How does land use and climate change affect soil organic carbon stocks and processes in

temperate grasslands?

Abstract: *Climate and land use changes have significant consequences on the global carbon (C) cycle. Changes to the C cycle in soils of temperate grasslands are important to consider because they often comprise regions of human agriculture and they may significantly alter global C cycles for hundreds to thousands of years. Experiments in temperate grasslands around Western Europe, Northern China, and the United States have shown either slight increases in soil organic carbon (SOC) stocks or no net change over the 20th century, possibly due to increased CO_2 stimulating plant growth, in turn offsetting increased SOC loss via soil respiration. There is little consensus in the scientific community over what causes these effects. Experiments testing hypothesis on some SOC factors, such as soil microbial communities, have yielded inconclusive or conflicting results. Uncertainties and lack of inclusion of certain SOC dynamics and experimental variables may explain why model simulations show widely varying predictions of future global and regional SOC stocks and dynamics.*

Introduction

Background

Human input of carbon dioxide to the atmosphere has been a major driver of global climate change since the Industrial Revolution. CO_2 concentrations may increase as much as 110% by the end of the century, potentially increasing global surface temperatures 1.1-6.4 °C (IPCC, 2013). As more CO_2 is released into the air, understanding the carbon (C) cycle and how it is impacted by climate change becomes increasingly important.

A major stage of the C cycle lies in the soil, where plants take up CO_2 and incorporate C into their biomass via photosynthesis, eventually depositing C as dead organic matter into the soil. Soil organic carbon (SOC) is released back into the atmosphere as heterotrophic microbes decompose the organic matter and respire (Figure 1). SOC can also be removed by major disturbances like fire and erosion. Thus, Earth's soils act as both sinks and sources of atmospheric CO_2 (Eglin et al., 2010).

Understanding how SOC responds to warming is important for sequestering C from the atmosphere and maintaining soil fertility. SOC and its associated organic matter affect soil water retention, nutrient availability, soil structure, and erosion, among other factors critical in maintaining agricultural productivity and ecological functioning (Trumbore and Czimczik, 2008). SOC can be affected by changes within myriad plant, atmosphere, or other earth system processes (e.g. photosynthesis, annual precipitation) to the point that positive feedback loops between the soil and climate change forces initiate and compound detrimental effects to the environment (Schuur et al., 2008).

SOC global distribution

The greatest soil stock of C in the world lies in the northern permafrost biomes (Figure 2). These biomes constitute almost a third of the global SOC stock and contain twice the amount of C found in the atmosphere. These stocks are very vulnerable to climate change since mean temperatures are rising faster in the high-north than anywhere else in the world (Dutta et al., 2006). Decomposition of formerly frozen organic matter has led to 40% and 78% increases in C released into the atmosphere (Schuur et al., 2009). Further thawing could significantly increase positive feedbacks to global warming.

Tropical forests contain the second largest SOC stock (~692 PgC) in the world. These ecosystems store more C in vegetation than anywhere else, making them the largest zones of CO_2 uptake (Eglin et al., 2010). Human demand for economically valuable food crops has increasingly turned these forests into agricultural regions that produce far less plant biomass and thus do not fix as much CO_2 from the atmosphere. Converting tropical forest to agricultural cropland causes approximately 41% of SOC to be lost from forest soil (Wei et al., 2014). Tropical forests' SOC stocks correlate with high plant productivity, but this is not the case for ecosystems where plants are harvested and C is prevented from depositing into the soil. Also, depending on the plants' structural composition, soil deposits may not decompose for extended periods (Eglin et al., 2010).

This review will focus on temperate grasslands. These regions contain approximate SOC stocks of ~172 PgC, with more than 80% of the total C in the ecosystem represented in the soil (Eglin et al., 2010). Since soil organic matter and its contained C may remain in grassland soils between 22 and 5,000 years (Scurlock and Hall, 1998) alteration of grassland SOC dynamics by climate or land use change may have long lasting effects on the global C cycle and intensify climate change forces. Much research on SOC dynamics in temperate grasslands has focused on those within the United States, Western Europe, and Northern China and Tibet. These areas provide insight on different stages of land use change and its effects on SOC due to their varying histories of human cultivation.

Uncertainties

Predictions of the effects of climate change on global SOC vary widely since SOC processes are not well understood, especially across time scales of decades to centuries or longer.

Primary and tertiary effects of climate change that occur or unfold over decades to centuries, such as ecological succession or major weather events, play important roles in C cycling but can be difficult to predict (Trumbore and Czimczik, 2008). For example, fires can alter the C cycle by shifting grassland plant communities to other species comprised of differentially degrading C, thereby affecting microbial communities and SOC release into the atmosphere. The cumulative effect on SOC dynamics in temperate grasslands of such occasional and difficult to predict events have not been widely examined in scientific literature. As a result, carbon-climate coupled models do not provide very accurate pictures of future SOC changes.

The relationship between climate change and terrestrial C dynamics can be explored through historical SOC records. Temperate grassland SOC does not constitute much of the average global SOC stock but these regions often have long records of human cultivation. Detailed historical data in these ecosystems allows for finer examination of long-term changes in terrestrial C cycles than in tropical rainforests and permafrost regions. This review will examine how climate and land use change may impact soil respiration and SOC dynamics in temperate grasslands.

Land use changes and field observations of historical SOC stocks and dynamics

Research by Bellamy et al. (2005) on SOC of England and Wales has sparked much discussion on what may have caused changes to their recorded SOC concentrations. Samples differentiated by soil type and land use type were collected 12 to 25 years after original sampling between the late 1970's and early 80's across 5,662 sites. Bellamy et al. (2005) found widespread C was losses at an average rate of 0.6% yr^{-1}. They concluded that climate change caused these losses.

Lack of data prevented the authors from exploring the effects of land use change on SOC dynamics. This omission has led to much criticism of their findings and conclusion. Lettens et al. (2005) suggests that instead of climate warming, the changes observed by Bellamy et al. (2005) may have been due to changes in farming practice. Such changes include improved technology and crop strains that reduced crop litter left on fields after harvesting and declining livestock numbers that decreased the amount of animal manure deposited in the soil. Reductions in animal manure deposition likely explain some of the SOC variations observed between 1960 and 2000 in Belgium. Other agricultural practices may have contributed to increases in SOC stocks over that period (Lettens et al., 2005).

Besides missing land use factors, another flaw in Bellamy et al. (2005) was their estimation of soil bulk density to derive SOC stocks. Bulk density (g soil cm^{-3} soil) may have changed over time due to changes in soil water content or change in net primary production (NPP). A 0.05 $Mg\ m^{-3}$ change in soil bulk density could lead to 25% changes in SOC stocks (Smith et al., 2007). Such lack of precision by Bellamy et al. (2005) was considered in an experiment in English grassland sites not subject to significant changes in land use. Steady managed of these sites for over a century provided appropriate background data on soil properties. Despite consistent air and soil temperature increases across these sites, SOC content of the plots was too variable to be attributable to climate change. Rather, SOC may have experienced no net change, and the observed variability may have been caused by changes in bulk density or statistical uncertainties (Hopkins et al., 2009). Indeed, other empirical and modeling studies in the UK have shown either soil C gains or no significant change over roughly the same period that Bellamy et al. (2005) examined (Smith et al., 2007). Modeling experiments conducted by Smith et al. (2007) suggest that climate change accounts for only 10-20% of SOC

losses in the UK.

Yang et al. (2010) observed changes in SOC in northern China between the 1980's and 2000's. Regional variations in SOC had a wide range between a maximum of 6.8 Pg C in the Tibetan Plateau and a minimum of 1.8 Pg C in the Inner Mongolian Plateau. (It is important to note that the authors used the same estimation as Bellamy et al. (2005) of soil bulk density for certain soil profiles lacking this information. Therefore, some of the SOC concentration derivations may have been exaggerated.) The variations in SOC stocks in this region of northern China may have stemmed from ruminant grazing activity. Samples were analyzed according to grazing and non-grazing activity but no significant differences in SOC stock change were found between the two conditions (Figure 4a). Differences in grassland type were another theoretical cause of the SOC dynamic variation. This hypothesis was ruled out upon finding no significant change in SOC stock between either grassland types (Figure 4b). The largest changes in stock occurred in soils with the most C (Figure 4c), suggesting that variation in stock may also reflect variation in SOC density across a region (Yang et al., 2010; Holmes et al., 2006). Averaging all the data collected across the landscape showed no significant change in SOC stocks. Given the vast climatic range of northern China and differences in SOC and temperature from other global temperate grasslands, a summation of regional data may not have been useful for forecasting SOC responses to climate change (Yang et al., 2010; Homann et al., 2007; Burke et al., 1989).

In the alpine grasslands of the Tibetan Plateau, SOC stock exhibited similar stability from the 1980's to 2004. Like in northern China, these grasslands exhibited considerable regional variations (Yang et al., 2009). The C cycle in soils may be in a steady state since the Tibetan Plateau experiences relatively little human intervention and the climate has steadily warmed. The range in SOC stocks and the differences between Tibetan and northern Chinese grasslands from

those of other temperate grasslands in the world suggests that analysis of SOC stocks should not be considered across the entire landscapes. Rather, SOC should be considered under narrower categories like type of grass, rainfall pattern, and human land use history (Yang et al., 2009).

Plant community impacts on SOC

Increased atmospheric CO_2 levels have a positive effect on plant productivity and by association, soil C storage (Pendall et al., 2010; Luo et al., 2006). The steady state of SOC stocks in the sites examined by Hopkins et al. (2009) may have been due to such an increase of NPP offsetting SOC losses (Hopkins et al., 2009). Similarly, in the Great Plains, U.S., no significant net change was observed in an experiment involving harvesting of tall prairie grasses growing in plots subject to gradual 2° C warming. Significant SOC loss via respiration occurred more on experimental plots than in ambient temperature control plots. However, warmed plots with unclipped and clipped grass increased 14% and 26% respectively in NPP, offsetting the SOC loss incurred by the increased soil respiration (Luo et al., 2009).

One reason for this stimulated growth was the displacement of C_3 grasses by C_4 plants. Warmer temperatures enhanced the photosynthesizing capacity of C_4 plants while also lengthening the growing season and increasing plant nutrient uptake efficiency. These conditions resulted in their greater plant biomass production (Figure 5). The woodier, lignin-heavy plant structure of C_4 litter is also slower to decompose than the nitrogenous, labile C structured C_3 plants, resulting in greater soil surface litter mass accumulation and greater input into the inert soil pool of recalcitrant C (Figure 6). This plant community shift and accumulation of recalcitrant C affected microbial community compositions and soil respiration rates (discussed further below). Comparisons of SOC concentrations in clipped versus unclipped plots showed

360 g C m^{-2} (6yr)$^{-1}$ and 683 g C m^{-2} (6yr)$^{-1}$ respectively, indicating that clipping the grass also had the effect of stimulating root growth, increasing NPP and rhizodeposits to the soil (Luo et al., 2009).

The findings of this experiment coincide with the findings of Yang et al. (2010): grass defoliation may have stimulated NPP to offset increases in soil respiration that may have occurred due to climate or land use changes. However, they also diverge from previously assumed aspects of SOC dynamics. For example, the higher rate and earlier onset of biomass production compared to soil respiration of this experiment suggested that NPP might be more responsive to climate warming than respiration (Cheng et al., 2010; Luo et al., 2009). Previous models had predicted that soil respiration would be more sensitive to warming than (Davidson and Janssens, 2006; Friedlingstein et al., 2006; Cox et al., 2000). A lack of consensus among researchers of the temperature-soil respiration relationship may be due to the differences in temperature levels, duration of study, and data analysis by researchers among several other widely varying parameters used in field experiments (Luo et al., 2009). The results of Luo et al. (2009) also conflicted with previous assumptions that labile C, the C that is most bioavailable and quickest to decompose, would decrease in warmer temperatures (Peterjohn et al., 1993; Niinisto et al., 2004). The authors observed increases of labile C by 373 mg C kg$_{dry\ soil}^{-1}$ in warmed and unclipped plots compared to control plots. (Clipped plots had less labile C because the C contained in the harvested biomass was taken out of the biogeochemical C cycle.)

Luo et al. (2009) examination of plant-soil responses under warmer temperature conditions did not include consideration of the direct relationship between CO_2 concentrations and plant growth. Increased CO_2 concentrations directly stimulate photosynthesis in C_3 plants. Experiments on plant-soil responses under coupled conditions of warmer temperature and

increased CO_2 concentrations have shown mixed results as to which functional type is favored. Pendall et al. (2010) observed increased C_4 biomass in Australian temperate grasslands subject to 2 °C warming and 550ppm free-air CO_2 enrichment over 6 years. Compared to control plots with ambient CO_2 and temperature, C_4 plots exhibited positive growth, more labile C, faster decomposition rates, and no change in SOC storage. C_3 plots did not change in these factors relative to control plots. These results confirmed that soil respiration by microbes may be enhanced by increased deposition of soil organic matter (an effect called "priming") and that this effect may have partially offset the increase of SOC by NPP (Pendall et al., 2010). The stability of SOC stocks observed in northern China and Tibet may partly be explained by this enhancement in respiration.

Microbial decomposition and SOC

The C cycle depends heavily on the decomposition of organic matter by microorganisms. Climate forces affect the five factors that control microbial decomposition rates: physical contact by microbes to organic matter clustered in soil aggregates or hydrophobic humic matter, chemical adsorption/desorption of organic matter to mineral surfaces that prevent decomposition, the solubility of C and extracellular enzymes, oxygen supply, and microbial kinetics.

Modeling and lab based experiments have led to the general conclusion that warming directly stimulates microbial activity, but it is not certain whether microbial decomposition of recalcitrant C (Figure 5) follows the same rule. A study of the microbial populations in the experiment by Luo et al. (2009) showed that they did not shift towards those better at decomposing recalcitrant C despite the shift towards more C_4 plants. This preference towards labile C degradation may have enhanced plant growth since nitrogen bound to labile C was made

more available. Therefore, recalcitrant C pools may remain largely stable under climate warming (Zhou et al., 2012). The increase in labile C pools under warmed and CO_2 enriched plots of C_4 plants in Pendall et al. (2010) may have experienced similar microbial community dynamics thereby increasing soil decomposition.

Higher temperatures may initially intensify soil respiration and then decrease with time. This trend may occur because once labile C leaves the soil recalcitrant C may not substitute into the microbial diet (Eliassen et al., 2005; Luo et al., 2001; Melillo et al., 2001; Rustad et al., 2001). Alternatively, microbes may have adapted to increased temperatures and returned to a starting metabolic rate (Davidson and Janssens, 2006). Zhou et al. (2012) confirmed this theory with their finding that microbes acclimated to the warming treatment after eight years.

A recent meta-analysis on the direct impact of increased CO_2 on soil microbes has found a significant 16.5% increase in decomposition rates. Whether this is true across all ecosystems or not is unknown (Figure 7; Van Groenigen et al., 2014). The amount of time C spends (the residence time) in soil decreased by 2.4 years under increased atmospheric CO_2, likely because the priming effect can allow microbes to decompose organic matter that would not normally be decomposed without increased plant litter. Priming may be widespread and prolonged under increased atmospheric CO_2. Increased CO_2 also increased microbial activity because plant water use efficiency increased, thereby increasing the amount of water in the soil.

Modeling feedback responses:

Given the lack of comprehensive historical data on SOC stocks, modeling studies provide the best picture of changes to SOC stocks under various experimental parameters. Common C cycle models, however, are missing some factors that field experiments have determined as

having important roles in global SOC cycling. For example, microbial decomposition factors are overly simplified in that they are correlated only with temperature and water content and not CO_2 or community feedback responses (Van Groenigen et al. 2014; Zhou et al., 2012; Bardgett et al., 2008). Conventional climate model projections also do not consider how microbial biomass and extracellular enzymes convert SOC to dissolved organic carbon (DOC), a critical process in soil respiration. One 30-year model incorporating these factors and microbial carbon-use efficiency (CUE; the uptake of C by microbes to increase biomass) showed more specific effects of warming temperature than conventional models. CUE declines led to microbial biomass declines, followed by soil respiration declines after initial increases. Conventional models predicted decreases in SOC stocks with warmer temperatures while this model predicted the opposite. If microbes acclimated to increased temperature, CUE would be less sensitive to temperature, and thus more C would be taken up by microbes to increase biomass. Putting these conditions into this microbial-enzyme model caused SOC decomposition to increase (Table 1; Allison et al., 2010).

Another parameter often ignored in modeling is land use change. In one global ecosystem model land use and climate change parameters were manipulated to estimate regional SOC and biomass C changes from 1901 to 2002. This "Organizing Carbon and Hydrology In Dynamic EcosystEms- Land Use Change" model (ORCHIDEE-LUC; Krinner et al., 2005) showed that soils experience a negative change in C stock under combined effects of climate, atmospheric CO_2 concentrations, and land use change (Eglin et al., 2010). This result differs from those simulated by 11 models of an international model comparison project called "Coupled Climate Carbon Cycle Model Intercomparison Project" (C4MIP) which did not incorporate land use change factors (Friedlingstein et al., 2006). Another model coupled with ORCHIDEE-LUC to

consider land use change effects on SOC from year 2000 to 2099 predicted SOC increases to a global total of 0.35 PgC Mkm^{-2}, with the greatest increase projected to occur in the region of the former Soviet Union. The greatest decrease was projected in Africa and South America due to increasing deforestation of tropical forests (Eglin et al., 2010).

A telling clue to the level of uncertainty in soil C modeling is in the global and regional projections of SOC change. The C4MIP models predict anywhere between -45.8 PgC to 310 PgC in global SOC change by year 2100 (Figure 8). Two models projected negative trends in global SOC stocks and tropical and temperate region C stocks. In these three areas of consideration, the other 9 models predict a wide spread of change, especially in the global C stock. The models agree the most in boreal regions.

Large uncertainties arise even in comparisons of models that consider how changing climate may affect vegetation, biogeochemical, and hydrologic cycles. The range in global SOC stock change in one such comparison of Dynamic Global Vegetation (DGV) models was between 169 PgC and -58 PgC. Wide variations are also seen between models of tropical, temperate and boreal regions. The C4MIP and DGV models show the greatest differences in projections of SOC stocks in tropical regions (Eglin et al., 2010).

Attempts have been made to calibrate models to empirical evidence. Xu et al. (2011) divided real soil samples into the theoretical SOC pools with different turnover rates found in the popular Rothamsted Carbon (RothC) model. The RothC model predicts effects of climate or land use change on SOC with consideration of types of plant matter, microbial biomass, and humus. The authors found that only some pools correlated strongly between measured and modeled values, likely because the measured pools reflect the subtle conditions in the actual environment, and thus the SOC content, better than the modeled pool. The newly calibrated model predicted a

2-6% decrease in SOC in temperate Irish grasslands over 40 years (Xu et al., 2011).

Conclusion:

Given the relative lack of field data, especially those recorded over long periods of time, model projections are valuable for understanding soil C cycling dynamics. However, there is uncertainty within both field data collection/analysis and modeling parameterization/analysis. For example, field results have shown that NPP may be more sensitive to warming than soil respiration (Luo et al. 2009; Janssens et al., 2001). Laboratory tests and models had previously led to assumptions of the opposite (Davidson and Janssens, 2006; Friedlingstein et al., 2006; Cox et al., 2000). Field results may offer more accurate basis for answering some questions on SOC dynamics and climate change, but lack of standardized sampling methods, incomplete historical background data, and reliance on other premature assumptions may affect analysis of field results. Xu et al. (2011) normalized modeling tests with field evidence in order to reduce such uncertainties. More such work should be done.

Plant production has an important role in the C cycle as a bridge between the atmosphere and soil. It is encouraging that several field experiments show that under warming conditions soils do not become a C source to the environment due to increased NPP, particularly with removal of above-ground plant matter such as during harvest or grazing (Luo et al., 2009; Yang et al., 2009). How climate change impacts the infrastructure that supports such agricultural land use practices (e.g. harvesting, grazing, fertilization) is important to monitor for effects on SOC. Development of cost effective methods of long-term sequestration of C in soils would benefit the agricultural industry through improved soil fertility and structure while potentially reducing the impact of climate warming by greenhouse gases.

The implications of plant communities shifting towards C_4 dominance are unclear but vital to future SOC stock and microbial community dynamics. Plant community impacts on SOC have already been studied extensively so better understanding of microbial community responses to climate warming and consideration of such responses in carbon-climate modeling studies is needed (Zhou et al., 2012; Allison et al., 2010). A correlation exists between decreased soil respiration sensitivity and altered microbial community composition and structure. Previously, the availability of labile C was thought to have a larger role than microbial community composition in the decreased soil respiration sensitivity (Zhou et al., 2010). Further advancements in metagenomic research on the mechanics of this relationship may reveal more about how microbes affect plant growth under climate warming.

Field tests have shown that historical SOC density has a positive correlation with SOC change over time (Yang et al., 2010, Holmes et al., 2006). More importantly, historical land use has been shown to be a strong indicator of later SOC stock changes. These cases warrant the need for consideration of land use change parameters in carbon-climate models. The ORCHIDEE-LUC model included climate, atmospheric CO_2 concentrations, and land use change effects and showed markedly different results from others models without land use change considerations in its projections of historical SOC stock changes (Eglin et al., 2010). The model structure and parameters that give rise to these differences are riddled with uncertainty themselves (e.g. the temperature sensitivity of labile versus recalcitrant C, changes in agricultural practices).

Furthermore, uncertainty lies in major events that typically occur in spans of decades such as fires, insect outbreaks, droughts, and successional changes in vegetation. Climate change is expected to increase the severity and frequency of these events. How do these events currently

affect the global SOC pool and how will their effects change under a warmer global climate? This is a difficult question to answer because how the climate will change with increased greenhouse gases is highly variable and uncertain, let alone the effect the climate will have on land use change or other factors impacting SOC. Researchers have observed or predicted conflicting outcomes in changing C cycling components. However, decadal span rare events and other uncertainties still must be considered in the context of long-term global SOC change and incorporated into model projections.
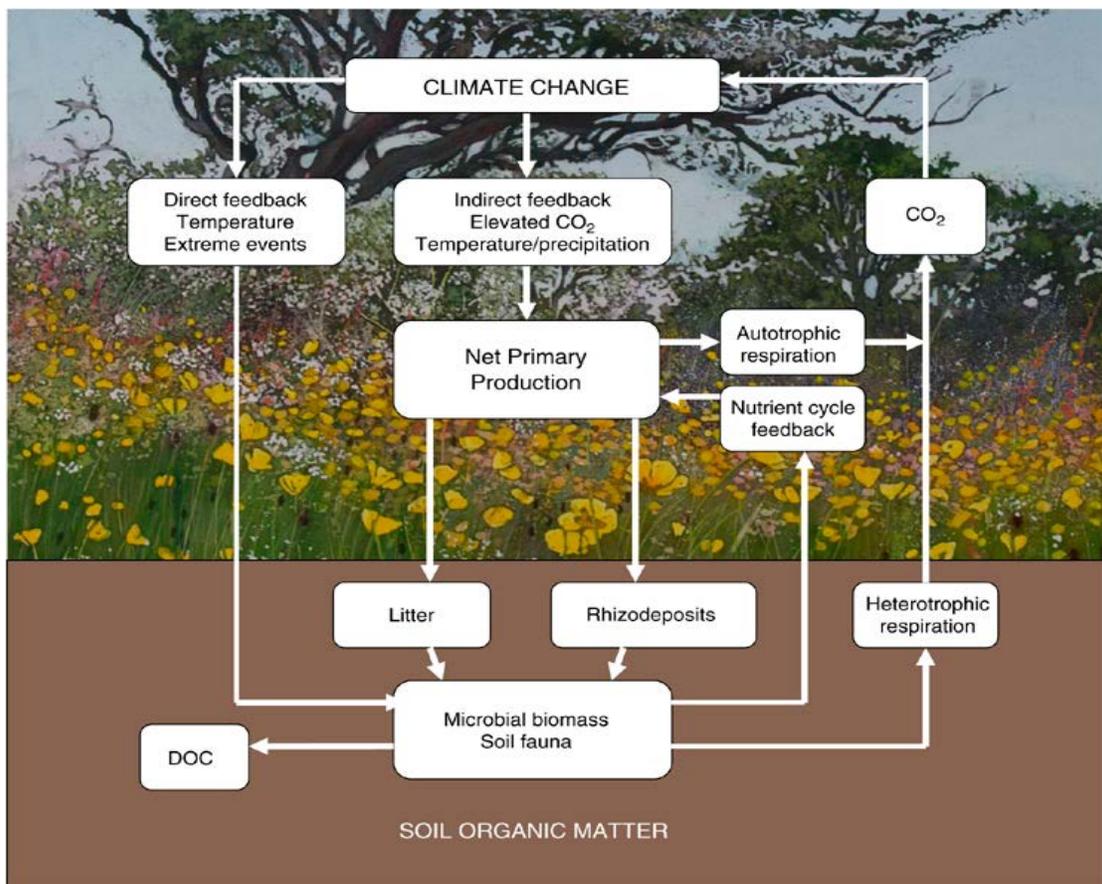

Figure 1: Climate change affects atmospheric CO₂ and SOC via complex direct and indirect mechanisms. Net primary production (plant growth) is a prominent factor in C deposition in soils, via plant litter (e.g. roots, leaves, stems) and C deposits to the rhizosphere (rhizodeposits). C leaves the soil via heterotrophic respiration and leaching of dissolved organic carbon (DOC; Bardjett et al., 2008)
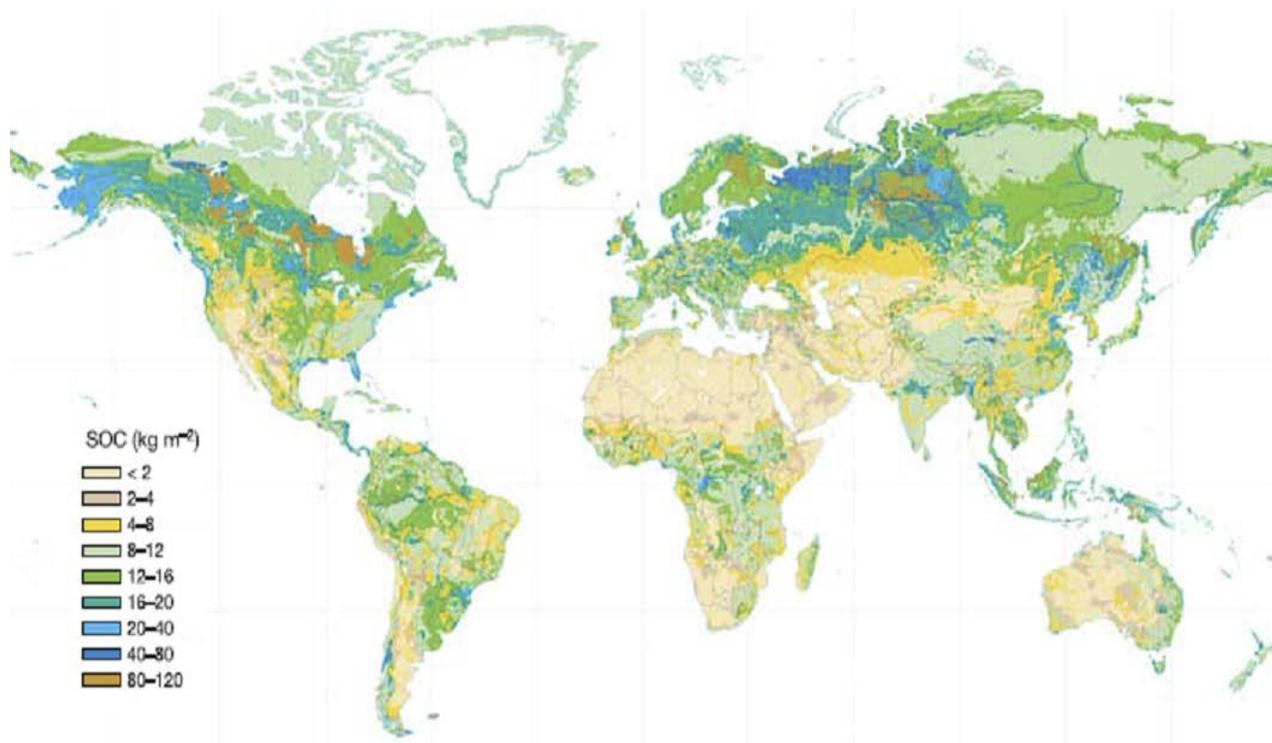
Figure 2: Global distribution of SOC stocks. Arctic permafrost regions have the most SOC in the world and are most apparent as the largely blue northern areas with patches of brown. Tropical forests (light blue/green areas of central Africa and South America) have the second largest global SOC stocks. Temperate grasslands fall within 20-50 degree latitudes and gnerally contain between 8-16 kr m^{-2} SOC (after Davidson and Janssens, 2006).
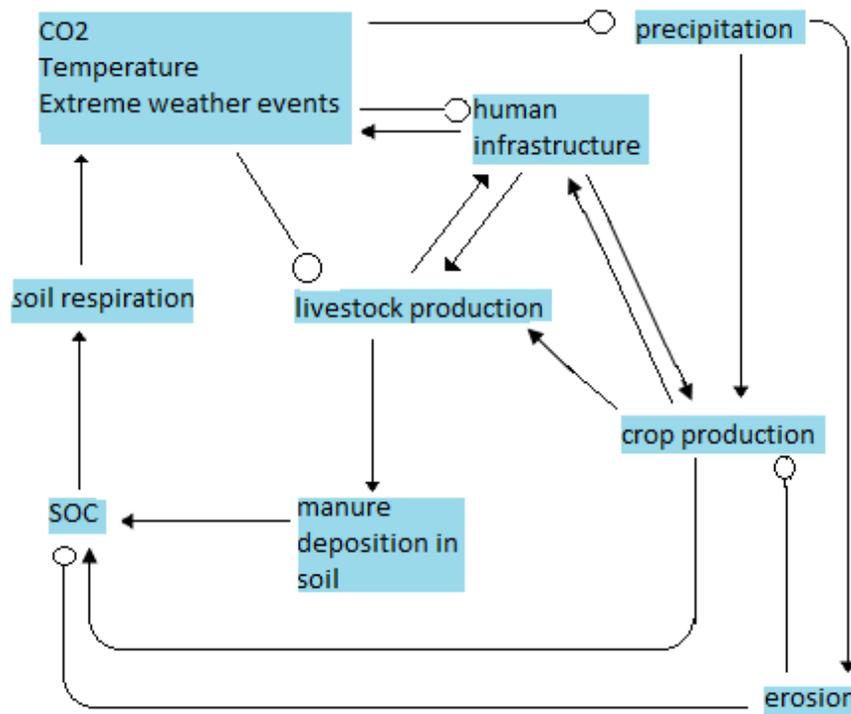
Figure 3: Simplified flow chart of climate change impacts on agricultural land use and SOC. The impacts of climate change on precipitation patterns and erosion will depend highly on location. Thus SOC stocks will also vary. Other factors relating to climate and agricultural land use change include pests/disease populations and C_3 versus C_4 plant community shifts. These factors may also variably impact SOC. For example, pests and diseases may proliferate and spread under warmer conditions, negatively impacting livestock and crop production as well as human health and infrastructure. Mass die off of crops by pests or disease may have a temporary positive effect on SOC stocks since more organic matter would be deposited into the soil. However, later NPP and the attendant organic matter deposition may decrease, leading to decreased SOC stock (C.Kim original figure).
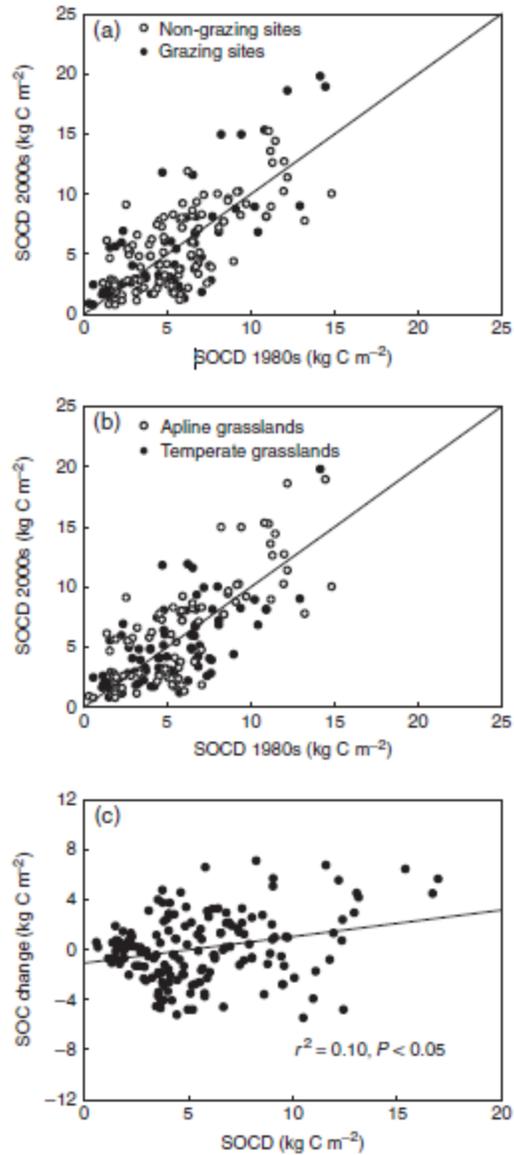
Figure 4: Comparison of SOC density (SOCD) according to (a) grazing activity, (b) grassland type, and (c) SOC change. Grazing activity and grassland type could not explain regional variation in SOC stocks in northern China because no significant change in SOCD was observed within these parameters. SOCD and SOC change have a positive correlation (Yang et al., 2010).
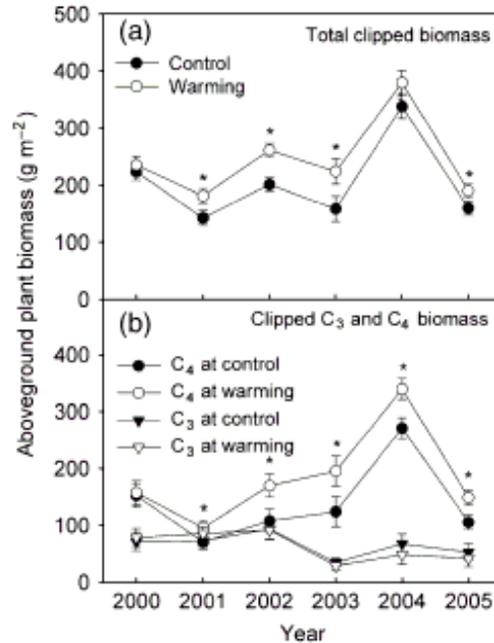
Figure 5: (a) Comparison of total clipped biomass between unwarmed control plots and warmed plots and (b) Comparison of C_3 and C_4 types of plants between unwarmed control plots and warmed plots. Warmed plots show consistently higher amounts of aboveground plant growth. C_4 came to dominate over C_3 plants after two years into the experiment. A spike in NPP in 2004 across control and experimental plots was likely due to higher than average yearly precipitation. Precipitation in 2005 was much lower than average and may explain the drop in plant biomass across all plots (Luo et al., 2009).
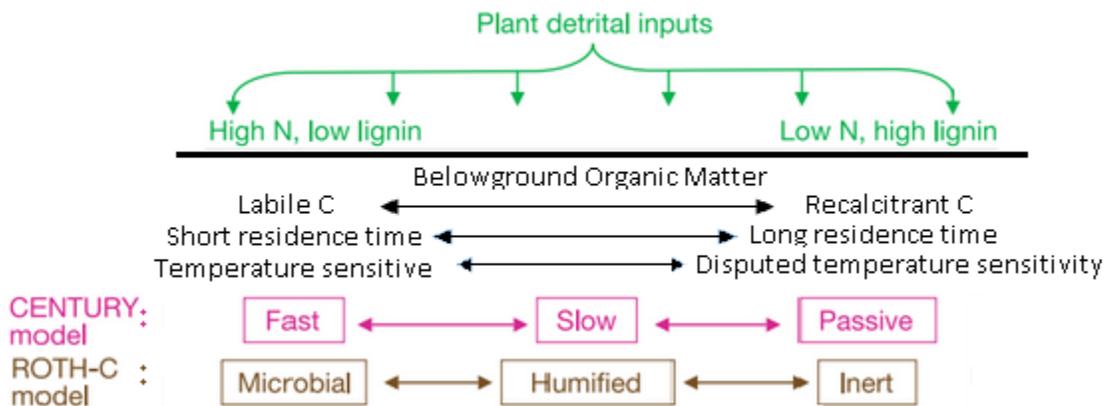

Figure 6: Range of categories of SOC and their properties. High nitrogen (N), low lignin detritus associated with C_3 plants decomposes into labile C. This C falls in the "Fast" and the "Microbial" labeled categories in the CENTURY and ROTH-C models, respectively. At the other end of the spectrum, low N, high lignin litter is associated with C_4 plants which decomposes into "Passive" and "Inert" recalcitrant C in the CENTURY and ROTH-C models, respectively (after Davidson and Janssens, 2006).

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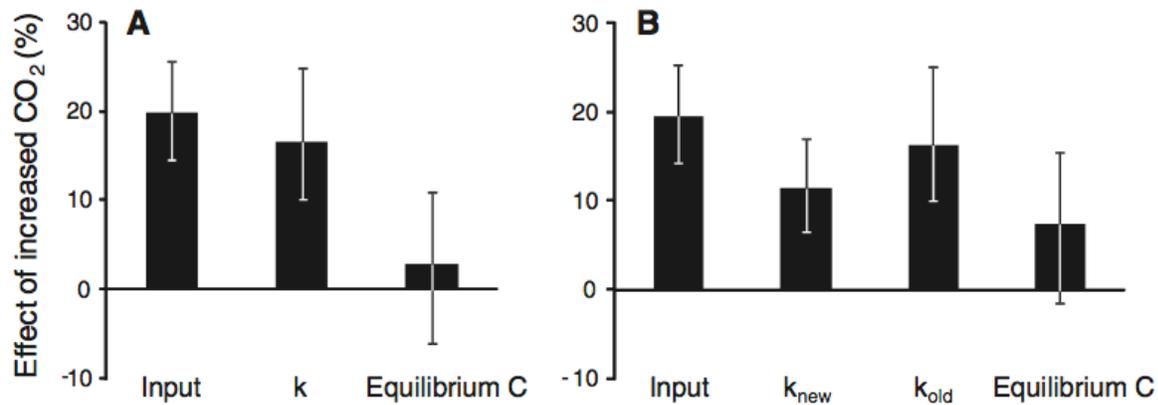
Figure 7: Effect of increased CO_2 on soil C input, decomposition and release (k), and projected equilibrium C based on a one-pool soil C model (A) and a two-pool soil C model (B) with 95% confidence error bars.

Scenario*	30 yr change in SOC pool size (%)
Control	0
CUE varies	+1
CUE acclimates	−16
CUE acclimates + enzyme acclimation	+3

Table 1: Comparison of 30-year changes in SOC pool size of a microbial-enzyme model study under different scenarios. Slight increases in SOC are predicted when CUE declines with increasing temperature (when CUE varies) because microbial growth is reduced, which reduced the rate of soil respiration. When CUE acclimated soil respiration increased leading to a loss of SOC. Enzyme acclimation is shown to counter the negative change of CUE acclimation (after Allison et al., 2010).
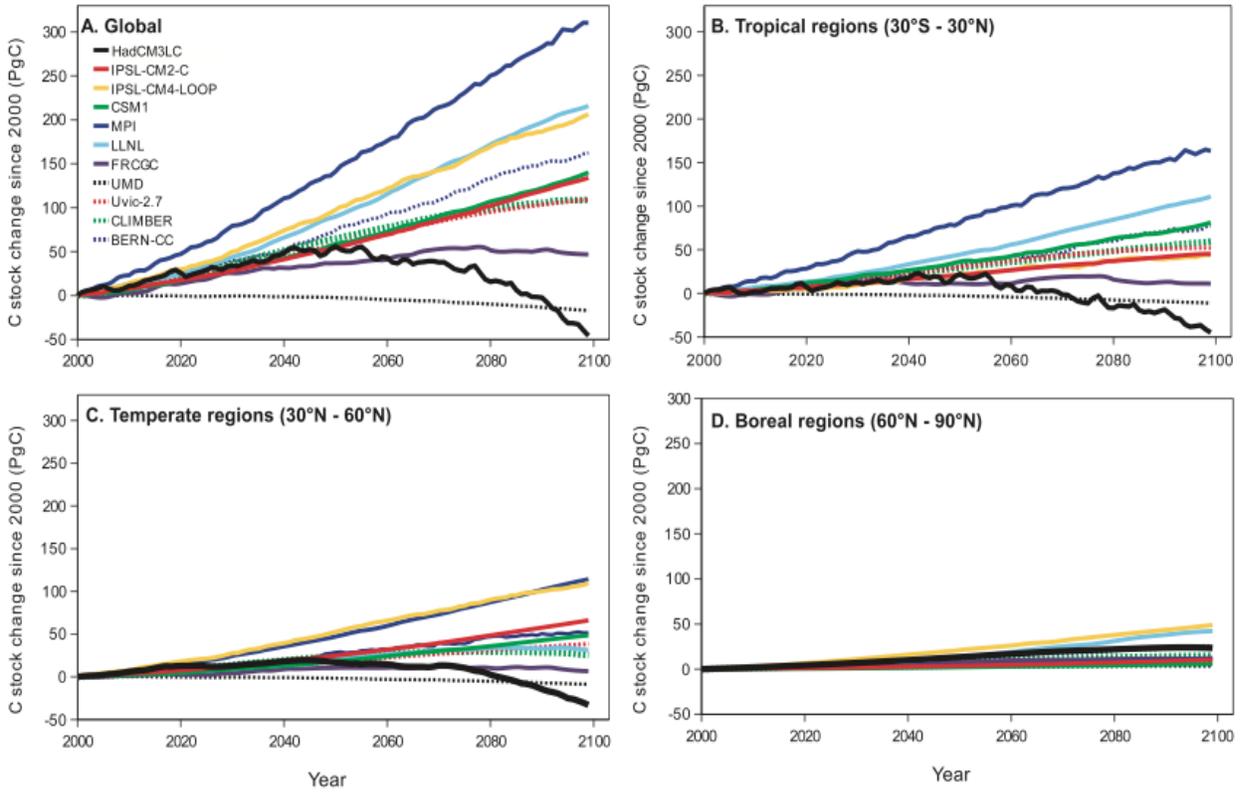
Figure 8: 11 C4MIP model projections of future global and regional SOC stocks.
These models start with known records of global and regional SOC stocks but diverge greatly with time. Most models assume NPP will increase with increases in atmospheric CO_2 and therefore project a positive change in SOC. (Eglin et al., 2010; Friedlingstein et al., 2006).

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