with rising temperature expected of non-acclimated plants.

We compare acclimation responses between experimental and natural seasonal temperature variation, boreal and temperate species, and angiosperm and gymnosperm species. On the basis of previous research[3,7,9–13,23,24], we expected to observe partial acclimation (of ~30–50%) that would be similar across species in response to both experimental and temporal temperature variation. We also anticipated that boreal species, which experience a greater temperature range in their native higher-latitude distributions, would show a greater acclimation than temperate species.

Calculating entire respiratory temperature response curves (rather than measurements at a single temperature) for all sampled leaves enabled us to discern whether the shape of the short-term response varies with thermal environment, or whether the elevation of the entire curve shifts over time as experienced temperatures vary. We tested five models to establish the best equation for quantifying R_{leaf} as a function of short-term leaf temperature variation (see Methods). Across all 1,620 curves, all models provided good fits. Exponential equations with a fixed Q_{10} coefficient (that describes the proportional change in R_{leaf} with a 10 °C temperature increase) and an Arrhenius model worked well (median $R^2 = 0.95$, Extended Data Table 1). By contrast, adding temperature-sensitivity did not improve the Arrhenius model, and two other temperature-sensitive models (a log-polynomial[20] and a Michaelis–Menton approach[21]) did not consistently show their expected decelerating forms (see Methods and Extended Data Table 1). Given that fits were best described as exponential, we present the data using the Q_{10} approach; however, results are similar if any of the other models are used.

The Q_{10} value differed among species, but was unaffected by experimental warming, as there were no differences in Q_{10} across the warming treatments for any of the 10 species studied (Extended Data Fig. 2 and Table 1). Thus, to assess acclimation for each species, we compared R_{leaf} at a standardized measurement temperature, which represents the overall elevation of each curve, given consistent Q_{10} values. We chose standard leaf temperatures of 20 °C and 23.4 °C, and derived respiration rates at those temperatures (R_{20} and $R_{23.4}$, respectively) for each temperature response curve. We chose 20 °C as a typical standard for comparing respiration rates[7,13,25], and 23.4 °C because it represents the average temperature above that standard due to the warming treatment[18,19,26].

We also assessed the acclimation response to seasonal variation in temperature by examining R_{20} in relation to the mean night-time temperature for the 5 nights before the measurement date. We chose this rather than the previous 10-day period[4,16,17], as evidence suggests acclimation can occur within a few days of temperature shifts[10,23,24], hence our response curves are perhaps more representative of leaf physiological status over the previous 5-day than 10-day period. Nonetheless, acclimation was similar (in fact, slightly stronger) if the previous 10-night mean temperature was used, and the results are not dependent on this choice.

Across species and sites, plants in the +3.4 °C treatment had significantly lower R_{20} values than ambient-grown plants (Extended Data Fig. 3 and Table 1), indicating acclimation to increased growth temperature[3,7]. The best statistical model included only treatment and species (see Methods), as the response to warming treatment did not differ with site (site × warming, $P = 0.74$; site × species × warming, $P = 0.69$). Species differed in their average R_{20} value, but the acclimation response to experimental warming did not differ significantly among species (Table 1), sites or species groupings (boreal/temperate; angiosperm/gymnosperm). Differences between ambient and warmed plants were similar if other metrics (for example, R_{leaf} measured at 25 °C) were used, or if R_{leaf} was estimated using temperature response functions from the alternative models (for example, Methods and Extended Data Figs 4 and 5).

As a result of this strong acclimation (Extended Data Fig. 3), individuals in each species grown in the +3.4 °C warming treatment had leaf respiration rates at 23.4 °C that were generally not notably greater than those of ambient-grown plants measured at 20.0 °C (Fig. 1). In fact, on average across species, plants grown in the +3.4 °C warming treatment had leaf respiration rates at 23.4 °C that were just 5% higher (±2% s.e.m. among species) on average than those measured at 20.0 °C for untreated plants (Fig. 2). By contrast, non-acclimated ambient-grown plants had rates at 23.4 °C that were 23% higher (±1% s.e.m. among species) on average than at 20.0 °C (Figs 1 and 2). Thus, thermal acclimation of warmed plants eliminated roughly 80% of the increase in leaf respiration expected of non-acclimated plants (see below).

Shifts in R_{20} in relation to seasonal variation in temperature (Fig. 3) also demonstrated strong acclimation that was consistent with shifts in R_{20} in response to warming treatments. This acclimation was statistically examined by evaluating the R_{20} response to prior 5-night mean temperature, warming treatment and species. The prior 5-night mean temperature was significant, whereas warming treatment was not, because the prior 5-night temperature metric fully accounted for its impact (Table 1). Thus, all 10 species showed pronounced acclimation of R_{20} to recently experienced temperatures (Fig. 3). The slopes of R_{20} versus recent temperatures did not differ between boreal and

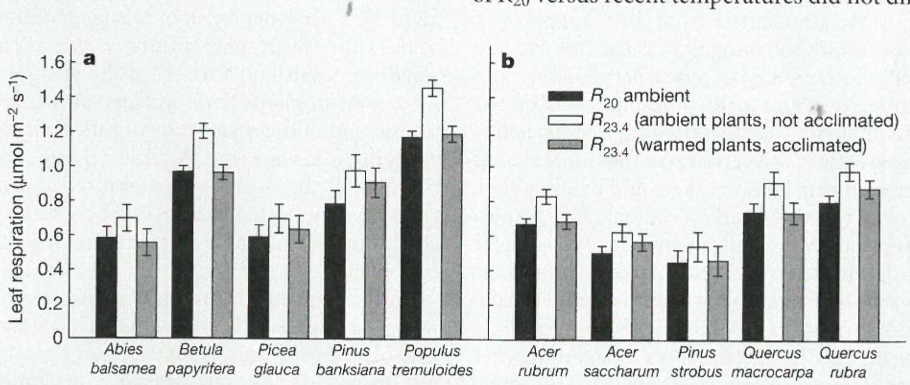

Figure 1 | Leaf dark respiration rate of ambient and experimentally warmed plants. a, b, Data are from five boreal (**a**) and five temperate (**b**) tree species. Respiration is shown at measurement temperatures of 20 °C and 23.4 °C for ambient-grown plants; respiration for plants grown at +3.4 °C conditions is shown at a measurement temperature of 23.4 °C. The two values for ambient plants show the increase in respiration with a +3.4 °C temperature increase for non-acclimated plants; comparison of ambient plants measured at 20 °C with warmed plants measured at 23.4 °C represents the increase in respiration with a +3.4 °C temperature increase for acclimated plants. Sample size by warming treatment and biome type (boreal, ambient = 363; boreal, warmed = 380; temperate, ambient = 434; temperate, warmed = 443). Data are mean and s.e.m. (s.e.m. values are from the full model).

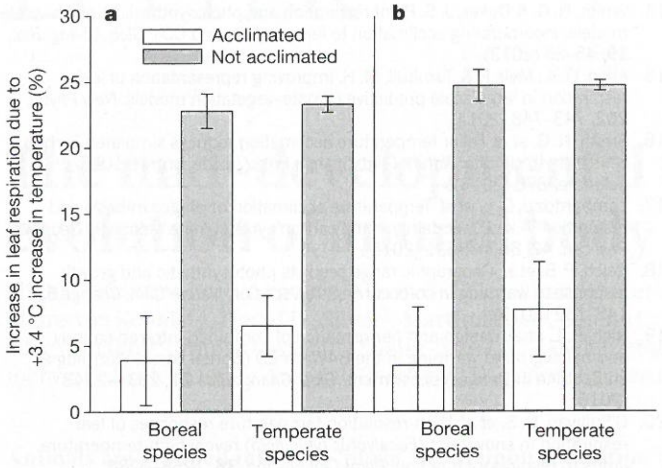

Figure 2 | Increase in leaf dark respiration (R_{leaf}) with +3.4 °C warming for acclimated and non-acclimated plants, among species, by biome of the species. a, b, Increase in R_{leaf} is shown on a percentage basis in response to both experimental warming (**a**) and seasonal temperature variation (**b**). For acclimated plants, response is calculated as: ((R_{leaf} of warmed plants at 23.4 °C per R_{leaf} of ambient plants at 20 °C) × 100) − 100. For non-acclimated plants, response is: ((R_{leaf} of ambient plants at 23.4 °C per R_{leaf} of ambient plants at 20 °C) × 100) − 100. Sample sizes are as in Fig. 1. Data are mean and s.e.m. (s.e.m. among species, by biome group and treatment).

temperate species, but were significantly steeper on average for the four gymnosperms than the six angiosperms (Methods and Extended Data Table 2).

On the basis of the species responses to seasonal temperature variation, plants that had experienced recent night temperatures of 23.4 °C would be expected to have R_{leaf} at 23.4 °C that was just 6% higher (±3% s.e.m. among species) on average than R_{leaf} at 20.0 °C for plants recently experiencing 20.0 °C nights (Fig. 2). By contrast, without acclimation (that is, for a plant that recently experienced 20.0 °C nights), rates at 23.4 °C would be 25% (±1% s.e.m. among species) higher on average than at 20.0 °C. Those acclimation responses to seasonal temperature variation were very similar to those noted above for plants acclimated to +3.4 °C experimental warming. In other words, the differences in growth temperatures due to experimental warming had the same effect on R_{leaf} value at any given measurement temperature as the changes in the prior 5-night temperature of the same extent. Thus, acclimation to temperature as it varied across time was similar to acclimation to experimental warming. If extrapolated to a 10 °C shift in temperature, acclimation would result in realized long-term (or 'apparent') Q_{10} value of ~1.2, despite a short-term Q_{10} of ~1.9.

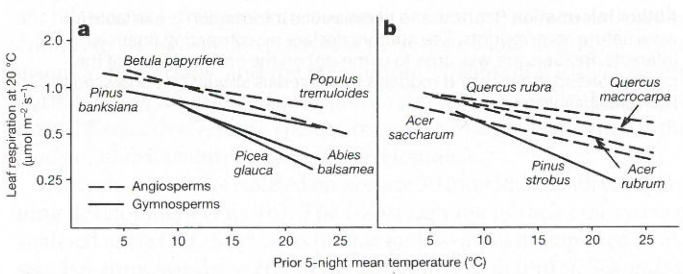

Figure 3 | Relationship between leaf dark respiration measured at 20 °C and the prior 5-night mean temperature, across seasons and years. a, b, Data are for five boreal (**a**) and five temperate (**b**) tree species. Sample sizes are as in Fig. 1. Data are the best fit regressions between the logarithm of R_{20} and the prior 5-night mean temperature per species, using data from both ambient and warmed treatments. Angiosperms and gymnosperms differed in slope ($P < 0.05$), but species within each group did not. Resultant species-specific equations are shown in Extended Data Table 2.

Table 1 | Q_{10} and R_{20} in relation to +3.4 °C warming and species

Source of variance	Q_{10}		R_{20}		R_{20}, 5-night T	
	F	$P>F$	F	$P>F$	F	$P>F$
Species	4.66	<0.0001	57.07	<0.0001	40.89	<0.0001
Treatment	0.66	0.4199	11.53	0.0012	2.59	0.1119
Species × treatment	1.09	0.3646	0.76	0.6557	1.17	0.3127
5-night T					38.95	<0.0001
5-night T × species					2.48	0.0081
5-night T × treatment					0.01	0.9265
5-night T × species × treatment					0.34	0.9626
Full model R^2	0.10		0.43		0.45	

Summaries of analysis of variance for Q_{10} (exponent of short-term temperature response function) and R_{20} (respiration rate at standard measurement temperature of 20 °C) are shown in relation to +3.4 °C warming treatment and species. Also shown is the model for R_{20} that includes the prior 5-night mean temperature (5-night T) and associated interactions. All models significant at $P < 0.0001$. F indicates the F-ratio used in the F-test of the significance of each factor or interaction among factors. Data for 10 species ($n = 1{,}620$). R_{20} was $\log_{10}$-transformed before analyses.

We also assessed percentage acclimation, a measure of how much of the respiratory increase expected due to short-term (minutes to hours) warming is eliminated by physiological adjustment of plants warmed by the same extent but for weeks or months. We quantified this acclimation for plants in response to warming treatment by contrasting the difference between the $R_{23.4}$ of plants in the +3.4 °C treatment and the R_{20} of those in ambient conditions with the difference between the $R_{23.4}$ and R_{20} of plants in ambient conditions (Fig. 1; see Methods for equation). The mean percentage acclimation to experimental warming across species was 78.2% (±7.7 s.e.m. among species), and the mean percentage acclimation to the 5-prior night temperature was 80.9 ± 9.5% (Extended Data Fig. 6).

Given the close coupling of respiration and photosynthesis[13,21,27,28], shifts in leaf respiration of plants growing under different thermal conditions could result from temperature-related shifts in photosynthesis[14]. Previous work with seedlings has found the ratio of leaf respiration to photosynthesis (R:P) to be stable in some cases, but to increase with growth temperature in others[14]. Data from our multi-year experiment indicate that the acclimation of R_{leaf} did not result from (or result in) a stable R:P ratio, because for all 10 species, R:P was higher in warmer conditions, whether seasonal or experimental (Methods). However, without acclimation, R:P would have been much more increased at higher mean daily temperatures compared to what was observed. Hence our results suggest that acclimation is part of a process that limits the size of the 'window' within which R:P varies, but does not support the idea of a complete homeostasis of R:P. Statistical analyses also showed that the response to warming treatment of Q_{10}, or R_{20}, could not be explained by concomitant shifts in photosynthesis (Methods).

As respiration in terrestrial plants (including root, stem and leaf fluxes) releases ~64 Gt of carbon per year to the atmosphere, offsetting ~50% of terrestrial GPP[5,6,16,17], autotrophic respiration and its acclimation to rising temperature are crucial to the global carbon balance[5,6]. Our experimental results are informative relative to this issue.

Our results demonstrated strong acclimation of leaf respiration to both a +3.4 °C warming and seasonal temperature increases, which profoundly reduced plant respiratory carbon loss compared to what would have occurred without acclimation. A recent meta-analysis[7], based largely on short-term studies of laboratory grown plants, found acclimation to be less than half as great as we observed (see Methods for details). Moreover, earth system models[14–17] typically simulate even weaker levels of acclimation, or none at all. For example, two recent modelling papers[16,17] based their acclimation routines on data from first-year seedlings in laboratory settings that showed ~30% respiration acclimation[4]. Despite this more modest acclimation than we observed here, acclimation alone still resulted in a 10% change in simulated global carbon stocks compared to a model that assumed no leaf respiration acclimation[17]. Given that we observed a much greater (~80%) acclimation of respiration, our results suggest that high latitude forests may show a more pronounced leaf respiration acclimation than expected[4,7,13] to increasing growing season temperatures associated with climate change.

If our realistic, long-term field results are broadly indicative, they suggest that leaf respiratory acclimation globally may have a larger ameliorating impact than expected on CO_2 losses with rising temperatures as climate changes. Such amelioration would be even larger if stems and roots showed similar acclimation as leaves, but whether this is so is highly uncertain owing to a scarcity of available data. Our results contribute to current efforts to improve the characterization and incorporation of thermal acclimation of respiration in land surface models[14,17] by providing robust field evidence on the nature and magnitude of leaf respiratory acclimation, thus aiding future models in improving estimates of respiratory acclimation in a changing climate, and of the consequences of acclimation for carbon cycling.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Author Contributions P.B.R., R.A.M. and R.L.R. designed the study. R.L.R. designed the warming system. R.L.R. and A.S. implemented the warming system and A.S., K.M.S. and X.W. the day-to-day field measurements. P.B.R. analysed the data. P.B.R. wrote the first draft and along with the other co-authors jointly wrote the manuscript.

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