Chapter 8

Climate change feedback and temperature sensitivity of soil organic carbon and its degradation kinetics

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Terrestrial ecosystems can release or absorb globally relevant greenhouse gases such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), they emit aerosols and aerosol precursors, and they control exchanges of energy, water and momentum between the atmosphere and the land surface. Ecosystems themselves are subject to local climatic conditions, implying a multitude of climate- ecosystem feedbacks that might amplify or dampen regional or global climate change. Of these feedbacks, that between the carbon cycle and climate has recently received much attention. Large quantities of carbon are stored in living vegetation and soil organic matter, and liberation of this carbon into the atmosphere as CO_2 or CH_4 would have a serious impact on global climate. By definition, the carbon balance of an ecosystem at any point in time is the difference between its carbon gains and losses. Terrestrial ecosystems gain carbon through photosynthesis and lose it primarily as CO_2 through respiration in autotrophs (plants and photosynthetic bacteria) and heterotrophs (fungi, animals and some bacteria), although losses of carbon as volatile organic compounds, CH_4 or dissolved carbon (that is, non-CO_2 losses) could also be significant. Quantifying and predicting these carbon-cycle-climate feedbacks is difficult, however, because of the limited understanding of the processes by which carbon and associated nutrients are transformed or recycled within ecosystems, in particular within soils, and exchanged with the overlying atmosphere.

Carbon dynamics

In carbon-cycle-climate models, the effect of the prevailing climate on the carbon balance in terrestrial ecosystems is described mostly by relatively simple response functions and kinetic concepts of CO_2 uptake by photosynthesis and loss by respiration. The fundamental paradigm adopted by researchers over the past two decades has been that photosynthetic uptake is simulated both by increasing CO_2 and, in boreal and temperate regions, by rising temperature, although both effects are expected to saturate at high levels of these variables. On the other hand, the biological processes underlying respiration are assumed to respond to temperature in an exponential way but are not affected by the CO_2 concentration. This leads to the conclusion that the biosphere is able to provide negative feedback to rising CO_2 and temperature until the temperature climbs so high that the stimulating effect on respiration exceeds the CO_2 fertilization effect. Although this conceptual model has provided valuable guidance for experimental and model design, evidence has accumulated in recent years that above- and below-ground processes are intimately linked, constituting a complex and dynamic system with non-negligible interactions. Hence, the situation is much more complicated than previously thought and might result in unexpected dynamics through interactions between physical, chemical and biological processes within the ecosystem- particularly in the soil. This implies that, beyond rising CO_2

levels and rising temperature, other climatic and environmental factors might modify, or even dominate, the carbon balance of the world's ecosystems. Furthermore, not only the long-term rate of change of mean values of parameters such as temperature but also alteration in their variability, including greater extremes, may be crucial to ecosystem carbon dynamics.

Climate changes feedbacks and soil organic carbon dynamics

Climate changes have both direct and indirect effects on the soil organic carbon (SOC) dynamics and its decomposition kinetics as well as microbial activities on SOC decomposition that provide a feedback to the gaseous-C concentrations to the atmosphere and contribute to global warming. Direct effects include temperature mediated soil respiration, SOC decomposition leading to gaseous-C emission, changes in precipitation and extreme climatic events. The indirect effects result from climate-driven changes in plant productivity and diversity that would alter soil physico-chemical conditions, the supply of carbon to soil and, structure and activity of microbial communities involved in decomposition processes and carbon release from soil.

As rates of soil respiration are thought to be more sensitive to temperature than primary production, it is predicted that climate will increase the net transfer of carbon from soil to atmosphere, there by creating a positive feedback to climate change. Growing stress tolerance species also contribute to a positive feedback to climate change. Increase of primary production (higher photosynthesis) and reduction of the length of growing season causes negative feedback to climate change by reducing the CO_2 emission to atmosphere and absorbing more CO_2 from atmosphere. The indirect effects which includes positive feed backs are i) percolation and runoff losses of dissolved organic carbon (DOC), ii) higher root exudation that causes faster SOC decomposition through "Priming effect" and promote methanogenesis and hence enhance the C losses from soil as CH_4. The indirect negative feedbacks include i) increasing plant-microbial competition for nitrogen (N) that causes ecosystem carbon (C) accumulation, ii) increasing growth of mycorrhizal fungi causing C accumulation and iii) stimulation of microbial biomass and immobilization of soil N causing limitation of N availability to plant and hence accumulation of C in soil . Another indirect effect on climate change (both positive and negative feedbacks) is through shifts in the functional composition and diversity of microbes and vegetation which occurs over longer time scales of decades and centuries.

Factors associated to carbon dynamics and climatic feedbacks

Primary productivity in more than half of the world's ecosystem is substantially limited by the availability of water. Hence, changes in precipitation will have direct effects on ecosystem C dynamics. In a warmer world, evaporation is expected to increase, leading to a more negative water balance, whereas decreased water loss through stomata in a CO_2-richer world will tend to mitigate this effect. The net effect (production minus respiration) of a more negative overall water balance probably depends on the water-holding capacity of the soil, the vertical distribution of C and roots in the soil, and the general drought sensitivity of the vegetation. For instance, if most of the soil C is concentrated at the top of the soil, while roots go deep into a soil with high water-holding capacity, or even tap the groundwater, soil carbon decomposition will initially be more strongly affected by drought than will vegetation productivity, as the topsoil dries out first. Water limitation may even suppress the effective ecosystem-level response of temperature on respiration. Conversely, if soil water-holding capacity is low, as in shallow soils, vegetation productivity will be strongly affected by a negative water balance. Hence, under drier conditions, there are predictions of increased sequestration by suppression of respiration and net loss of C through decreased productivity.

A second important interacting factor is the available N, which often determines the magnitude of the CO_2 fertilization effect and may suppress it completely if N is limiting. There are also indications of strong interactions between water and N, with N becoming more limiting under

drier conditions. Other factors to be considered are changes in the amount and quality (direct or diffuse) of light, which can alter vegetation productivity, and increases in air pollutants and ozone, with their detrimental effects on primary production.

Feedbacks in the carbon-cycle-climate system

As discussed above, the net effect of any environmental change on the carbon balance in an ecosystem depends on the reactions of both photosynthesis and respiration; in other words, on above-ground and below-ground processes. Below-ground processes in particular are still poorly understood yet provide a number of potentially important feedbacks in the carbon-cycle-climate system.

Current estimates of carbon stored deep-frozen in permafrost regions amount to at least 400 petagrams (4×10^{11} tonnes) of carbon that is relatively unprocessed and labile as the frozen state protects it from microbial decomposition. Moss and turflayers provide very good insulation against the atmosphere. With rising summer temperatures, these soils begin to melt, the carbon becomes metabolized and microbial metabolism may release enough heat (the 'during heap-effect) to facilitate further melting, providing a nonlinear positive-feedback mechanism to enhance permafrost melting and, though CH_4 and CO_2 emissions, to increase the greenhouse effect.

Another mechanism for potential mobilization of large amounts of carbon is the so-called 'microbial priming effect'. It has been shown in several experimental systems that the addition of substrates with readily available energy (for example, glucose and cellulose) to the soil stimulates the decomposition of 'old' soil carbon. Fontaine et al. (2004) showed that simply by adding cellulose to the soil they could mobilize carbon from the subsoil of grasslands that was assumed to be stable, whereas other factors such as temperature, nitrogen addition or increasing oxygen concentration had no effect. Addition of such material even induced a net loss of carbon from the soil samples, as the soil carbon stock is large. In the context of climate change this effect may induce a positive-feedback effect, particularly in grassland soils. Increasing CO_2 concentrations can lead to enhanced below-ground allocation of labile carbon through roots and root exudates, which can enhance microbial activity and foster decomposition of carbon material that has been deemed stable but was in fact not being attacked because microbes were not active. Also, if rooting patterns change, either because of altered precipitation or a part of general vegetation dynamics, carbon input into deeper layers that were not rooted before might induce release of old carbon through this mechanism.

The interaction of the carbon and nitrogen cycles offer a plethora of mechanism that could alter expected ecosystem carbon response to the prevailing trend in climate change. In nitrogen-limited ecosystems, nitrogen nutrition limiting the CO_2 fertilization effect on canopy assimilation is regularly found after a few years of increasing CO_2 levels. There are also indications that nitrogen availability influences the decomposition of soil organic matter. Fungi use lignin, an abundant, stable organic substance found in plant cell walls, as a nitrogen source under conditions of limited nitrogen availability. Enhanced decomposition of lignin may lead to a positive feedback in response to rising atmospheric CO_2. On timescales longer than a few years, however, acclimation or change in species composition, or, for example, increased nitrogen fixation through increased carbohydrate input into the soil, may relax or even overcompensate for the nitrogen-limitation effects. Also, an interaction with microbial 'priming' through more intensive and deeper plant rooting is not unlikely, as a decrease in nitrogen availability often leads to a larger allocation of carbon to roots.

Temperature sensitivity of soil organic carbon

The temperature sensitivity of decomposition of the enormous global stocks of SOC has recently received considerable interest. Interest in this topic is high because of its importance in the global carbon cycle and potential feedbacks to climate change. This recent controversy has focused primarily on organic matter in upland mineral soils. These soils have reasonably good

drainage and aeration, allowing roots and soil fauna to penetrate into mineral soil layers, thus mixing SOC with mineral particles. Conditions in upland mineral soils are also favourable for decomposition, resulting in relatively low carbon densities. In contrast, in wetlands and peatlands where anaerobic conditions frequently persist, decomposition proceeds much more slowly, and deep layers of organic matter accumulate on top of mineral layers.

Factors controlling decomposition of organic carbon

The stocks of organic carbon in soils result from the balance between inputs and outputs of carbon within the belowground environment. Inputs are primarily from leaf and root detritus. Outputs are dominated by the efflux of CO_2 from the soil surface, although CH_4 efflux and hydrological leaching of dissolved and particulate carbon compounds can also be important. The production of CO_2 in soils is almost entirely from root respiration and microbial decomposition of organic matter. Like all chemical and biochemical reactions, these processes are temperature dependent. Root respiration and microbial decomposition are also subject to water limitation. Hence, most empirical models relate the efflux of CO_2 from soils (often lumping microbial and root respiration together as 'soil respiration') to temperature and often also to some scalar of soil water content or precipitation. This much is not controversial.

The kinetics of enzymatic reactions in well-mixed media is also not controversial. Activation energies are related to the ambient temperature and to the molecular structure of the organic-C reactant. The temperature sensitivity of decomposition increases with increasing molecular complexity of the substrate. The reaction rates are also modified by substrate concentrations and affinities of the enzymes for the substrates.

Soils contain thousands of different organic-C compounds, each with its own inherent kinetic properties. Not only do plants produce a wide range of carbon substrates, but plant detritus also undergoes transformations by microbial degradation or by abiotic condensation reactions that produce new aromatic structures, larger molecular weights, insolubility, or other molecular architectures that affect the types and efficacies of enzymes that can degrade them. These complex molecular attributes are characterized by low decomposition rates, high activation energies, and inherently high temperature sensitivity. The inherent kinetic properties based on molecular structure and ambient temperature could be called as the 'intrinsic temperature sensitivity' of decomposition.

On the other hand, the enzymes for decomposition may be physically or chemically excluded from many of the organic-C substrates within the heterogeneous soil environment, causing substrate limitation at reaction microsites. The observed response to temperature under these environmental constraints, which we shall call the 'apparent temperature sensitivity', may be much lower than the intrinsic temperature sensitivity of the substrate. Conversely, if a temperature-sensitive process alleviates an environmental constraint to decomposition, then the subsequent increase in substrate availability could result in the apparent temperature sensitivity temporarily exceeding the intrinsic temperature sensitivity of the substrate. The environmental constraints that can temporarily or indefinitely affect apparent temperature sensitivities of decomposition include the physical, chemical protection, drought, flooding, freezing etc.

The intrinsic temperature sensitivity of soil organic carbon decomposition

Arrhenius equation and Michaelis-Menten kinetics

The temperature sensitivity of soil respiration is expressed as the van't Hoff's temperature coefficient Q_{10}, which describes the factor by which the rate increases with a 10°C rise in temperature. The Arrhenius equation Eq. 1 describes changes in relative reaction rates (like decomposition rates) as a function of temperature:

$$k = A \exp(-Ea/(RT)) \qquad \ldots \ldots \ldots (1)$$

where, k is the reaction rate constant; A is the frequency factor; Ea is the required activation energy in joules per mole; R= 8.314 $JK^{-1}mol^{-1}$ gas constant and T is the temperature.

Soil organic matter with complex molecular attributes (e.g. recalcitrant SOM, adsorbed SOM, complexed SOM) is characterized by low decomposition rates, high activation energies and, therefore, an 'inherently' high temperature sensitivity. The activation energy Ea is a constant that is related to an ambient temperature and to molecular attributes of the organic C compound (Davidson & Janssens, 2006). With increasing temperature, there is a declining relative increase in the fraction of molecules with sufficient energy to react, and consequently, the Q_{10} value decreases (Davidson & Janssens, 2006; Tjoelker et al., 2001). This implies highest temperature sensitivities in colder regions where also largest C stocks are found (Post et al., 1982; USDA, 2000). The Arrhenius function also shows that the temperature sensitivity of decomposition increases with increasing stability of organic compounds because stabilized substrates are less reactive due to higher activation energies. This means that the stable pool is more temperature-sensitive than the labile pool, which is characterized by low activation energies.

The application of Arrhenius kinetics is limited under conditions of low substrate availability. As described by Michaelis-Menten kinetics (Eq. 2), the reaction rates are further modified by substrate concentrations [S] and affinities of the enzymes for the substrates Km:

$$k= Vmax * [S] / (Km + [S]) \qquad .... (2)$$

where, k is the reaction rate; Vmax is the maximal rate of enzymatic activity at a given temperature; Km is the Michaelis-Menten constant, representing the affinity of enzymes for the substrates expressed as substrate concentration at which the reaction rate equals Vmax/2 and [S] is the substrate availability (substrate concentration at active site of the enzyme).

Substrate availability is directly affected by stabilisation of organic compounds (e.g. by interaction with mineral surfaces and metal ions, spatial inaccessibility due to aggregation and hydrophobocity (Sollins et al., 1996; von Lutzow et al., 2006)) or indirectly by external control factors (e.g. water, oxygen and nutrient supply, temperature, pH) that restrict decomposition. *In situ* temperature insensitive processes such as seasonal litter fall, drying rewetting and tillage alter the release of easily decomposable substrates.

Canceling effects

When substrate [S] is abundant and larger than Km ([S]>Km) and the temperature does not exceed the optimum temperature, Km becomes insignificant (the term [S]/(Km + [S])) and the temperature response of Vmax determines the decomposition rate, which depends only on the catalytic effect exerted by enzymes according to Arrhenius. However, when substrate availability [S] is low- as in most soils, Km becomes relevant and the decomposition rate depends on the enzyme concentration as well as on the substrate concentration. Because Km and Vmax increase with temperature (Arrhenius, 1889), the temperature sensitivities of Vmax and Km (nominator/denominator in Eq. 2) can nutralise each other (Davidson et al., 2006). This 'cancelling effect' becomes significant when substrate concentration [S] is low and also within the range or lower than Km and if both Km and Vmax have similar temperature sensitivities (Larionova et al., 2007). Results by Gershenson et al. (2009) show that addition of readily available substrates significantly increases Q_{10} values because substrate saturation eliminates the canceling effect of Km on the measured Q_{10} values. When Vmax and Km cancel each other out, respiration is controlled by temperature-sensitive processes that alleviate substrate limitation, e.g. decomposition of stabilized SOC pools is a process that produces available substrate.

As most soils are C-limited (Cheng et al., 1996; Ekschmitt et al., 2005), the cancelling effect can be an important factor controlling the 'actual' temperature sensitivity in soils *in situ*. The cancelling effect is short-lived if the time delay between Vmax and Km changes is significant, whilst synchronous alterations of these parameters lead to the Vmax and Km cancelling each other out in the long term.

Conclusions

The picture of a gradual increase in CO_2 and temperature, with separable, non-interactive effects on assimilation and respiration, needs to be replaced by a multifactor view, by more sophisticated characterization of changes in environmental factors, including their variability and extremes, and, maybe most importantly, by stronger integrative consideration of complex interactions between ecosystem processes at different levels of organization. Most of these emerging characteristics point to a lower CO_2– sequestration potential than estimated by current models and highlight the vulnerability of soil carbon that has accumulated over millennia. A positive feedback of ecosystem carbon to climate change might occur earlier and more strongly than currently predicted in coupled carbon-cycle-climate models.

Both the Arrhenius equation and Michaelis-Menten kinetics demonstrate different temperature sensitivities of differently stabilized SOC pools. In the Arrhenius equation, temperature sensitivity of decomposition increases with increasing stability of organic compounds because stabilized substrates are less reactive due to higher activation energies (e.g., recalcitrant SOC compounds, complexed SOC and adsorbed SOC). Stabilization of SOC by spatial inaccessibility (e.g., occlusion of SOC by aggregation, hydrophobicity) for microbes and enzymes is considered by Michaelis-Menten kinetics.

In most current C turnover models, the reaction of SOM pools on variations in temperature is considered to be equal ($Q_{10} = 2$ at 30-35°C; $Q_{10} = 4$-6 at 5-10°C; based on measurements of the CO_2 efflux from short-term laboratory incubations of bulk soils by Kirschbaum (1995)). Handling bulk SOM as one homogeneous pool ignores the variation in relative abundances of differently stabilized SOM pools and the underlying temperature dependencies in decomposition rates. In addition, the use of fixed Q_{10} values in C turnover models describes a potential temperature sensitivity, but not the actual temperature sensitivity, which is modified by cancelling effects *in situ*.

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