TROPICAL SOILS COULD DOMINATE THE SHORT-TERM CARBON CYCLE FEEDBACKS TO INCREASED GLOBAL TEMPERATURES

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Abstract. Results of a simple model of the effects of temperature on net ecosystem production call into question the argument that the large stocks of soil carbon and greater projected warming in the boreal and tundra regions of the world will lead to rapid efflux of carbon from these biomes to the atmosphere. We show that low rates of carbon turnover in these regions and a relatively greater response of net primary production to changes in temperature may lead to carbon storage over some limited range of warming. In contrast, the high rates of soil respiration found in tropical ecosystems are highly sensitive to small changes in temperature, so that despite the less pronounced warming expected in equatorial regions, tropical soils are likely to release relatively large amounts of carbon to the atmosphere. Results for high-latitude biomes are highly sensitive to parameter values used, while the net efflux of carbon from the tropics appears robust.

Introduction

The resolution of biological feedbacks in the global carbon cycle is essential to robust predictions of future climate. The pool of carbon in soils and terrestrial vegetation exceeds that in the atmosphere by threefold (Schlesinger, 1991), and annual fluxes of carbon between the terrestrial biosphere and the atmosphere are roughly ten times greater than the annual efflux of CO_2 via the burning of fossil fuels (Mooney *et al.*, 1987). At steady-state, fluxes to and from terrestrial biota are roughly equal, but even a small disruption of this equilibrium could alter carbon dioxide concentrations in the atmosphere substantially.

One possible imbalance in the carbon cycle arises from the differing responses of production and decomposition to changes in temperature. Respiration and decomposition are believed to be more sensitive to temperature than are photosynthesis and production, raising the concern that global warming could trigger a net release of carbon dioxide from soils to the atmosphere. Attention has focused upon the boreal and tundra regions of the world, where large stocks of soil carbon coupled with a greater predicted warming could result in a massive efflux of CO_2 (Woodwell, 1990; IGAC, 1990). The tropics, with their smaller soil carbon reserves and lower anticipated warming, have not been emphasized. However, the basic pat-

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terns of variation in photosynthesis and respiration versus temperature suggest the potential for a significant release of soil carbon from tropical ecosystems.

Photosynthetic rates as a function of temperature increase most rapidly at low temperatures, with the response saturating as conditions become warmer (Gates, 1980; Fitter and Hay, 1981), and comparisons of net primary production (NPP) with mean annual temperature (Lieth, 1975) or with latitude (Prentice, 1986) yield a similar pattern. Inputs of carbon to ecosystems via primary production are therefore likely to be most sensitive to changes in temperature in cold, higher latitude ecosystems, while tropical and subtropical regions should have little or no response. In fact, Brown and Lugo's (1982) detailed analysis of tropical forests yields no significant effect of temperature on NPP.

In contrast, rates of soil respiration increase exponentially with temperature (Reiners, 1968; Medina and Zelwer, 1972; Singh and Gupta, 1977; Schlesinger, 1977), with no upper bound that appears relevant to any real or predicted climate. This means that a given increase in temperature will cause a much greater absolute effect on carbon dioxide efflux in a warm region compared to a cooler one. Put another way, carbon dioxide effluxes from tropical systems should increase markedly with a small change in temperature, whereas an increase in flux of similar magnitude in the arctic would require substantially greater warming. Soil carbon stocks in the tropics average somewhat less than those in the high latitudes, but the difference is relatively small (less than a factor of two; Post *et al.*, 1982), while differences in rates of carbon turnover can exceed an order of magnitude. Since the tropics have such high rates of carbon turnover and comprise 40% of the world's land area, they could have a significant overall effect on atmospheric carbon dioxide. In fact, Marston *et al.* (1991) found that measured CO_2 anomalies at Mauna Loa between 1958 and 1987 were highly correlated with temperatures averaged over equatorial regions. This correlation was better than that for global mean temperatures, and much better than that for non-equatorial latitudes.

The Model

We constructed a very simple model – almost a thought experiment – to explore the potential sensitivity of ecosystem-level carbon balance to temperature changes in the major biomes of the world. Total soil carbon values for each biome were taken from Post *et al.* (1982). Inputs to this pool of carbon via NPP and effluxes via soil respiration were initially assumed to be equal, and values for these fluxes were obtained from values summarized by Raich and Schlesinger (in press). No effort was made to separate root from soil respiration, and soil carbon was considered to be a single undifferentiated pool.

We assumed that changes in temperature would increase NPP linearly (Lieth, 1975; Prentice, 1986) and soil respiration in an exponential fashion (Reiners, 1968; Medina and Zelwer, 1972; Singh and Gupta, 1977; Schlesinger, 1977). Global temperature was increased exponentially over a 100 year period, with an overall increase of 2 °C in tropical regions, 3 °C in temperate regions, and 4 °C in the boreal forests and tundra. These values are reasonable estimates for temperature increases in a 2 × CO_2 world (IPCC, 1990).

The annual net change in soil carbon was calculated from

$$C_s = P_0 + M(T - T_0) - K_i C_s Q(T - T_0/10)$$

where P_0 is the initial NPP value (in g/m^2), M is the increase in NPP per °C as adapted from the photosynthetic capacity function of Prentice (1986), $T - T_0$ is the temperature change at any given time step, Q is the van 't Hoff Q_{10} factor, and K_i is ratio of initial carbon flux to initial soil carbon pool size. M was equal to 19.05 g/m^2 for tundra, boreal, and temperature biomes, and 8.98 g/m^2 for tropical biomes. The change in soil carbon at each time step was multiplied by the world area of each biome (Atjay *et al.*, 1979) to get the annual net flux of carbon between the biome and the atmosphere due to surface warming. All simulations were performed using the Stella software package and employed an annual time step.

Results and Discussion

Results at Q = 2 for All Biomes

Reported mean values for Q (van 't Hoff's Q_{10}) center around 2 (cf. Singh and Gupta, 1977; Raich and Schlesinger, in press), so one set of model runs was performed with $Q = 2$ in all biomes. Figure 1a shows the simulated change in soil carbon over a 100 year run in six biomes: tundra, boreal forests, tropical moist forests, tropical dry forests and savannas, temperate forests, and temperate grass-

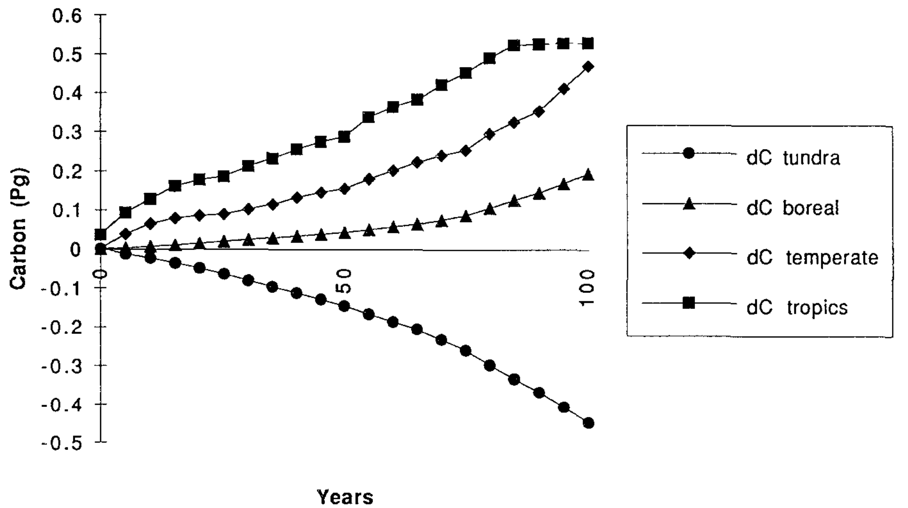

Fig 1a. Simulated annual soil carbon fluxes from 6 major biomes. Q (van 't Hoff's Q_{10}) = 2 for all biomes. The results for tropical moist forests and dry forests/savannas are combined, as are those for temperate forests and grasslands.

lands. Since the qualitative behavior of each tropical biome and of each temperate biome was similar, their results are combined here. The results differ from previous discussions of carbon balance in a warmer climate in several ways. Tropical regions release a substantial amount of carbon to the atmosphere despite a small temperature change due to the exponential response of an already high flux. Results for the temperate zone are similar to those for the tropics, but lag slightly behind them.

In all four tropical and temperate biomes, the rate of soil carbon loss increases exponentially early in the simulation. This imbalance cannot persist indefinitely: as soil carbon is lost, decomposition eventually must become substrate limited. The structure of the model contains this constraint, because respiration is calculated as a fraction of the remaining soil carbon. This effect can be seen in Figure 1a, where the efflux from the tropics levels off towards the end of the 100 year period, while temperate regions, where decomposition rates are slower and greater amounts of soil carbon are available, continue to show an exponential increase in the rate of carbon loss.

In contrast, initial losses of soil carbon from the boreal forest biome are relatively small. The massive carbon storage in this biome, however, means that ever higher temperatures eventually would increase the loss rate beyond that of the tropics. Finally, our results suggest that tundra soils will represent a significant net storage of carbon throughout the 100 year period. Given the low initial temperature of the tundra, a 4 degree warming increases NPP more than decomposition.

Finally, Figure 1b shows the net global flux between soils of all biomes (not just the six summarized in Figure 1a) and the atmosphere over a 100 year period. Despite the pronounced carbon storage of tundra soils in this scenario, the combined response of terrestrial soils is a linear increase in the release of carbon to the atmosphere.

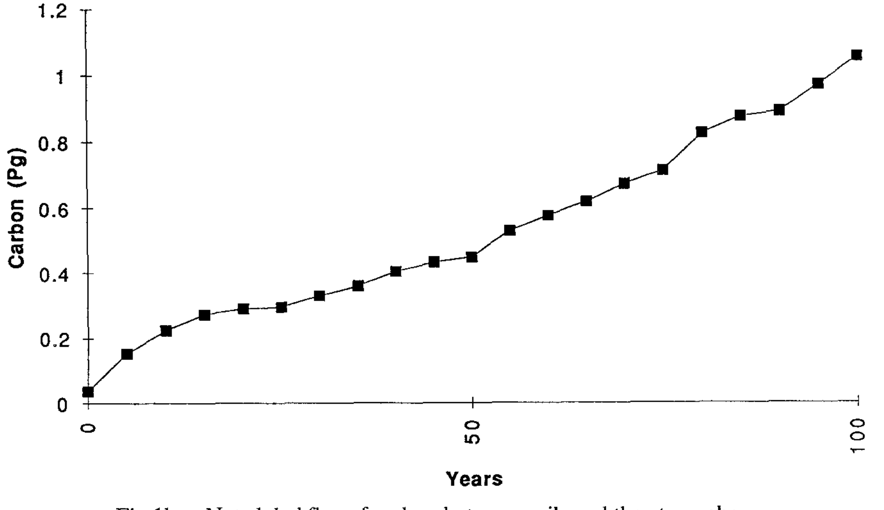

Fig 1b. Net global flux of carbon between soils and the atmosphere.

Results for Biome-Specific Q Values

We also used literature values to estimate a separate Q for each biome. These data are far from comprehensive even at regional scales, and comparisons among studies of soil respiration are subject to a variety of problems (Schlesinger, 1977; Meentemeyer, 1984; Raich and Nadelhoffer, 1990), but the patterns resulting from this analysis are nevertheless interesting. We used the Q_{10}'s derived by Fung *et al.* (1987) for tropical and temperate biomes. These values were derived by comparing dozens of reported CO_2 fluxes from the field against a detailed climate database. Such information was not available for the boreal and tundra regions, however, so we calculated a Q for each biome by averaging all the reported Q_{10} values we could find for these regions. A summary of the values used may be found in Table II.

Figure 2a shows the effects of increasing temperature (as above) on net carbon balance for the same six biomes, with these biome-specific mean Q values used in place of a global average. Table I shows calculated net ecosystem production (NEP, defined as net primary productivity minus respiration) in g/m^2 carbon at 25 year intervals under each modeling scenario. Little change in soil carbon loss from the $Q = 2$ simulation occurs in the tropical and temperate regions, largely because the new values for Q are all within 5% of $Q = 2$. Substantial changes in soil carbon as compared to the earlier runs, however, occurred in the boreal region. Here, the lower Q leads to a positive NEP up to a change in temperature of 3.5 degrees, at which point respiration begins to exceed production and loss of soil carbon commences. Overall, boreal soil carbon changes very little over the 100 year simulation. Finally, the tundra, despite its much higher Q, continues to have a positive NEP throughout the simulation, although the total amount of carbon stored is less than in the $Q = 2$ scenario. Figure 2b shows the global net flux with biome-specific Q

TABLE I: Net Ecosystem Production in g/m^2/yr (= NPP − Respiration)

			Biome-specific Q's				
Year	tundra	boreal	temp gl	temp for	savanna	dry for	rain for
25	5.77399	0.68535	−3.3298	−4.5718	−3.2535	−4.433	−9.54
50	12.3345	0.88339	−6.4062	−7.7484	−4.7436	−6.62	−14.285
75	19.8732	0.38453	−10.368	−10.939	−6.4749	−8.9905	−19.314
100	27.1717	−1.8469	−17.136	−17.9	−9.0299	−12.557	−26.823
			$Q = 2$				
Year	tundra	boreal	temp gl	temp for	savanna	dry for	rain for
25	8.07858	−1.72	−3.0988	−5.1413	−3.4772	−4.7332	−10.118
50	17.983	−3.7823	−5.9732	−8.6947	−5.0637	−7.0609	−15.135
75	31.2098	−7.1944	−9.6987	−12.218	−6.901	−9.5756	−20.436
100	50.0388	−14.103	−16.099	−19.895	−9.6016	−13.347	−28.327

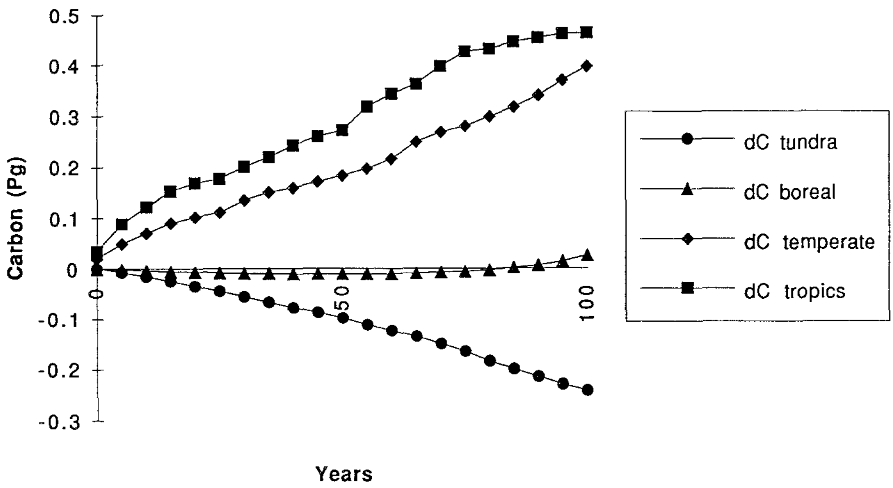

Fig 2a. Simulated soil carbon fluxes from 6 major biomes. Q values are biome-specific, as calculated from literature values (Table II). The results for tropical moist forests and dry forests/savannas are combined, as are those for temperate forests and grasslands.

TABLE II: Summary of Q values used in biome-dependent Q simulations

Biome	Q_{10} Value	Source
Tropical Forests	1.96	Fung *et al.* (1987)
Temperate Forests	1.93	Fung *et al.* (1987)
Grasslands	2.03	Fung *et al.* (1987)
Boreal Forests	1.3, 1.6	Berg (1984)
	2.42	Cowling and MacLean (1981)
	1.24, 1.73	Gordon *et al.* (1987)
	1.61, 1.68, 1.91	Schlentner and Van Cleve (1985)
Boreal mean	1.71	
Tundra	2.78	Stewart and Wheatley (1990)
	1.5–15.6	Svensson (1980)
Tundra mean	3.88	

* Values given by Fung *et al.* (1987) are derived from dozens of reported field values for soil respiration.

values. Despite the differences in the results for the tundra and boreal biomes in this scenario as compared to the $Q = 2$ simulation, the overall response of terrestrial soils is again a linear increase in the net flux of carbon to the atmosphere.

Global Trends and Discussion

The sensitivity of these simulations to changes in parameter values varies considerably with latitude. Figure 3 shows the effects of Q on the total 100 year flux be-

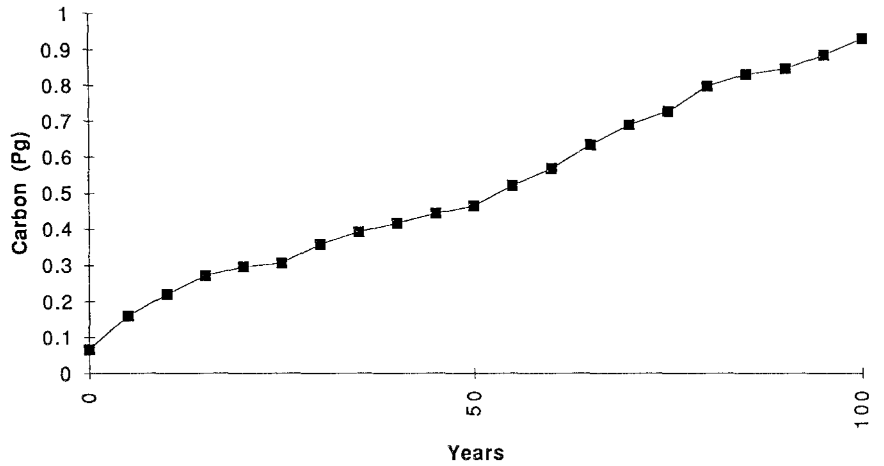

Fig 2b. Net global flux of carbon between soils and the atmosphere.

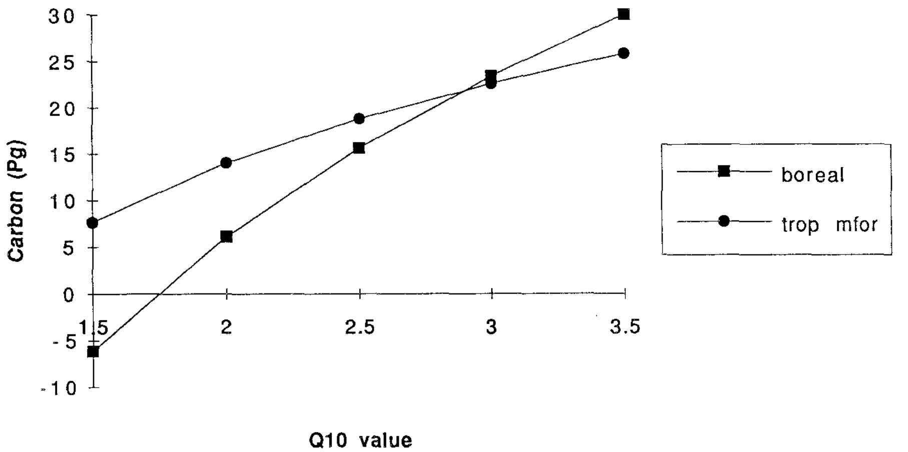

Fig 3. The effects of Q_{10} on the 100 year integrated flux of carbon between soils and the atmosphere for boreal and tropical moist forests.

tween soils and the atmosphere for the boreal and tropical moist forest biomes. The results for tropical regions are quite robust; lower Q values do result in a lower total flux, but substantial losses of soil carbon occur throughout the range. At the highest values, most of the carbon loss occurs in a few decades after which substrate availability limits further loss. At the lowest values, the initial losses are less, but the imbalance can persist for a longer period of time. In contrast, carbon balance in the boreal is far more sensitive to Q_{10}. Below 1.75, there is a net increase in soil carbon, while at values greater than 1.75 the total flux to the atmosphere increases rapidly. The results for temperate biomes lie between the boreal and tropical values. Clearly, uncertainties in the temperature response of boreal and tundra biota contribute most to our overall uncertainty about terrestrial carbon balance in a warmer climate.

This simple model is not a comprehensive analysis or prediction of carbon balance in a changing climate. While temperature is generally the most important controller of soil respiration rates, other factors are critical in determining the magnitude of soil CO_2 effluxes. Chief among these is moisture, and moisture effects on soil respiration in the tundra are particularly important. The variability in reported Q_{10} values from the tundra is largely due to differences in moisture, with one study reporting a more than a 30-fold variation in Q_{10} across a range of soil moisture (Svensson, 1980). Moreover, NPP is also closely linked to moisture availability.

A third major variable in any analysis of soil carbon balance and climate change is substrate quality. Decomposition rates are dependent on the resistance of the organic matter being decomposed (Van Veen and Paul, 1981; Flanagan and Van Cleve, 1983; Parton *et al.*, 1987), and the steepness of the temperature response may also vary with substrate quality. One possible example of this variance is the relatively low Q in boreal regions, where the coniferous litter is known to be highly resistant to decay (Berg, 1984; Berendse *et al.*, 1987). Moreover, existing studies of temperature controls over soil respiration have tested the response of the most labile component of soil organic matter, which accounts for only a few percent of the total. Most carbon in soils is contained in pools which are more resistant to decay (Parton *et al.*, 1987). Roughly 30–50% of soil carbon is stored in highly recalcitrant organic-mineral complexes, with a mean turnover time that should render it relatively unimportant to climate change on the decadal time scale (Trumbore *et al.*, 1990), and most of the remainder is in more labile forms whose mean turnover time is on the order of decades (Schimel, 1986; Parton *et al.*, 1987). It is the response of this large intermediate pool of carbon to both temperature and moisture that will determine the amount of carbon stored in or released from soils in a warmer climate. If the temperature response of this pool is significantly lower than that suggested by short term studies of soil respiration, vast losses of soil carbon to the atmosphere as the earth warms would be less probable.

Finally, our analysis has focused on storage of carbon in soils. If warming leads to a significant increase in carbon storage above-ground either within extant biomes (Bonan, 1991), or as high-biomass biomes migrate into regions that now have low above-ground carbon storage (i.e., boreal forest into tundra), the net effect of warming on soil carbon loss could be reduced or eliminated. Moreover, carbon to nutrient ratios of soil organic matter are much lower than those in plant tissue, and where nutrients limit biomass accumulation, their release via warming-driven increase in decomposition could stimulate NPP and carbon storage (Pastor and Post, 1986; Schimel *et al.*, 1990; Kittel *et al.*, in press). Nitrogen limitation is a strong constraint on primary production in most temperate and high-latitude ecosystems (Aber *et al.*, 1989; Vitousek and Howarth, 1991). Most tropical forests, however, appear to be phosphorus or calcium limited (if at all by nutrients). Due to adsorption on soil surfaces, increased decomposition will not produce a proportional increase in available phosphorus or calcium to nearly the same extent as it will for nitrogen. Additionally, tropical forests are relatively enriched in nitrogen (Vitousek and Sanford, 1986), so any increase in nitrogen release from accelerated decomposition may also increase fluxes of nitrogen trace gases (Matson and Vitousek, 1990). Overall, storage of additional carbon in plant biomass as a consequence of elevated temperature is unlikely in tropical forests and quite likely at higher latitudes. In this respect, the differences between tropical and high latitude biomes reported here may be conservative, as the model does not store any of the increases in NPP in biomass.

Two major conclusions can be drawn from this work. First, even a slight warming of the tropics produces substantial losses of soil carbon, causing tropical biomes to dominate the early response (several decades) of terrestrial carbon balance to warming. Temperate systems may also produce a large soil carbon efflux within a century. Second, the large carbon reserves and substantial warming in high-latitude ecosystems may not necessarily lead to significant releases of carbon in a warmer climate. Instead, the low rates of carbon turnover and the relatively greater responsiveness of NPP could lead to a positive NEP over some limited range of warming. Predictions of high-latitude carbon balance are highly sensitive to the parameter values used, and therefore it is crucial that these be known accurately. In contrast, the projections of rapid net release of carbon from tropical soils appear robust.

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