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Roots exert a strong influence on the temperature sensitivity of soil respiration

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The temperature sensitivity of soil respiration will largely determine the effects of a warmer world on net carbon flux from soils to the atmosphere. CO_2 flux from soils to the atmosphere is estimated to be 50–70 petagrams of carbon per year and makes up 20–38% of annual inputs of carbon (in the form of CO_2) to the atmosphere from terrestrial and marine sources[1,2]. Here we show that, for a mixed temperate forest, respiration by roots plus oxidation of rhizosphere carbon, which together produce a large portion of total effluxed soil CO_2, is more temperature-sensitive than the respiration of bulk soil. We determine that the Q_{10} value (the coefficient for the exponential relationship between soil respiration and temperature, multiplied by ten) is 4.6 for autotrophic root respiration plus rhizosphere decomposition, 2.5 for respiration by soil lacking roots and 3.5 for respiration by bulk soil. If plants in a higher-CO_2 atmosphere increase their allocation of photosynthate to roots[3–6], these findings suggest that soil respiration should be more sensitive to elevated temperatures, thus limiting carbon sequestration by soils.

The response of soil carbon fluxes to global warming is sensitive to slight changes in the relationship between soil temperature and soil respiration[7,8]. Simulation models of regional and global carbon cycling generally use a single, fixed Q_{10} coefficient for the exponential function between soil respiration and temperature[9–11]. However, Q_{10} varies among ecosystems and across temperature ranges, in part because the various components of soil respiration have different temperature sensitivities[12–14]. These components include respiration by live roots (allowing their growth and maintenance) and associated mycorrhizae, and the oxidation of plant detritus (for example, roots, leaves and woody inputs), root exudates and humified organic matter by soil heterotrophs. We show here that variations in soil respiration through the growing season in a temperate hardwood forest are determined mainly by temperature responses of root respiration and rhizosphere heterotrophs (those in the area of soil immediately surrounding and influenced by plant roots). Microbial respiration outside the rhizosphere, although a significant fraction of total soil respiration, is less responsive to temperature than is root and rhizosphere respiration.

We used a long-term litter-manipulation experiment initiated in 1990–91 at the Harvard Forest, Petersham, Massachusetts, USA (42° 30′ N, 72°12′ W), to examine the biological and physical controls on the dynamics of soil organic matter. The study site is an 85-year-old mixed-hardwood stand growing on a gentle, northwest-facing slope (4%) pastured in the 1800s. Soil is a well-drained stony, fine sandy loam, with a C_d horizon (hardpan) at 65 cm depth. Mean annual air temperature is 6 °C; annual precipitation is 1,100 mm, distributed evenly through the year. Litter manipulations (3 m × 3 m plots, $n = 3$, except for control where $n = 6$) include 'control' (normal litter inputs), 'no litter' (above-ground litter excluded from plots annually), 'double litter' (above-ground litter doubled annually), 'no roots' (roots excluded from plots by fibreglass-lined trenches), 'no inputs' (no above-ground litter and no roots), and 'OA-less' (organic (O) horizons and upper mineral soil (A) horizon (to 20 cm depth) removed and replaced with subsoil).

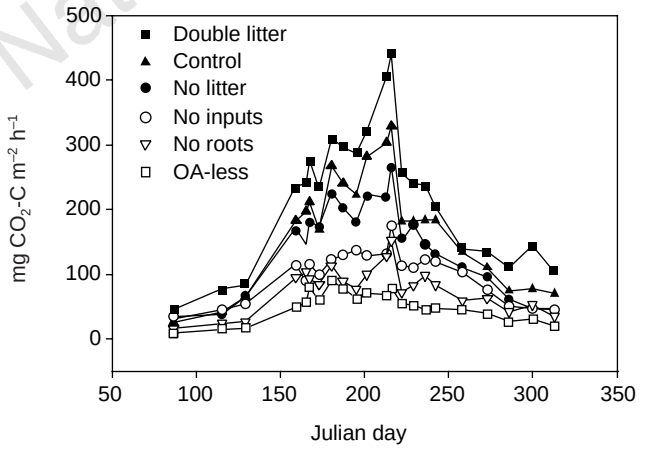

Figure 1 Soil CO_2 efflux per treatment for Harvard Forest litter-manipulation plots. Measurements were made over a one-year period from 16 June (Julian day 167) 1994 to 14 June (Julian day 165) 1995. Values are treatment means ($n = 3$ except for control, for which $n = 6$) of two measurements (early morning and late afternoon) within the same day. The means of coefficients of variation over the sampling period ranged from 10% to 15% by treatment. CO_2-C, carbon in the form of carbon dioxide.

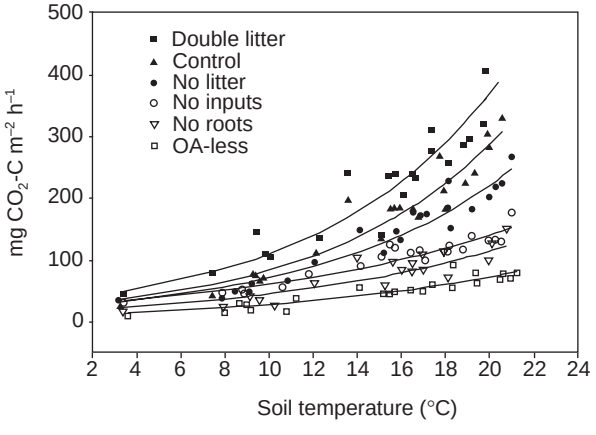

Figure 2 Relationship, for each treatment, between mean daily soil CO_2 flux and soil temperature at 5 cm depth. An exponential function of the form $y = \beta_0 e^{\beta_1 T}$, where $y = CO_2$ flux, β_0 and β_1 are fitted constants, and T = temperature, was applied to the data.

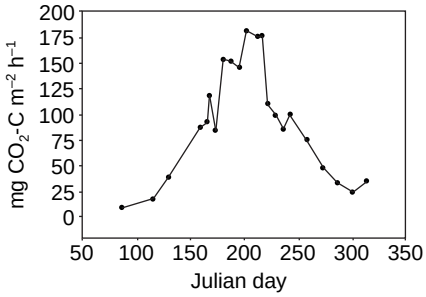

Figure 3 Soil CO_2 efflux by Julian day for 'roots', calculated as the difference in daily mean respiration between the control and no roots plots.

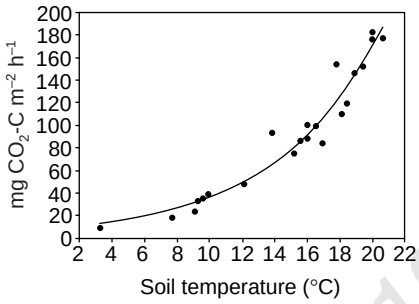

Figure 4 Relationship between mean daily CO_2 flux (calculated) from 'roots' and soil temperature at 5 cm depth. Soil temperatures are the means of control and no roots plots. An exponential function (Fig. 2) was applied to the data.

Measurements of soil respiration made in 1992 indicated that any increase in soil respiration due to decomposition of fine roots killed by the 1991 trenching of the 'no roots' and 'no inputs' plots was largely completed within one year of trenching[15]. We studied soil CO_2 efflux, temperature and moisture measured at the plots from June 1994 to June 1995.

Soil respiration (Fig. 1) varied by treatment, markedly tracked seasonal soil temperature (peaking in August for all treatments except OA-less) and was unrelated or weakly related to seasonal soil moisture. Soil temperature showed no treatment differences and ranged from 3.2 °C in late March to a maximum of 20.6 °C in early August, declining to 9.3 °C in late October. Soil moisture content (water volume in cm^3 per soil volume in cm^3) ranged from 0.21 to 0.54 for all treatments except OA-less and from 0.15 to 0.25 for OA-less; treatment means over the sampling period were 0.30–0.38 (all but OA-less) and 0.19 (OA-less). Soils generally were driest in July and wetter in spring and autumn. Soil moisture was always below saturation ($\sim$0.80 $cm^3\,cm^{-3}$) and above the level (0.12 $cm^3\,cm^{-3}$) identified previously for similar Harvard Forest soils as the break-point for a water limitation on respiration[16]. Multiple regression analysis using soil temperature and soil moisture as independent variables showed that soil water content (relatively constant during the measurement period) was unrelated to soil respiration for the litter treatments and was weakly related ($R^2 = 0.86$, temperature alone; $R^2 = 0.90$, temperature plus moisture) for the control plots.

We applied an exponential curve of the form $y = \beta_0 e^{\beta_1 T}$, where y is the carbon flux, β_0 and β_1 are fitted constants and T is the temperature, to compare the relationship between soil respiration and soil temperature (Fig. 2) and calculated Q_{10} values, where $Q_{10} = e^{10\times\beta 1}$. We calculated 'roots' respiration (Fig. 3) as the difference in daily mean respiration rates between the control and no roots plots, and derived a 'roots' Q_{10} value (Fig. 4). Within each treatment there was a strong correlation between temperature and respiration, but the sensitivity of the relationship (indicated by Q_{10} values and regression slopes) varied among treatments (Fig. 2 and Table 1). Q_{10} values and slopes changed nonsignificantly with either addition or exclusion of leaf litter, whereas treatments without roots had lower Q_{10} ($P = 0.053$, no roots; $P < 0.05$, no inputs) and slopes ($P < 0.05$) than those for the control. The 'roots' Q_{10} value and slope were significantly greater ($P < 0.05$) than those for the control and the treatments without roots. The Q_{10} value for the control plots (3.5) was close to the values for soil respiration determined elsewhere at the Harvard Forest ($Q_{10} = 3.9$; ref. 16) and for hardwood forests globally ($Q_{10} = 3.1$; ref. 10). The Q_{10} values for plots without roots are within the limits reported for soils (without roots) incubated in the laboratory over a similar temperature range[17,18].

Table 1 R^2 and Q_{10} values for the relationship between soil respiration and temperature

Treatment	R^2	Q_{10}
Control	0.91	3.5 (0.4)
Double litter	0.90	3.4 (0.4)
No litter	0.91	3.1 (0.3)
No roots	0.73	2.5 (0.4)
No inputs	0.89	2.3 (0.2)
OA-less	0.82	2.6 (0.3)
'Roots'	0.95	4.6 (0.5)

For R^2 values; $P < 0.01$; Q_{10} values are means (± s.e.m.). Q_{10} values were obtained from the exponential curve of the form $y = \beta_0 e^{\beta_1 T}$, where $Q_{10} = e^{10\times\beta_1}$. Standard error for Q_{10} is calculated as $Q_{10} \times 10 \times$ s.e.(β).

Our Q_{10} value for 'roots' (4.6) is much higher than that reported previously for root respiration[19–23]. However, there is an important difference between our approach and others. Previous measurements for root Q_{10} values have been for autotrophic root respiration alone, determined by assays of roots (often excised) that were free of *in situ* rhizosphere soil. Our Q_{10} values reflect not only root respiration but also respiration associated with the roots, including respiration by mycorrhizae and the decomposition of labile root-derived organic material (detritus and exudates) by microbiota in the rhizosphere. Increased production of root exudates (perhaps due to higher membrane permeability) at higher temperatures may be another contributing factor. If root respiration *per se* at our site shows typical temperature sensitivity (for example, Q_{10} values in the range 2–3), the temperature sensitivity and Q_{10} values for the mycorrhizae and rhizosphere heterotrophs together must be much higher than 2–3.

The seasonal pattern in soil respiration probably resulted in part from changes in root biomass and production. However, such changes would confound results only if they are unrelated to soil temperature. The synchronicity in soil respiration in the control and no roots plots indicates that root phenology is probably not independent of temperature.

The higher Q_{10} value for roots plus associated rhizosphere has implications for analysis of how soil CO_2 efflux may be affected in a warmer world. The results indicate that the temperature sensitivity of soil respiration may depend on the relative contribution that roots and associated rhizosphere microbiota (including mycorrhizae) make to total soil CO_2 efflux. Systems most sensitive to temperature rise should be those in which roots and the associated rhizosphere contribute the largest portion of total CO_2 flux. We would also expect that soil Q_{10} values should rise if higher atmospheric CO_2 were to lead to higher below-ground carbon allocation[3–6]. The factors that determine the relative contribution of roots and rhizosphere to CO_2 flux (this contribution can range from 20% to 90% of the total flux[15,24–28]) have not been well evaluated. The contribution of rhizosphere versus non-rhizosphere microorganisms to soil respiration is also poorly understood. More information across ecosystem types on the temperature sensitivities of soil CO_2 sources and their relative contributions to total soil respiration, and on how global change may influence below-ground photosynthate allocation, is essential to allow us to predict how increased temperature affects soil CO_2 efflux. □

Methods

Soil CO_2 efflux, temperature and moisture were measured at the plots from

June 1994 to June 1995. Soil CO_2 efflux was determined with an infrared gas analyser (IRGA, LICOR Model 6262) and a flow-through chamber. CO_2 concentrations were recorded every 6 s over a 4-min period in a tube-shaped chamber (0.25 m diameter × 0.10 m height) placed on a permanent collar inserted 1 cm into the soil; air was circulated by rotary pump through the system at 0.85 l min^{-1}. The chamber was vented with a capillary tube to allow equilibration of air pressure. Measurements were taken at sunrise during minimum flux and in the afternoon during maximum flux, as determined by previous diel sampling. Soil respiration rates reported here are the means of the two measurements for each treatment. Soil moisture at the time of the CO_2 measurements was determined using time domain reflectometry (TDR) probes (0–15 cm depth) positioned vertically through the forest floor and mineral soil. Soil dielectric values for all but the OA-less plots (no forest floor) were converted to volumetric water content on the basis of a calibration derived for nearby similar soils[29]; a calibration for mineral soil[30] was used for the OA-less plots. Soil temperature was measured hourly using Campbell 107-B temperature thermistors (5 cm depth); those reported are treatment averages of 24 measurements taken hourly on the day of the CO_2 flux measurements. CO_2 flux measurements were made weekly from June to August, biweekly in September and October, and monthly in all other months except December, January and February, when no measurements were taken. Q_{10} values and regression slopes of respiration ($\log_{10}$-transformed) versus temperature were compared by Student's *t*-test.

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Selective sweep of a newly evolved sperm-specific gene in *Drosophila*

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The pattern of genetic variation across the genome of *Drosophila melanogaster* is consistent with the occurrence of frequent 'selective sweeps', in which new favourable mutations become incorporated into the species so quickly that linked alleles can 'hitchhike' and also become fixed[1]. Because of the hitchhiking of linked genes, it is generally difficult to identify the target of any putative selective sweep. Here, however, we identify a new gene in *D. melanogaster* that codes for a sperm-specific axonemal dynein subunit. The gene has a new testes-specific promoter derived from a protein-coding region in a gene encoding the cell-adhesion protein annexin X (*AnnX*), and it contains a new protein-coding exon derived from an intron in a gene encoding a cytoplasmic dynein intermediate chain (*Cdic*). The new transcription unit, designated *Sdic* (for sperm-specific dynein intermediate chain), has been duplicated about tenfold in a tandem array. Consistent with the selective sweep of this gene, the level of genetic polymorphism near *Sdic* is unusually low. The discovery of this gene supports other results that point to the rapid molecular evolution of male reproductive functions[2–4].

Our initial observation was that the genetic organization of region 19DE on the X chromosome of *D. melanogaster* differs from that of other species in the *melanogaster* subgroup[5,6]. The *D. melanogaster* genome contains an additional ~70 kilobases (kb) of DNA, consisting of ~10 tandem repeats of a unit ~7 kb in length. The tandem repeat is flanked at its 5′ end by *Cdic*, which encodes the cytoplasmic dynein intermediate chain, and at its 3′ end by *AnnX*, which encodes annexin X. The repeating unit is formed from a fusion of the central region of *AnnX* with the 3′ region of *Cdic*. One possible scenario (Fig. 1) is that the *Cdic–AnnX* region became tandemly duplicated; then, a deletion fused *AnnX* exon a4 with *Cdic* intron 3, another deletion eliminated the 5′ end of *AnnX* extending into exon a2, and a third deletion with breakpoints in *Cdic* introns 5 and 7 eliminated exon v2. This new structure was then tandemly duplicated. We designated the repeating unit *Sdic* because subsequent studies showed it to encode a sperm-specific axonemal dynein intermediate chain.

Nucleotide sequence analysis of complementary DNA clones gave unambiguous evidence for transcription of the *Sdic* unit[6]. Only the *Cdic*-derived sequences in *Sdic* are transcribed, and the *Sdic* messenger RNA contains four of the five *Cdic* exons present in the repeat. Exon v1 is not included; this exon is alternatively spliced in