

**The Role of Soil CO₂ Efflux in the Global Carbon Cycle:
An Evaluation of Importance and Controls**

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Abstract

The global carbon cycle includes biotic and abiotic processes that shape and reshape the face of the Earth. Through a delicate balancing of incoming fluxes of carbon (e.g. photosynthesis) and corresponding outgoing fluxes (e.g. respiration), a dynamic equilibrium has been naturally established for terrestrial systems. In the face of global temperature increases and elevating atmospheric CO₂, this balance is becoming destabilized. In order to assess the future state of the biosphere, it is necessary to monitor rates of carbon fluxes. One important and easily measured flux is soil respiration, or soil CO₂ efflux. This flux is anticipated to be the component of the carbon budget most sensitive to warming and most likely to see prolonged impacts on the order of centuries. Understanding the controls on this flux of carbon will be important in approaching the issue of future global carbon balance. Soil temperature produces direct fluctuations in rates of soil CO₂ efflux, with effects visible over short as well as long time frames; precipitation, soil moisture, and soil nutrient status are responsible for seasonal and interannual variability in these rates. Additional considerations must be given to environmental aspects, such as topography as well as the biotic community structure in order to encompass a wide range of heterogeneity. Issues of scaling from site-level observations to global predictions are substantial, but further improvements in the available technology utilized in both measurement and analysis of soil CO₂ efflux, as well as the inclusion of more empirical data from unique ecosystems, may lead to a better understanding of soil carbon response to environmental change.

Table of Contents

List of Figures and Tables	4
Introduction	5
The Carbon Cycle	5
Climate Change	10
Monitoring the Carbon Budget	17
<i>Eddy Covariance</i>	18
<i>Soil CO₂ Measurements</i>	21
The Nitrogen Cycle	24
Controls on Soil CO₂ Efflux	28
Temperature	28
Soil Moisture and Precipitation	32
Soil Characteristics	41
Biota	45
<i>Microbes</i>	48
<i>Vegetation</i>	51
Topography	55
Soil CO₂ Efflux: The Need for a New Perspective	60
Scale of Observation	64
<i>Plant-level Perspective</i>	64
<i>Site-level Perspective</i>	66
<i>Watershed-level Perspective</i>	67
<i>Global Perspective</i>	69
<i>Gaining Perspective on Soil CO₂ Efflux</i>	70
Modeling the Carbon Cycle	71
Future Considerations	74
Conclusion	78
References	80
Acknowledgements	89

List of Figures and Tables

Figure 1: Carbon Cycle	6
Figure 2: Trends in Climate Warming, 1900-2009	11
Figure 3: Eddy Covariance Apparatus	19
Figure 4: Nitrogen Cycle	25
Figure 5: Interaction of Carbon and Nitrogen Cycles	27
Figure 6: Seasonal Variation of Temperature and Soil CO ₂ Efflux	29
Figure 7: Relationships among Temperature, Soil Moisture, and SCE	32
Figure 8: Diurnal Hysteresis	36
Figure 9: Controls on Soil Carbon Stocks	59
Figure 10: Predicted Changes in Mean Annual Precipitation	62
Figure 11: AmeriFlux Network	76
Figure 12: Interaction of Controls on Soil CO ₂ Efflux	79

Introduction

The essential component to life on Earth, carbon is one of the most heavily discussed topics in environmental research. Carbon represents the basic building block of all biological systems and as such warrants much investigation. In general, carbon cycling across the atmospheric-terrestrial interface is largely understood. However, it is the changes in the size of carbon pools and the magnitude of the transfers among them that is of interest. Each aspect of the carbon cycle has demonstrated, in essence, a form of dynamic equilibrium, defined by frequent though gradual changes in the composition of carbon pools; however, in the face of rapidly approaching climate change, this trend of change and subsequent environmental adaptation is unlikely to be maintained. Only through the development of a more thorough knowledge of the global carbon budget and its components can the fate of the biosphere be understood.

The Carbon Cycle

Figure 1 demonstrates a simplified version of the terrestrial carbon cycle. Representing the major pools and fluxes associated with the global aggregate land surface, this diagram is seen in one form or another across a wide range of textbooks and scientific literature. What is important to take away from this diagram are the relative sizes both of carbon pools (atmosphere, vegetation, and soil) and of the fluxes between pairs of these pools. It is generally accepted that carbon residing in soils constitutes the largest reservoir of active carbon linked to terrestrial processes, with estimates ranging from 1550 Pg C (Raich and Potter, 1995; Batjes, 1996) to 2300 Pg C (Davidson and Janssens, 2006). In contrast, estimates of the atmospheric carbon pool suggest values of

approximately 750 Pg C (Schlesinger, 1997), representing only between 33-50% of the total carbon retained within soils. Living vegetation also constitutes a relevant proportion of the global carbon budget, though this biomass amounts to only about 50% of even the most conservative estimates of total soil carbon (Schlesinger, 1997). As such, vegetation

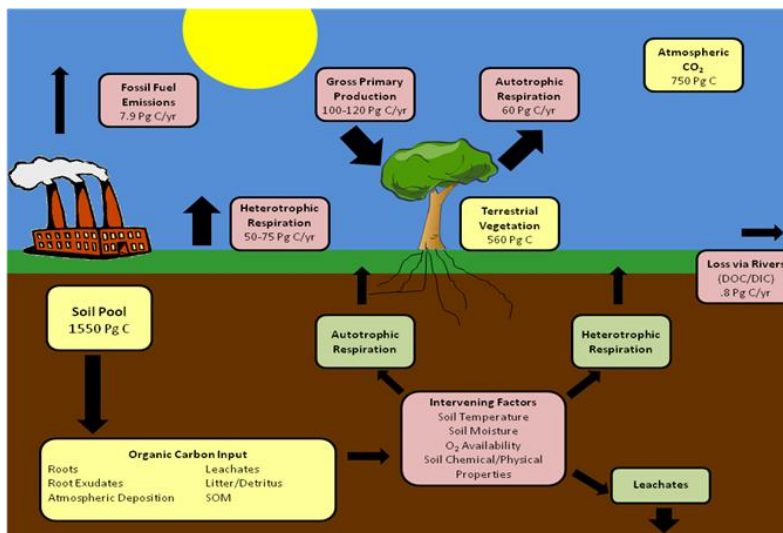


Figure 1: Terrestrial carbon cycle, including belowground components; adapted from Schlesinger (1997) and Anderson (1973).

plays a more minor role in carbon storage, though it is the primary vehicle for sequestration in terrestrial systems. Regardless of exact dimension, each of these pools is critical to the functioning of terrestrial ecosystems and

must be considered carefully. For the most part, the size of these pools is approximately static from year to year, though decadal and century-long time frames may allow for considerable variability in the face of transitioning climates and changing landscapes. Operating under the assumption that interannual variation in pool size is limited, however, understanding the principles governing fluxes between the pools becomes significant.

Primary productivity is the dominant biological means by which carbon is sequestered in terrestrial systems. Measured in terms of gross primary productivity (GPP), it is the total amount of CO₂ removed from the atmospheric pool annually and incorporated into living systems. Estimates of average annual GPP range from 100-120

Pg C/yr for the biosphere as a whole (Box, 1978; Bolin, 1983; Houghton and Woodwell, 1989). This flux represents the largest single-pathway flow of carbon within the terrestrial cycle and is typically thought to be solely derivative of atmospheric CO₂; though this assumption is strong, plants are capable of acquiring carbon, both in organic and inorganic forms, through root uptake (Jassal et al., 2004). Despite this capability, this mode of sequestration provides carbon to vegetation in quantities orders of magnitude less than that derived from the atmosphere and thus is often considered negligible when quantifying flow of carbon into vegetative pools. It is important to note that measurements of GPP only consider the total amount of carbon taken up by a landscape; there is no inclusion of carbon losses due to respiration, biomass removal, or death. In order to conceptualize total system carbon flux, researchers often consider the positive annual carbon gain for plants in a more collective term rather than separately identifying GPP and plant respiration. Net primary productivity (NPP) represents this total accumulation of biomass by autotrophs (i.e. GPP) less whole-plant respirative losses, providing a more succinct idea of net carbon change by autotrophs.

Ecosystem respiration, collectively produced by autotrophic and heterotrophic biota, is the largest vector of carbon loss from the biosphere annually. Second in size of flux only to GPP (Yuste et al., 2004), respiration is a major factor in determining terrestrial carbon balance. Total ecosystem respiration is defined as the combination of autotrophic and heterotrophic respiration from both aboveground and belowground sources. Belowground respiration is typically considered collectively and includes both heterotrophic respiration, resulting in large part from the decomposition of soil organic matter by microbial communities, as well as belowground autotrophic respiration from

roots. Estimates for annual global soil respiration range between 50-75 Pg C/yr (Schlesinger, 1977; Raich and Schlesinger, 1992; Schimel et al., 1996). As aboveground ecosystem respiration is difficult to measure independent from soil CO₂ release, estimates of global aboveground respiration tend to reflect the disparity between the more readily quantifiable fluxes of GPP and soil respiration, and are considered to be ~60 Pg C/yr (Schlesinger, 1997).

Comparing the average productivity of an environment with its annual respiration rate can be useful in understanding the carbon dynamics of the area. In particular, identifying net carbon gains (where NPP > heterotrophic respiration) or net losses (where NPP < heterotrophic respiration) will illustrate whether a system is operating as a net sink or net source of carbon, respectively. This distinction is critical to interpreting the growth of a system and will prove to be a key consideration in monitoring terrestrial environments in coming decades as climate change threatens to alter carbon relations on an expansive scale.

Global fluxes of NPP and soil respiration are governed by a variety of environmental and resource gradients. Where productivity is concerned, vegetation type, air temperature, soil moisture, and nutrient availability represent the main forces determining carbon sequestration (Janssens et al., 2001). These factors are also vital to recruitment and establishment success (Weltzin et al., 2003), both of which are critical to the maintenance of ecosystem productivity. Though some local variability exists concerning ambient concentration of CO₂, it is unclear whether its impact on productivity is significant in calculations of NPP. Some variability is inevitable as a result of canopy formation, especially in situations demonstrating understory and overstory layers;

however, where a whole-system or global perspective is sought, the atmosphere is considered nearly homogeneous, and thus little inter-site variability is anticipated in growing conditions. In light of changing CO₂ concentration, a distinct response is expected between C₃- and C₄-dominated landscapes, with C₃ species anticipated to increase in total GPP to a much greater extent than C₄ species (Ehleringer et al., 1991). In the case of soil respiration, the magnitude of flux is dependent largely on soil temperature, soil moisture, and nutrient availability; it is unclear, however, whether increases in the ambient concentration of CO₂ in coming decades will play any significant role in directly modifying soil respirative flux, as it is anticipated to do with GPP (Schimel et al., 1995). Terrestrial systems are bound primarily by biological pathways as a means of carbon exchange with the atmosphere, in contrast to oceanic systems, which utilize biological as well as physiochemical mechanisms; heterotrophic activity is thus limited not by the concentration of CO₂ in the atmosphere, but rather the availability of soil organic matter (Falkowski et al., 2000). Impacts on rates of soil respiration seen from increased CO₂ will more likely be attributable to increases in soil and air temperature than in the size of the atmospheric pool. A discussion on the nature and interaction of these environmental variables and their impact on soil respiration is provided in greater detail in later sections.

Natural fluxes of carbon within terrestrial systems tend to exist in relative balance with one another in that inputs of carbon to the landscape are balanced largely by the respirative losses of both autotrophic and heterotrophic organisms. Though fluctuation invariably exists, pronounced shifts do not tend to occur swiftly, allowing the environment the capacity to adapt to changes, such as through dissolution in oceanic

waters or through increased sequestration in soil organic matter pools. Since the advent of the industrial revolution, however, the rate of change of the global climate has been substantially high and has begun to demonstrate its impact on the biosphere. Largely induced by human activities, introduction of an additional significant carbon flux resulting from the consumption of fossil fuels has greatly unbalanced the former dynamic equilibrium of the carbon budget. It is estimated that annual emissions of CO₂ are on the order of 7.9 Pg C/yr (Raupach et al., 2007). In comparison to relative totals contributed by soil respiration and NPP, this new flux represents only about 10% of the carbon associated with each of the established fluxes (Post et al., 1990). Nevertheless, continuing input due to human usage without a compensating removal either by sequestration within terrestrial and aquatic systems or through sediment burial has created an unaccounted surplus of CO₂ in the atmosphere. The amplified greenhouse effect of elevated CO₂ has begun to, and is expected to continue to, promote warming of air and soil temperatures, a fact which may lead to drastically altered landscapes and novel feedbacks for the carbon cycle in the next century.

Climate Change

As ambient concentrations of carbon within the atmosphere increase, a response is anticipated for both terrestrial systems as well as global climate. This phenomenon represents an entirely new paradigm on which scientific thought is based. Providing the foundation for many relevant environmental studies within the past decade, climate change has come to shape both the approach to and analysis of scientific research. Though it is often described by the term global warming, this mild misnomer does not do

justice to the broader environmental responses that are expected within the next century.

By the year 2100, it

is anticipated that

mean global

temperature will

have increased 1.1-

6.4°C (IPCC, 2007).

However, a shift in

temperature regime

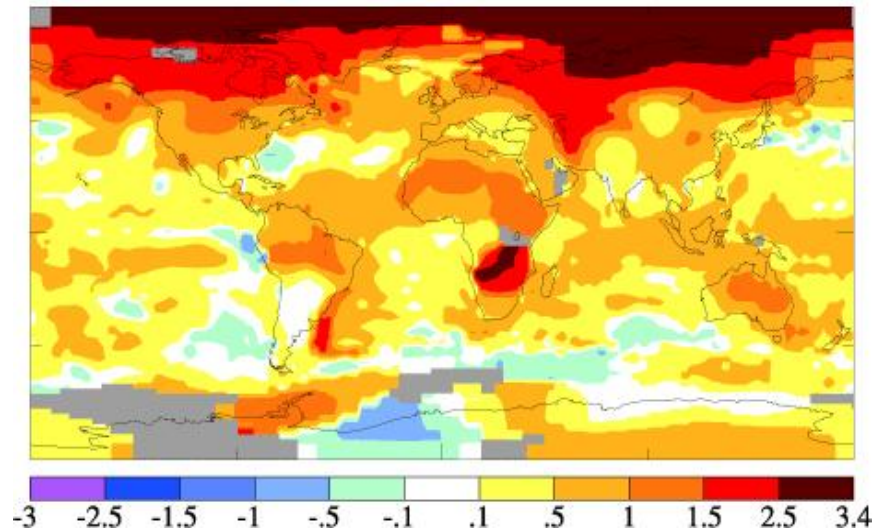


Figure 2: Trend in global temperature change, 1900-2009; Source <http://geology.com>

is only one aspect of climate change that must be considered. Effects are predicted to extend outward, generating new patterns of precipitation, altered nutrient availability, and changes in the magnitude and direction of carbon fluxes for terrestrial ecosystems.

Productivity is dependent on a series of environmental and resource gradients, among them the temperature of air. Temperature is a major factor determining the success of photosynthesis within foliage. In C_3 plants, where RuBisCO is the dominant enzyme responsible for fixing carbon within plant cells, temperature changes can play a significant part in the discrimination process. RuBisCO, as its name implies, is both a carboxylase and an oxygenase, meaning that it can bind effectively with either CO_2 or O_2 . In C_3 autotrophs, this presents a challenge in that enzymatic binding with oxygen molecules inhibits carbon fixation. In order to free a RuBisCO molecule from oxygen, the plant must then undergo photorespiration, which effectively causes the organism to utilize energy in order to overcome the bond and enable the enzyme to engage in carbon fixation. Photorespiration represents a major obstacle to carbon gain in C_3 plants

(Ehleringer et al., 1991). As air temperatures increase in response to predicted climate change, the enzymatic affinity of RuBisCO for CO₂ becomes significantly less, thus increasing the probability of oxygen binding to it (Jordan and Ogren, 1984; Brooks and Farquhar, 1985). As such, increased rates of photorespiration are expected to accompany temperature rise. In C₄ plants, however, spatial separation of RuBisCO from the point of carbon fixation ensures that photorespiration is almost nonexistent within cells. There has been some suggestion that this critical difference between C₃ and C₄ plants may lead to a gradual expansion in the ranges of C₄ plants as a result of reduced competition; instances of C₄ expansion have occurred in response to similar global changes in the past (Ehleringer et al., 1991). Some research, however, has suggested that C₃ plants will in fact see an increase in overall biomass accumulation due to higher concentrations of atmospheric CO₂. FACE (Free Air Carbon dioxide Enrichment) projects, in which atmospheric carbon levels are raised to mimic anticipated change scenarios, have revealed that C₃ plants respond more significantly to higher CO₂ concentrations than do C₄ counterparts (Ehleringer et al., 1991). This is largely due to reductions in overall photorespiration, as increases in ambient (and thus internal leaf) CO₂ decrease the probability of RuBisCO binding with O₂. However, the results for these experiments are often inconclusive where ecosystem carbon gain is concerned; they do not account for the host of other environmental shifts that are expected to occur in conjunction with CO₂ increase. Temperature rise, for example, will lead to higher rates of evapotranspiration and may more heavily impact areas predicted to encounter increased frequency and duration of drought in the future. As C₄ plants exhibit noticeably higher water-use efficiencies than C₃ individuals (Sinclair et al., 1984), water stress may become a limiting

factor in the ability of plants to adequately sequester carbon and limit the extent of biomass increase.

As water availability is critical to the magnitude of the fluxes of both NPP and soil respiration, understanding trends in precipitation and their expected modification by climate change becomes essential. According to Weltzin et al. (2003), anticipated increases in mean annual precipitation are expected for the tropics and midlatitudes, whereas the subtropics are likely to see a decrease in rainfall. Globally, precipitation is predicted to increase by an average of 7% over the next century (Weltzin et al., 2003), with an anticipated increase of 2-3% for every degree (C) increase in surface temperature (Andrews et al., 2010). Should this prediction prove to be true, the consequences for both productivity and heterotrophic respiration could be tremendous. In terms of vegetation, increases in mean annual precipitation are correlated directly with increases in NPP (Hanson and Weltzin, 2000); however, elevated precipitation also correlates positively with soil respiration (Riveros-Iregui et al., 2007). Quantifying the change in both fluxes is difficult given current level of understanding of the variables involved, leading some to speculate on the ability of the global environment to balance these new vectors of biosphere inputs and outputs. What may be of more interest to researchers at this point is the nature of precipitation events in response to climate change. The intensity of rainfall is anticipated to increase (Weltzin et al., 2003), meaning more precipitation will fall over a fewer number of days. Inevitably, changes in the severity of these events will alter the proportion of water infiltrating soils. In high intensity events, heavier and more rapid rainfall will likely result in increased overland flow. In effect, soil water recharge may be limited despite overall increases in mean annual precipitation. Increased runoff will also

lead to higher rates of erosion and removal of topsoil from watersheds, which could negatively impact soil respiration rates through limited nutrient availability. In contrast, areas currently experiencing drought are anticipated to see more prolonged and more severe drought in the future (Weltzin et al., 2003). In such cases, soil respiration rates may be greatly depressed (Borken et al., 1999). The fate of terrestrial systems in response to shifting precipitation patterns is poorly understood and will require further empirical investigation.

Linked intimately to both NPP and soil respiration, the nutrient status of the soil is a major determinant in the growth and functioning capacity of a region. In particular, zones characterized by high mineralization rates are associated with high total biomass. In the face of climate change, mineralization rates are expected to increase as a result of increased temperature (Jin et al., 2008). Higher rates of respiration coincide with shorter turnover times and increased availability of key nutrients. In the case of terrestrial systems, which are characteristically N-limited, accelerated rates of nitrogen mineralization can increase both the productivity of vegetation and the metabolic activity of microbial communities.

Climate change scenarios also predict an increase in the demand for key nutrients (van Veen et al., 1991); initial increases in N may result in rapid yet unstable consumption of soil organic matter that would lead to an overall reduction in soil respiration rates with time (Jin et al., 2008). This situation raises questions about the sensitivity of soil communities, with primary focus being given to subsurface soils. Though categorized by their low mineralization rates and overall stable moisture and temperature regimes, deep soil zones are highly sensitive to perturbation and as such may

become centers of dramatically increased respiration rates in the near future. It is worth noting that, despite increases in mineralization rates, N-limitations may become more prevalent (Hyvonen et al., 2007; Reich et al. 2006) if utilization rates of available nitrogen are accelerated in response to higher ambient concentrations.

In light of the numerous changes that are expected to accompany global climate change as it unfolds over the next 100 years or more, there is some suggestion as to the limited ability of the biosphere to cope. A large, unutilized capacity for carbon sequestration in terrestrial vegetation is believed by some to help compensate for CO₂ increases in the atmosphere; current values of NPP do not demonstrate saturation under present concentrations (Schimel, 1995) and may therefore increase over time as carbon becomes less limiting. Initial results from experiments fertilizing landscapes with CO₂ also seem to agree that significant increases in biomass accumulation can occur under elevated ambient concentrations (Luo et al., 2001; Melillo et al., 2002). However, after prolonged periods of fertilization, both vegetative and microbial communities demonstrate a degree of acclimation to their new growing environment, at which point continued response of these groups to elevated CO₂ becomes less pronounced (Chapin et al., 1986). In addition, ambient CO₂ is anticipated to reach levels of 800-1000ppm by the end of the century (Houghton et al., 1996), which may prove too much for the biosphere to counterbalance. This new evidence gives researchers pause, as it was once conceived that considerable biomass increases would result from elevated atmospheric carbon and thus stave off the more serious effects of temperature increase. Similar outcomes were demonstrated for nitrogen as for carbon; acclimation of terrestrial systems to nutrient

status changes in response to a climate shift was observed (Heimann and Reichstein, 2008).

Although it is unlikely that any region of the globe will entirely escape the effects of CO₂ increase and temperature rise anticipated in coming decades, there are several key regions of the globe that are expected to see greater than average modifications to the landscape. High latitude and high altitude regions are predicted to experience more severe shifts in ecosystem function than the mid-latitudes, particularly in terms of soil respiration (Schleser, 1982). High latitude environments, especially, have already begun to change in response to current rates of temperature increase. Both plant growth and establishment success have been augmented (Tape et al., 2006). As annual air and soil temperatures increase, the length of the growing season is extended, as is the time that soils are not subject to complete freezing. Additionally, as frozen soils retreat, plant community compositions are altering in response (Tape et al., 2006), with progression of timberlines northward. There is much discussion in the scientific community concerning northern latitude ecosystems and in particular the effect global warming will have on rates of soil respiration. Given that soil temperatures are characteristically low, turnover rates are significantly less than those of lower latitude systems. As these colder systems are anticipated to see the most dramatic increases in temperature, it is uncertain to what extent soil respiration will accelerate, though large amplifications in total soil CO₂ efflux are expected. At these low temperatures, even small increases can have dramatic effects on increasing the rate of soil respiration (Yuste et al., 2003). Furthermore, temperature increases are predicted to impact not only surface, but also deep soil environments, thus expanding the active heterotrophic respiration zone and compounding the issue of soil

organic matter conversion to CO₂ (Bunn et al., 2007). This enhancement of soil respiration invariably serves as a positive feedback mechanism for global warming.

Given the series of complications quickly mounting, what can be done in the face of climate change? In truth, preventative measures at this juncture are powerless to stop the cascade of environmental impacts already revealing themselves. It now falls to the scientific community to observe and assess the changes that are currently taking place globally. By developing a greater understanding of the interactions among biotic and abiotic factors within an environment, predictions can be made as to the fate of the carbon budget. In particular, monitoring of nutrient fluxes and changes in carbon balance is necessary to develop the knowledge and background required to comprehend precise ecosystem functions. Though countless techniques have been employed over the years to describe both productivity (NPP) and soil respiration, few are broad enough to consider implications on a global scale.

Monitoring the Carbon Budget

Here, techniques for the monitoring and assessment of carbon pools associated with the atmosphere and soils are presented. Though these methods are not necessarily representative of the carbon cycle-based literature as a whole, they do demonstrate commonly utilized strategies for understanding complex ecosystems. Where terrestrial atmospheric carbon is concerned, eddy covariance has emerged as an invaluable tool for estimating total system carbon exchange. Deployable across a wide variety of terrestrial ecosystems, this approach utilizes technological advancements and novel methodology to monitor gaseous fluxes across the terrestrial-atmospheric interface, and can account for

both net ecosystem production and total system respiration. For consideration of soil CO₂ efflux alone, a few different methods will be discussed in brief. Soil respiration chambers provide instantaneous *in situ* readings that offer accurate results for a snapshot in time. Solid-state CO₂ probes, designed to provide continuous measurements *in situ*, provide detailed information on soil CO₂ concentrations within a given area. Simulated respiration in lab settings has also been used and is helpful in attempting to isolate contributions to total soil respiration by autotrophic and heterotrophic components. Each of these methods offers a unique view on carbon fluxes and useful insight into ecosystem processes.

Eddy Covariance

Studying entire landscapes is often difficult to accomplish. Without a method to sample across the extent of the target environment, scaling up from smaller plot- or site-based measurements introduces a large possibility for error as unknown instances of heterogeneity are potentially overlooked. Where fluxes of some gaseous substances are concerned, eddy covariance provides an alternative to individual sampling methods that encompasses entire system fluxes.

Eddy covariance operates on the principle that transfers of molecules across the interface of the land surface and the atmosphere are detectable; by analyzing the covariance of vertical air mass movement and CO₂ concentrations in the air, measurements of total ecosystem exchange can be acquired (Baldocchi et al., 1988; Baldocchi, 2003). There are several benefits to employing eddy covariance as a means of assessing carbon fluxes. First, this technique is capable of providing reliable data



Figure 3: A typical eddy covariance setup – a 3-D , sonic anemometer coupled with an open-path infrared gas analyzer (IRGA) – measuring fluxes of CO₂ underneath a forest canopy; Source: <http://www.campbellsci.co.uk>

applicable over a large relative area, and can yield information on whole-system exchange. This fact enables simple detection of the status of a landscape; identifying an area as a net source or sink of carbon will prove beneficial in coming decades as climate change threatens to alter these patterns within terrestrial

environments. Second, this method enables researchers to gather observations continuously over lengthy durations on the order of years to decades (Baldocchi et al., 2001). Through long-term measurements, dynamics associated with modulating climatic conditions, such as variation in annual precipitation totals or increases in mean annual temperature, can be observed and their impact on the landscape can be quantified.

Eddy covariance, though most often employed as a tool for observing CO₂ exchange, is unique in that the same method can be applied to the study of other substances, such as water, methane, or isoprene. Each of these gases, as well as their related fluxes, has been identified as a useful consideration for terrestrial systems in the face of climate change. The ability to monitor ecosystem production and exchange of molecules beyond CO₂ may provide useful information when considering a landscape and its patterns of nutrient cycling.

This technique, however, is not without its assumptions. Due to the method of gathering carbon flux data, eddy covariance functions most reliably in areas displaying a

high degree of homogeneity. With this, there is a necessary oversight concerning site-specific activity that may affect fluxes such as NPP or respiration. In addition, when applied to terrain made complex either by topography or variability in vegetative height, systematic errors are introduced into the data (Baldocchi et al., 2003). When considered over an extended period of time, these biases compile to produce more substantial errors that must be corrected and accounted for (Montcrieff et al., 1996). As such, eddy covariance operates most reliably over landscapes that are largely flat, relatively consistent in canopy height, and have sufficient vertical turbulence to enable accurate measurements of gas flux. In the application of this technique to the study of soil respiration, it is required for flux towers to be erected below the canopy; in such scenarios, vertical flow of air is often restricted, thus preventing an adequate measurement of gas exchange by eddy covariance methods (Jassal et al., 2004). In light of this, eddy covariance is limited in its ability to separate out the individual components of a flux; aboveground and belowground respiration inputs are considered together as ecosystem respiration. To account for this, some estimates have been provided to help quantify the relative contributions of soil respiration independent of aboveground respiration. Nighttime emissions measured as upward fluxes of CO₂ by eddy covariance, typically used as a baseline measurement for total ecosystem respiration, have been considered to be 50-80% soil respiration (Buchman, 2000); however, this quantification often requires understanding the physical controls on soil respiration, which may be difficult to do particularly over complex and heterogeneous terrain. This technique might be better served in the future if it could be coupled with direct measurements of soil CO₂ efflux to allow for distinction between respiration components. As such, utilizing

effective methods for observing soil respiration will prove useful in identifying variation in total soil production independent of variation in whole ecosystem respiration.

Soil CO₂ Measurements

Ecosystem respirative flux is derived from two main sources: autotrophic respiration and heterotrophic respiration. Though estimates of NPP already consider total autotrophic respiration, including aboveground and belowground inputs, it is often difficult to adequately distinguish between sources of belowground activity (Carlyle and Ba Than, 1988). Experiments have attempted to observe root respiration directly through *in situ* root cuvette measurements (Gansert, 1994) or through lab procedures (Burton et al., 1998) in the hopes of quantifying autotrophic CO₂ without the influence of microbes; however, these methods impose a significant degree of disturbance to the soil matrix or even complete removal from the system in order to obtain data, which can alter rates of respiration in response to altered conditions. Similar attempts have been made in an effort to isolate microbial communities from soil and have met with similar issues. Removal of root biomass from soil alters its structure as well as the equilibrium of the plant-microbe-soil environment. As these inputs to total soil respiration by belowground sources are difficult to quantify separately, they are often considered jointly. Soil CO₂ efflux (SCE) collectively describes the contributions by autotrophic and heterotrophic biomass within the soil, and additionally includes inputs resulting from the dissolution of carbonate minerals. SCE is only a measurement of the emission of carbon from the soil into the atmosphere; therefore, it does not consider losses associated with leaching nor does it account for soil storage of CO₂. Though both of these overlooked components may prove

important in understanding the terrestrial carbon budget, it is the direct exchange of carbon at the soil-atmosphere interface that is of greatest interest.

Early methods of measuring soil CO₂ efflux utilized chemical strategies. Soda-lime, a mixture of ammonium hydroxide and slake lime, characteristically binds with CO₂ irreversibly (Carlyle and Ba Than, 1988). By containing soda-lime within a chamber of known diameter and creating a sealed contact point with the surface of the soil, carbon emitted from the ground is then funneled into the chamber where it reacts with the chemical compound. By simply measuring the dried weight of the chamber and soda-lime before and after application to the soil surface, an accurate estimation of SCE can be achieved (Edwards, 1982). This method, however, is only sufficient for observing fluxes on short time scales. Above a threshold of absorption, the soda-lime must be discarded so as to maintain reaction efficiency with CO₂; as determined by Carlyle and Ba Than (1988), this threshold resides around 7% absorption and suggests a great deal of material is required to achieve results. Absorption experiments such as these had durations on the order of an hour, making observation of diurnal and seasonal trends limited.

More contemporary methods of observing instantaneous measurements of SCE employ the use of sophisticated technology. Similar to the technique utilized by eddy covariance methods, IRGAs are coupled with soil chambers to monitor rates of CO₂ production from the soil. Each chamber of known volume creates a seal while in contact with the soil surface. This chamber, initially flushed with air to provide a background concentration of CO₂, is able to measure the rate at which carbon is emitted from the soil. As the concentration of carbon dioxide increases in the chamber itself, the rate of increase is fitted to an equation (typically quadratic, though linear is used as well) until a

constant rate of increase is determined (Riveros-Iregui et al., 2008). Both in this method and with the soda-lime approach, it is important to constrain measurements to a particular range of times during each day of sampling; fluctuations in SCE occur throughout the day in response to changes in temperature that must be minimized to maintain comparability between sites (Riveros-Iregui, 2007).

In an attempt to examine soil respiration over extended time periods, solid-state CO₂ probes can be integrated into a soil matrix. These probes provide the opportunity to gather continuous measurements of soil CO₂; however, there is a clear distinction between this technique and those previously described. Soil chamber measurements, for instance, sample soil CO₂ efflux, and therefore capture only the gas emitted from soil. Solid-state probes are designed to measure *in situ* concentrations of CO₂, and therefore do not give any direct indication of SCE. SCE relies on the combination of two factors: production and transport. CO₂ probes do not consider transport to the surface, which suggests that data achieved through them are not directly relatable to surface SCE measurements; however, these tools do provide the opportunity to measure within-soil migration of CO₂ by calculating vertical flux between two probes buried at different depths. The results these probes produce are also highly dependent on the depth of burial. A strong stratification exists with depth that serves as a proxy for transport efficiency of gas within the soil matrix. Deeper soils are expected to have higher overall concentrations of CO₂ as exchange with the atmosphere is more limited. Nevertheless, solid-state probes present a unique and high-frequency view on soil carbon that other methods do not.

The true significance behind studying soil CO₂ efflux is the predicted volatility of soil carbon pools in response to environmental conditions. With the array of climatic

changes that are anticipated in the next century, rates of SCE are likely to see large increases and thus promote further warming through elevated atmospheric CO₂. Highly responsive to local heterogeneity, it is difficult to assess patterns of soil respiration without a more complete understanding of the factors that control it. By employing one or more of these methods of observing soil CO₂ efflux, researchers may be able to achieve just such an understanding.

The Nitrogen Cycle

Closely linked to the activity of the carbon cycle, nitrogen (N) is a crucial element in the production and survival of terrestrial life. Not only is nitrogen responsible for the formation of compounds such as chlorophyll, which serves as the primary pigment by which carbon from the atmosphere is sequestered, it is also a necessary building block in structural material of autotrophic and heterotrophic organisms. As such, the nitrogen cycle is of critical importance to terrestrial systems and understanding the global pools and fluxes of nitrogen can provide insight into the functioning of biota within their environments.

Nitrogen is the most common gas in Earth's atmosphere, representing approximately 78% of the total volume. Although nitrogen is abundant, it exists primarily in a non-reactive form (N₂), which is not utilizable by a significant proportion of terrestrial organisms. In order for it to be sequestered and converted into inorganic forms readily taken up by both plants and microbes, it requires transformation through a process known as fixation. In soils, this feat is accomplished by a number of pathways. Two common constituents through which nitrogen is fixed are: *Nitrosomonas spp.*, a

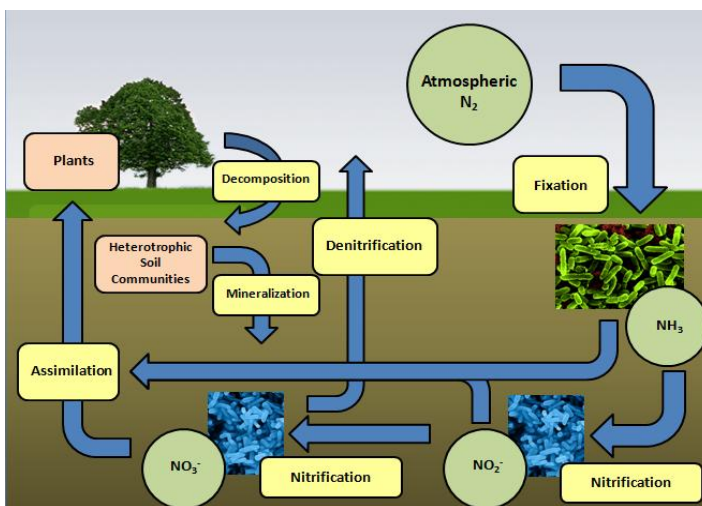


Figure 4: Nitrogen Cycle; adapted from EPA - <http://www.epa.gov/maia/html/nitrogen.html>

classification of microbacteria; and mycorrhizae, symbiotic fungal associations commonly developed with plant roots. Both of these classes of biota are able to convert N_2 into a usable form, NH_4^+

(ammonium), which is ideal for

uptake by other, non-fixing organisms. Still, alteration of nitrogen compounds can occur within soils through additional microbial pathways that allow for the conversion of ammonium into other inorganic forms (NO_2^- and NO_3^-) through a process called nitrification; NO_3^- is also readily taken up by soil organisms. Just as N can be extracted from the atmosphere and incorporated into living systems, either within tissue or within soil reservoirs, it can also be transformed from inorganic forms back into inert N_2 . Denitrification, as this step is termed, is a major focus of active research as rates and their associated controls are proving significant for areas affected heavily by anthropogenically-induced N-fertilization of soils.

In general, denitrification in soils and in coastal systems such as salt marshes is responsible for removing a large proportion of excess nitrogen incorporated into riverine effluent as a result of processes such as direct deposition or leaching from soils, to name a few (Warren et al., 1979). Recent decades have demonstrated increases in nitrogen in many terrestrial systems, largely as a result of acid deposition. Acid deposition, though a natural chemical process by which nitrogen in reactive forms is removed from the

atmosphere and incorporated into soil and aquatic systems, has seen dramatic accelerations in rates as a result of human-induced emissions of NO_x . NO_x , a generic term for numerous nitrogen and oxygen-bearing gaseous compounds, is produced by both industrial and personal consumption of fossil fuels. As a result of increased NO_x formation and thus acid deposition, terrestrial ecosystems are experiencing greater inputs of nitrate, which can promote leaching rates within soils. Despite elevations in total input to coastal marshes of nitrate and ammonium derived from these leachates, only a fraction of this increase appears in aquatic systems offshore, suggesting that these specific environments have an incredible capacity for denitrification, as well as a large potential for nitrogen uptake by vegetation, that may prevent high frequency of aquatic N-fertilization. However, recent evidence shows a significant reduction in the total land area of these systems, and thus the total area available for denitrification, over the past several decades; furthermore, in light of anticipated sea level rise in response to global temperature increase, coastal systems will become increasingly inundated, further limiting the land surface area capable of providing this ecosystem service.

Though the activity involved in the nitrogen cycle is both fascinating and complex, terrestrial ecology is forced to recognize that no system can function in isolation. It is the interconnectivity between the nitrogen and carbon cycles that helps to create a mosaic of environments on scales ranging from micro to global in size. Some overlap in these two cycles is based solely on chemical interactions and is removed from influence by organisms; however, the major links that exist between C and N are induced by biotic processes. In general, it is worth noting the significance of nitrogen in both the sequestration and respiration of CO_2 . Where autotrophic productivity is concerned,

nitrogen forms an essential building block responsible for the capturing and processing of photosynthetically-active radiation (PAR). Increases in the abundance of nitrogen within a soil matrix have been tied to increases in overall aboveground productivity (Weltzin et al., 2003). Likewise, nitrogen represents a limiting factor in soil respiration. Fertilization experiments have demonstrated that improved nitrogen availability provides a positive feedback for microbial activity (Jin et al., 2008).

The variability of C:N among different tissues, autotrophic and heterotrophic included, in terrestrial environments is indicative of the highly complex interactions

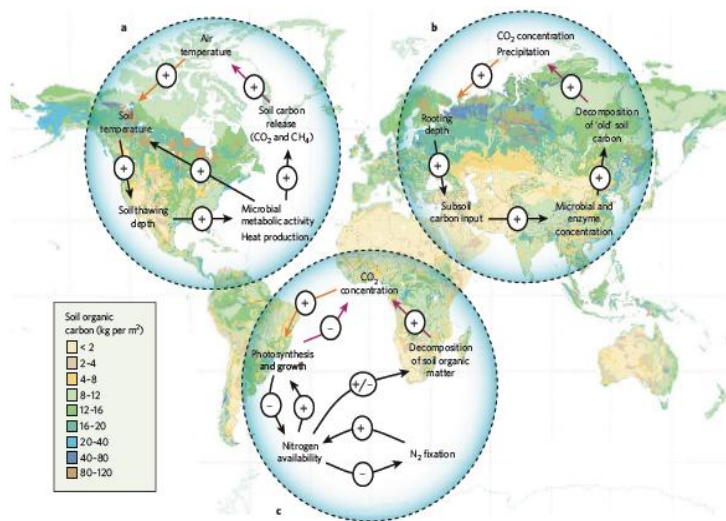


Figure 5: Interconnectivity of the carbon and nitrogen cycles in the face of predicted climate change; Source: USDA-NRCS.

between these elemental cycles. However, it is not the goal of this paper to consider the intricate relationship behind the carbon and nitrogen cycles; rather it is necessary to contemplate their interwoven nature in order to understand

responsiveness within an ecosystem. Where future dynamics are concerned, though both carbon and nitrogen are expected to see responses in turnover rates within terrestrial systems, it is the role of carbon as both a biological unit and as a direct influence on climate that brings it to the foreground of studies aimed at monitoring the development of the biosphere.

Controls on Soil CO₂ Efflux

Within a watershed, landscape characteristics can change on both spatial and temporal scales. Particularly in complex systems, the degree of variability in space and time can be quite high and can lead to the development of specialized habitats and the juxtaposition of environments that are seemingly contrasting. This certainly holds true when considering soil CO₂ efflux (SCE), a process that is ubiquitous across terrestrial ecosystems. However, it is very difficult to generalize when discussing SCE, as the determinants of the rates of CO₂ production and transport are themselves highly variable. In an effort to better understand this concept, a critical eye must be applied to a host of factors directly and indirectly associated with rates of soil respiration. Though some elements of control may demonstrate greater dominance over carbon evolution from terrestrial systems than others, it is truly the interaction among these elements that generates the most significant and often most complex influence on SCE.

Temperature

Of all the factors that have been considered to date, temperature imposes the greatest control on SCE across terrestrial systems (Dorr and Munnich, 1987; Raich and Schlesinger, 1992; Epron et al., 1999; Yuste et al., 2004; Riveros-Iregui, 2007). Serving primarily as a determinant of respiration rates, both for autotrophic and heterotrophic biomass, increases in soil and air temperature have demonstrated exponential increases in the associated CO₂ efflux (Jin et al., 2008). Figure 6 demonstrates the diurnal fluctuation of soil temperature and soil respiration; as seen, these two factors display covariance, maintaining approximate similarity throughout the sample period. When plotted against

temperature, SCE demonstrates dependency of an exponential nature. Though the exact

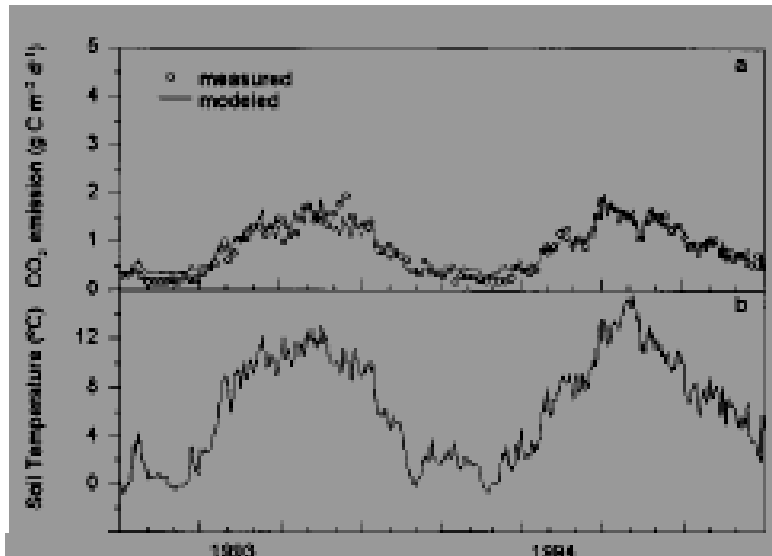


Figure 6: Seasonal changes of a) measured and modeled CO₂ emission and b) soil temperature at surface: Source: Moore (1986).

form of this curve can vary substantially across the spectrum of environments, the exponential nature of the relationship between temperature and SCE continues to hold.

Temperature also serves as a control on a number of

other properties important to consider when analyzing a soil community. For example, there exists a large degree of heterogeneity within soil horizons (Pumpanen et al., 2003); temperature means and maxima within each horizon can dictate the production of both aboveground and belowground biomass as well as determine microbial community structures within the soil (Jin et al., 2008).

It is important to note that fluctuations in temperature throughout the day can produce significant changes in rates of efflux. Diurnal variation plays a significant role in the transformation of carbon (Stenberg et al., 1995; Sprugel et al., 1995). SCE demonstrates a diurnal pattern similar in form to that of soil temperature (Riveros-Iregui et al., 2007). Increases in soil temperature produce increases in the rate of soil CO₂ efflux, provided that soil moisture is not a limiting factor. As such, daily maximum values of SCE are typically found shortly after midday; there is a slight lag in the timing of these maxima behind that of radiation due to the time necessary for heat to propagate

to deeper zones in the soil (Riveros-Iregui et al., 2007). The pattern seen on a diurnal basis can also be applied to temperature variation seasonally. As soil temperature increases toward the middle of the growing season, total SCE is seen to increase as well (Carlyle and Ba Than, 1988). It is important to note, however, that despite the control temperature imposes on rates of CO₂ efflux from the soil throughout the growing season, it is not uncommon for this factor to be superseded by other limitations to the rate of production and transport within the system; temperature effects are therefore most consistently associated with diurnal and even hourly variation (Howard and Howard, 1993; Riveros-Iregui et al., 2007).

One of the factors important when considering the specific temperature-dependency curve of a location is illustrated by its associated Q10 value. A Q10 value, simply put, describes the specific influence of an increase in soil temperature on the rate of efflux; presented as a unitless number, it states that for every increase of 10°C, the rate of efflux increases by a factor equal to the Q10 value. In the case of SCE, this Q10 value is far from constant. Research has shown that this factor decreases as temperatures increase (Yuste et al., 2003), suggesting that increases of already high soil temperatures will have a less dramatic impact on soil CO₂ evolution than similar increases of low soil temperatures. This fact is of primary importance for high latitude systems. These environments, characterized by heavy frost, prolonged snow cover, and short growing seasons, are considered to be sizeable reservoirs for soil organic matter (SOM). Given that decomposition rates are strongly depressed by low mean annual temperatures within these systems, much of the carbon that is sequestered in northern environments experiences long residence times. It is believed that predicted increases in temperature

over the next century will greatly accelerate the release of CO₂ from high latitude soils and shorten the residence time of SOM, thus exacerbating the issue of globally increasing atmospheric carbon. As Schlesinger (1977) pointed out, the annual exchange of carbon resulting from SCE amounts to 50-75 Pg C/yr while emissions due to fossil fuel consumption are only about 10% of this value (Post et al., 1990) at approximately 7.9 Pg C/yr (Raupach et al., 2007); even a small shift in the climate could increase total annual SCE in an amount on par with anthropogenic inputs, effectively doubling the total carbon entering the atmospheric pool that is unbalanced by gains in NPP or storage in SOM (Schlesinger, 1977; Raich and Schlesinger, 1992; Schimel et al., 1996).

Temperature effects are also of concern, not only for determining rates of respiration, but also for controlling rates of nutrient mineralization. Increased soil temperature can lead to an increase in the mineralization of nitrogen (Jin et al., 2008), which in turn elevates the capacity of an environment to support both autotrophic and heterotrophic life. As such, the feedback effects of accelerated N-mineralization produce an environment that not only promotes a higher rate of soil respiration, but also a subsequently higher rate of utilization of mineralized nitrogen and carbon. Furthermore, augmenting the availability of soil nutrients has been shown to increase the frequency of symbiotic interactions, such as root infection of mycorrhizae (Bowen, 1987), which could promote the growth of roots. A temperature-induced increase in mineralization rates could thus redefine nutrient status within soils and alter the biotic community structure substantially.

Though temperature is a major control of SCE in terrestrial environments, it must be stressed that temperature is not the sole factor contributing to this flux; rather it has

consistently been demonstrated to be the strongest control on rates of efflux. Interactions of this factor with other soil conditions like soil moisture and texture often dictate large portions of mass loss from the Earth. Likewise, considering variables in conjunction with temperature has increased the predictability of SCE patterns across select terrestrial systems (Raich and Schlesinger, 1992; Borken et al., 1999). Extensive research has sought to establish additional controls on SCE beyond temperature in an effort to understand function within soils more thoroughly.

Soil Moisture and Precipitation

Another major control on the rate of decomposition within soils, and thus the conversion of organic carbon into CO_2 , is the amount of water present. Typically measured in terms of soil moisture or soil water content (SWC), water acts as an essential catalyst for heterotrophic activity, promoting higher rates of soil respiration through increases in microbial biomass, as well as a driver of abiotic degradation of carbon-containing compounds. Typically, increases in the availability of water lead to higher rates of soil respiration; this generalization breaks down at very high values of soil moisture, however, as limitations in gaseous exchange

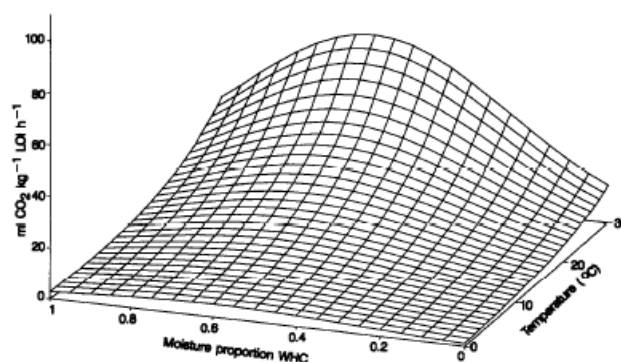


Figure 7: Interrelation among soil CO_2 efflux, soil moisture (as a proportion of water holding capacity, WHC), and temperature; Source: Howard and Howard (1993).

across the soil-atmosphere interface and across pore spaces develop, particularly concerning rates of O_2 diffusion into the soil matrix. Despite the necessity of water for

the production of CO₂, its effect is moderate in comparison with that of temperature; changes in soil moisture do not alter SCE as dramatically as similar magnitudes of temperature change. However, inclusion of soil water parameters is crucial to understanding the evolution of soil CO₂.

Seasonal changes in soil moisture play a major role in the carbon budget. As soil moisture in temperate zones declines throughout the growing season in response to evapotranspiration, a clear shift in the sourcing of CO₂ production in the soil takes place. Early on in the growing season, when soil moisture is typically at a high level due to snow melt and/or precipitation events prior to initial plant production, soil respiration is dominated largely by microbial activity. Root mass is not yet at its seasonal apex, and the abundance of water leads to high rates of decomposition and thus generation of gaseous carbon by microbes. As temperatures increase within the soil and water becomes more limiting within the system, microbial activity begins to retard while autotrophic production (i.e. root respiration) accelerates in response to increased air temperatures encountered by aboveground components of plants (Riveros-Iregui et al., 2007). This general shift in peak production from heterotrophic to autotrophic sources later in the season may be indicative of shifts in soil nutrient status; microbial mineralization of nitrogen, for example, might be diminished, thus creating a harsher and more competitive environment for growth for biota in general. Though this trend in seasonal drydown and shift in CO₂ production between heterotrophs and autotrophs can be present in many temperate systems, environments consistently characterized by either high or low soil moisture may show divergence from these patterns. Understanding the comparatively extreme nature of water relations in such systems and their impact on rates of soil

respiration will be essential to developing a global perspective on carbon-water interactions.

Not only is soil moisture a critical control of soil respiration, it also modulates soil CO₂ efflux by altering the diffusivity of gas through soil pores. The second of the two main components involved in SCE is transport (the first being production). In general, SCE increases as soil moisture increases, largely because higher water content lends itself to greater metabolic activity. In the event of soil inundation, however, SCE is limited by the ability of CO₂ and O₂ to migrate vertically within the soil matrix. As soils begin to dry down, SCE begins to increase in direct association with soil moisture decrease, as soil water is limiting neither to the production of CO₂ by heterotrophs nor to the diffusion of gases within the system. Below a certain moisture threshold, which is unique to the characteristics (e.g. texture) of the soil, SCE becomes nearly independent of soil water content and regains a strong association with temperature. This interesting relationship among water content, temperature, and soil CO₂ efflux has led in some cases to the exclusion of soil moisture as a meaningful control of SCE; only in cases where soil experiences significant seasonal drying or long-term flooding was it of critical value to incorporate both temperature and moisture. Nevertheless, inclusion of both parameters enhances the predictive power of attempts to model CO₂ efflux. This is especially true where complex terrain is considered, as heterogeneity within a watershed can create highly unique zones with distinct water and temperature relations.

Soil moisture also acts indirectly to affect rates of respiration within the soil, as well as soil CO₂ efflux. Where respiration rates are concerned, soil water content can modulate soil temperature; a reduction in the moisture level can alter the thermal

diffusivity, thus affecting the depth that solar heating can reach. Drier soils lead to increased thermal diffusion, resulting in one of two possibilities. First, higher soil temperatures accelerate microbial respiration rates, thus elevating SCE. Alternatively, if the system does not possess soil moisture significant enough to promote decomposition, microbial respiration, as well as survival, is inhibited. This is particularly true with extended periods of low soil moisture (e.g. drought) when microbial biomass may already be depressed (Borken et al., 1999). In both scenarios, however, heat transfer occurs to a greater depth, thus increasing temperatures for subsurface soils. Currently it is estimated that as much as 50% of the total soil CO₂ efflux is generated in soils classified as subsurface (Jin et al., 2008). Furthermore, it has been suggested that subsurface soils are more sensitive to moderate increases in temperature than even surface soils, and thus SCE values could be greatly affected by higher thermal diffusivities promoted by drying (Lomander et al., 1998). This occurrence, coupled with the fact that Q₁₀ values for soil respiration increase with depth, could greatly accelerate CO₂ evolution (Jin et al., 2008). This pattern of Q₁₀ values raises an interesting question. Given that microbial differentiation occurs between different soil layers and depths, is it possible that these unique strata of biota may in fact operate under different thermal maxima (Jin et al., 2008)? If this is in fact the case, changes in thermal diffusion could result in a redistribution of microbial communities within soil layers, thus changing the specific respirative activity that can be expected at each level. As such, soil moisture might play a significant role in creating this new differentiation as well as moderating the effects of soil temperature at depth; however, this indirect control of soil moisture on microbial communities has not been well understood.

A recent phenomenon has been observed when considering patterns of CO₂ efflux from soils. The relationship between temperature and SCE displays some predictable trends throughout a diurnal cycle; increases in soil temperature throughout the day lead to higher rates of efflux. However, these trends begin to shift in response to an additional factor. Riveros-Iregui et al. (2007) define this daily pattern as hysteresis. In essence, hysteresis is used to describe the nature of a parameter whose response to a second parameter is seen to lag due to additional variables; in the case of soil respiration, daily

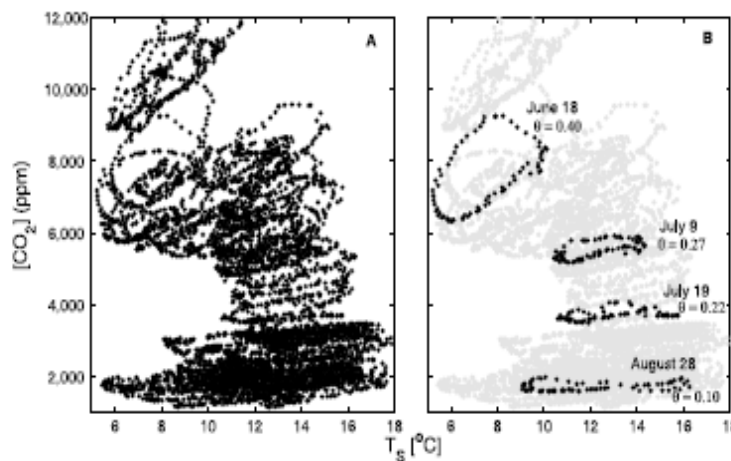


Figure 8: Diurnal hysteresis charted over the course of a growing season – each closed loop represents one day's fluctuation in CO₂; Source: Riveros-Iregui et al., (2007).

production of CO₂ is dependent on temperature, though transport is a function of soil moisture. Peak soil respiration is dependent on the

timing of maximum root respiration, which is a function of air temperature, and maximum heterotrophic respiration, which is a function of soil temperature. As soil temperature maxima lag behind those of air due to the time needed for heat propagation through the medium, peak heterotrophic respiration lags behind that of roots. As such, maximum total soil CO₂ efflux occurs between the independent maxima of these two sources of respiration, which does not correspond directly to the timing of peak daily temperature. When plotted, this hysteresis materializes itself as a series of closed loops; each full loop can be linked directly with the activity of a specific day. The extent of

hysteresis (i.e. the aperture of the loop) was seen to be associated most closely with soil moisture. As wetter conditions limit both the propagation of heat from the surface to deeper soils as well as the transport of CO₂ to the surface, days with higher soil moisture demonstrated more pronounced hysteresis. With progressively drier soil conditions, the degree of soil respiration lag behind temperature was less noticeable, thus resulting in a corresponding narrowing of the aperture of daily loops (Howard and Howard, 1993). Lower moisture provided conditions less inhibiting to the transfer of heat and CO₂ throughout the soil column, thus shortening the delay of maximum soil temperature, and the associated peak in heterotrophic respiration, behind that of air temperature.

Soil organic matter (SOM) comprises a vast amount of the world's carbon. Containing approximately 1550 Pg C (Raich and Potter, 1995; Batjes, 1996), SOM accounts for two times more carbon than the atmosphere, and thus provides a considerable resource for the facilitation of decomposition (Jin et al., 2008). Decomposition of organic matter is responsible for 20-50% of the total soil respiration from a temperate forest during the growing season, with contributions reaching nearly 100% during the non-growing season (Wang et al., 2000). However, it is not simply the mass of this pool that is significant, but it is the quality of SOM, which contributes to the rate at which materials are converted from organic to inorganic compounds (Jassal et al., 2004). Labile SOM is much more readily processed than is recalcitrant SOM, and thus the turnover rate of the former is much faster. Labile organic matter is the preferred source of several key nutrients for growth, carbon being only one of them. Given this preference, the exact proportion of SOM classified as labile can play a major part in controlling SCE. In areas with greater quantities of labile material, decomposition and

thus respiration are able to proceed at much higher rates than in areas with lower amounts. Typically, ecosystems displaying a large amount of aboveground biomass, particularly biomass that senesces seasonally, will possess a high degree of labile organic matter. However, the quality of the litter is important not only because of direct impacts on microbial respiration, but also because of its effects on soil leaching of key nutrients (e.g. nitrogen). In zones with high quality litter, compounds within organic matter can readily be broken down, both by microbial processes and chemical weathering. This pool of SOM is in large part subjected to variations in water availability. Regions that feature both high quality litter and high soil water content can experience a significant amount of soil nutrient leaching (Schimel et al., 1997). Such leaching is not only responsible for the removal of key nutrients like nitrogen, but it has also been noted to depress readings of SCE as CO_2 enters solution with water and is removed from the soil through groundwater outflows (Reardon et al., 1979; Wood and Petraitis, 1984).

Precipitation plays a secondary role in controlling soil CO_2 efflux. Inputs to the soil predominantly dictate soil moisture, though there is some direct effect of precipitation on the transport of gases within the soil matrix linked to displacement of material during infiltration events. Patterns of precipitation in an ecosystem can be correlated to carbon exchange within a region on a seasonal basis, as well as an interannual basis (Epron et al., 1999). Precipitation is strongly linked to net primary productivity as well, and can therefore moderate the flux of CO_2 . Additionally, precipitation can play a significant part in determining both soil organic matter and autotrophic respiration (Hanson and Weltzin, 2000). Precipitation can be considered as a series of three independent events: interception, infiltration, and runoff (Weltzin et al., 2003). For the purposes of soil CO_2

efflux, only infiltration will be considered here. Though interception and runoff may impact SCE, their significance is not considered in depth here as direct interaction with water throughout the soil matrix may be adequately defined through infiltration.

Infiltration is the primary mechanism for rewetting of the soil matrix and serves a number of important roles, from recharging the water table to altering microenvironments within soil pores. Through increasing soil moisture, this process can generate a resurgence of activity for both autotrophic and heterotrophic biota in residency there; this occurrence is of great significance for soil CO₂ efflux in terrestrial systems and has become a driving topic of study in recent years. Following a precipitation event, there is a spike in SCE, partially due to displacement of trapped CO₂ from soil pores and partially due to an increase in respiration generated by the addition of water to the system (Cable and Huxman, 2004). These pulses are particularly noticeable in hot, dry areas, where optimal temperatures for maximum soil respiration are already achieved or exceeded (Cable and Huxman, 2004). The size and timing of these pulses will be topics of great interest in coming years as precipitation frequency and intensity is expected to be modified in response to global climate change (Smith et al., 2000).

Though it is fairly well documented that soil efflux increases after a precipitation event, it is less well defined how different environments change in the time following that event (Weltzin et al., 2003). In particular, the effect on soil respiration of progressive soil drydown in the weeks subsequent to precipitation has been identified as a major gap in knowledge concerning ecosystem processes. Additionally, the impact of mid-season precipitation events and their role in elevating soil CO₂ efflux as well as the primary sources of CO₂ in periods following rainfall is poorly understood. Differentiating

between displacement of CO₂ from soil pores and newly generated soil respiration is difficult to do, as both processes are seen to lag behind the initial input of water due to limitations in gaseous exchange with the atmosphere. Further complicating this issue is the poor understanding of factors such as soil evapotranspiration, lateral transport of gases, and the redistribution of water throughout the soil matrix (Weltzin et al., 2003). Without incorporating these functions into estimates of SCE, sizeable releases of CO₂ could be overlooked.

Though precipitation events are themselves important in generating soil respiration, spatial and temporal variability of these events can have considerable influence on local rates of efflux. Understanding precipitation frequency and intensity on a regional scale can lead to better awareness of an ecosystem's responsiveness. The frequency and intensity of rainfall events are significant not only for respiration rates, but also for rates of export through groundwater flow. Areas characterized by high mean annual precipitation are often associated with elevated rates of soil nutrient leaching (Schimel et al., 1997). Increasing flow laterally through a soil matrix can increase the total dissolution of gaseous CO₂ in water or similarly the rate of formation and removal of bicarbonate. Even in the absence of biotic processes, carbon can be transported out of a system via lateral redistribution and potentially see removal through stream flow (Rosenbloom et al., 2006). This component of CO₂ export is often neglected and in regions experiencing high rainfall this could account for a relevant portion of total SCE.

Soil Characteristics

In order to gain a better understanding of soil CO₂ efflux, the medium itself must be understood. Soil properties vary significantly between ecosystems and often demonstrate a high degree of heterogeneity even within a given locality, though the extent to which a particular system experiences heterogeneity is far from consistent as well. Characteristics ranging from soil texture to nutrient content are major determinants of both rates and sources of soil respiration. Functioning in conjunction with environmental gradients such as soil moisture and temperature, the soil matrix and the variability inherent within it are essential elements of any terrestrial system, which must be incorporated into schemes attempting to understand the nature of SCE.

Soil texture, though generally only seen as a secondary control on soil CO₂ efflux rates, can have a dramatic impact on the production environment of CO₂. Specifically, soil texture is responsible for moderating a number of primary factors within the soil that directly affect soil respiration, namely soil moisture, soil organic matter, and biotic communities. Concerning soil moisture, knowledge about soil texture can bolster the predictability of functioning within the system. Texture correlates directly with pore size, which serves as a good indication of the capacity of a soil to store water. It dictates the porosity of a soil as well as both field capacity and wilting points, which are significant factors affecting soil biota and their ability to access water resources. Soils with larger pores are able to support greater rates of infiltration during precipitation events, but are also more likely to experience rapid drainage and more considerable lateral redistribution. As such, these systems may not be as capable of providing adequate nutrient status to promote large standing microbial biomass. On the other hand, larger pores help to

facilitate the exchange of gases between the atmosphere and the surface soils. This would allow a speedier release of CO₂ following production and could prevent O₂ limitations from occurring within the system. Soils characterized by smaller pores, though better able to retain water and nutrients, tend to negatively influence rates of heterotrophic decomposition of SOM by shielding this material from microbes; this shielding causes a faster rate of use of root exudates, though where this source of material is limiting, SCE can be depressed (van Veen et al., 1991).

Soil texture is strongly linked to nutrient availability. In soils with sandy textures, nutrient retention within the soil matrix is often limited due to high rates of flushing; soils poor in nitrogen could see minimal SCE despite significant inputs of carbon (van Veen et al., 1991). As such, sandy soils are not typically associated with vastly productive systems and therefore do not see a substantial amount of litter formation on an annual basis, which might inhibit the generation of an ample standing pool of soil organic matter. Soils rich in silt and clay tend to promote higher rates of SCE due to more expansive nutrient stocks. Soils capable of maintaining consistently higher soil water contents such as clays can likewise sustain higher volumes of dissolved organic matter (DOM), which is in turn a significant contributor to the annual availability of carbon, nitrogen, and various other essential nutrients (Qualls and Haines, 1991; Michalzik and Matzner, 1999). Increases in the amount of water in a system, as would be expected following a precipitation event, can elevate dissolved portions of carbon and nitrogen (Tipping et al., 1999). These forms of organic molecules, important for microbial communities that degrade them rapidly, are central to short-term biogeochemical cycles within forest soils (Jandl and Sollins, 1997). In terms of nitrogen, the magnitude of

leaching from a system can have dramatic consequences for local biota. Diminishing these standing stocks can limit NPP as well as microbial respiration (Schimel et al., 1997). Where carbon is concerned, leaching may not have as significant an impact on soil respiration (Schlesinger and Melack, 1981; Schlesinger, 1985). It is unclear, however, whether removal of dissolved organic and inorganic carbon through groundwater flow is truly negligible in studies of SCE (Band et al., 1993).

Nitrogen, generally, is the primary limiting nutrient in terrestrial systems (Vitousek and Howarth, 1991). It serves as a restriction not only to autotrophic production, but also to microbial activity, and can reduce the total annual SCE by impacting these processes simultaneously. Controlled primarily by the soil moisture regime and rate of mineralization, nitrogen availability in soil horizons is a large determinant of autotrophic and heterotrophic productivity and additionally serves to dictate future nitrogen mineralization. Deeper soils often experience lower rates of nitrogen mineralization and microbial activity; fertilization of these zones showed a significant increase in both rates in comparison to surface soils (Jin et al., 2008). It is possible that N-limitation is in fact present in subsurface soils; however a number of other factors including microbial community composition may prove to be more apt explanations (Fog et al., 1988). Nitrogen content of the soil is a strong factor in regulating microbial activity especially, and pending climate change may affect the rate at which nitrogen is cycled and consumed within soils. Little clarity is yet available as to whether increases or decreases in soil N will occur, though it remains a topic of much interest (van Veen et al., 1991; Schimel et al., 1997; Weltzin et al., 2003; Jin et al., 2008).

Depth within a soil column is indicative of unique soil conditions. Soils positioned directly at the interface between the terrestrial and atmospheric environments are necessarily different from subsurface soils. Progression away from the surface alters elements of soil moisture, temperature, and soil organic and mineral contents, each of which is responsible for impacting the rate of SCE. It is generally accepted that a large majority of soil CO₂ is produced in the upper layers of the soil matrix, typically considered between 0-20cm in depth (Pumpanen et al., 2003; Jassal et al., 2004). Upwards of 90% of total soil respiration is thought to occur within only the uppermost 10cm (Glinski and Stepniewski, 1985; Pietikainen et al., 1999). However, some research has been presented suggesting that, despite elevated rates of CO₂ production within the upper layers in response to temperature augmentations, only 50% of total SCE is generated in this surficial zone. Jin et al. (2008) noted that the significantly larger area comprised by subsurface soils compensates for the slower rate of CO₂ production. When compared directly with rates and total area of near-surface soils, it is possible that contributions by both zones are approximately equal. In addition, given the higher degree of temperature sensitivity of subsurface soils (i.e. that Q₁₀ values increase with depth), deep layers within these systems may become areas of focus in future years should soil temperatures increase as predicted by climate change models and these zones become more active in terms of CO₂ production.

Changes in both soil temperature and soil moisture occur with depth. Variation in both of these factors is in part due to a distance from the soil surface where the drying effects of solar radiation and atmospheric warming are greatest. As heat input and moisture alter with depth, the associated thermal diffusivity of the soil becomes a primary

control on the advancement of heat through the soil matrix, and likewise rates of soil respiration. As the influence of air temperature is greatest in shallow soils, upper layers are both the most responsive to environmental stochasticity and the most vulnerable; this tendency toward fluctuation in environmental conditions on short time scales tends to decrease with depth. Understanding the nature of the stratification produced by temperature and moisture within soils can improve predictability of total SCE for entire soil columns. It is important to note that each of these factors is controlled simultaneously by depth as by soil texture; this fact makes generalizations in strata among sites limited in value. Small amounts of heterogeneity in a soil matrix can produce vastly different conditions for heterotrophic microbes as well as for autotrophs, which can in turn alter values of SCE. As a complete knowledge of soil variability is largely unknowable, assumptions about the nature of soil influences on soil CO₂ efflux must be made.

Biota

The abiotic environment is only one component of the overall picture. Biotic communities that comprise a region are responsible for the vast majority of CO₂ produced from a landscape. Furthermore, they are hugely important in moderating a number of factors, including soil moisture and soil temperature, which in turn act to increase or decrease soil respiration. As such, it is necessary to consider these biotic components of the terrain, given their significance, to properly understand SCE within the ecosystem as a whole.

Soil carbon efflux is a product of two main sources: microbial communities and living roots. Microbial activity is directly related to the type and abundance of carbon

compounds within the soil, in addition to soil moisture and temperature. Hereafter termed heterotrophic respiration (HR), this activity is the primary process responsible for the conversion of soil organic matter into inorganic forms. Living roots, responsible for generating the vast majority of autotrophic respiration (AR), contribute to total SCE in two distinct ways: root respiration, which is largely dictated by air temperature; and the release of root exudates, which are often highly labile forms of organic carbon that are readily converted by soil fauna (van Veen et al., 1991). Both of these sources (HR and AR) can contribute significantly to the overall rate of CO₂ efflux. However, the relative contribution by each of these components varies widely across systems (Amundson and Davidson, 1990; Boone et al., 1998), limiting understanding of the exact components of production from microbial and root respiration. It has been suggested that the ratio of autotrophic to heterotrophic inputs to total SCE can range from 1:9 – 9:1, denoting a high degree of site-specificity (Buchmann, 2000). As such, AR can constitute between 10-90% of total SCE (Hanson et al., 2000). Understanding exact levels of activity by autotrophs and heterotrophs continues to be a challenge as current methodology is limited in its ability to distinguish between sources. As the structure and function of these living components is highly dependent on their growing environment, it is no small wonder that soil moisture and temperature would emerge as the main controls on rates of metabolism for these two groups. Just as seasonality exists for moisture and temperature, the comparative contributions of AR and HR also fluctuate seasonally as well (Widen and Majdi, 2001).

Interestingly enough, the two factors demonstrate some degree of divergence. HR follows a pattern nearly identical to the typical seasonal patterns characteristic of soil

environments. Dependent on soil temperature and soil moisture, microbial communities increase rates of respiration along with temperature and water content; should water become a limiting resource, HR values may be only a fraction of the regional maximum. The bulk of microbial activity that is responsible for HR occurs in the top 20cm of the soil column (Jassal et al., 2004). This zone of soil is also the first to experience both heating and drying; the former results from proximity to the surface and incident solar radiation, while the latter results from a combination of vertical drainage, evapotranspiration, and storage by autotrophic life forms. Microbial activity can easily become depressed in the upper reaches of soil as seasonal drying takes place. HR is also dependent on another factor, the quality of soil organic matter. Higher proportions of labile carbon in the total soil pool will enable higher rates of conversion from organic to inorganic forms. Contrastingly, AR is primarily a function of air temperature and photosynthetically-active radiation (PAR) (Riveros-Iregui et al., 2007). As such, AR increases and decreases in response to ambient climate conditions. This distinction in temperature dependency between HR and AR allows for the two to vary independently. AR rates can continue to increase throughout the growing season when HR rates are suppressed, as costs of biomass maintenance are similarly temperature-dependent. In the case of forested ecosystems, AR may also demonstrate independence from drying that occurs in the upper 20cm of the soil. Deep roots that can tap into more permanent sources of groundwater help to free perennial autotrophs from soil moisture controls (Baldocchi et al., 1997). The rates of both AR and HR show a great deal of diurnal variation as well, though each responds to a different aspect of the environment. As AR is directly associated with PAR, peak rates of production of autotrophic respiration occur around

midday when radiation is at its highest. HR, linked inevitably to soil temperature, peaks later in the day as soil temperature maxima lag behind those of air temperature (Riveros-Iregui et al., 2007). Despite considerable possibility for divergence in these two components of total soil respiration, HR and AR are bound by environmental factors to respond in similar fashions. In light of this, conceptualizing both collectively as soil respiration is prudent, though consideration must always be given to the independent nature of each flux.

Microbes

Microbial communities show a great deal of specialization and can be found in virtually every terrestrial environment yet explored. Responses of these organisms to a variety of conditions enable massive potential for differentiation in function, even within a single ecosystem. No single control on the growth and activity of microbes has been discovered, demonstrating the variability inherent within this classification of life. Adaptable to nearly any situation, these biota will only become more important to the global carbon cycle in the coming decades with the advent of global climate change.

Understanding of soil microbial communities and their composition is surprisingly limited, particularly at depths greater than ~25cm below the surface (Fierer et al., 2003). A large majority of studies have focused on surface soils, viewing the uppermost layers as the most active and responsive to changing environmental conditions. However, as suggested by the work of Jin et al. (2008), these surface soils may only account for 50% of the total SCE from an area. Given that research on subsurface soils is relatively sparse, the true nature of microbial activity in deeper soils is unclear. In truth, a great degree of

specialization in microbial communities may occur within deeper zones, as it is clear their functioning and utility is distinct from communities in shallower soils (Fritze et al., 2000; Blume et al., 2002). As such, the capacity of these microbes to respond to changing environmental conditions could be huge and understanding their limits may prove imperative. The first step, though, in deciphering the distributions of microbes within a soil profile, prior to considering their specific niches, is classifying heterogeneity within soils and applying it as a foundation for understanding differentiation.

Microbiota respond to a number of gradients within soils, both environmental- and resource-based. It is often suggested that communities develop in association with ambient growing conditions, and, in particular, favorable soil moisture and soil temperature. Certainly, soil moisture plays a huge role in determining the ability of a community to flourish, as it is essential to the functioning of individual cells. In the absence of sufficient soil water content, microbial biomass decreases (Riveros-Iregui et al., 2007). This can be seen through an investigation of microbial response to hillslope aspect; compared to south-facing slopes, microbial biomass was found to be significantly greater in north-facing slopes, with the key distinction between the two environments being higher soil moisture in the latter (Sveshnikova et al., 2001). Additionally, scenarios that present microbial communities with extreme water stress, as would be expected in drought conditions, are indicative of dramatically suppressed values of SCE (Widen and Majdi, 2001). Soil temperature simultaneously plays a part in determining total community activity at different depths within the soil, as increases in temperature lead to accelerations in the rates of heterotrophic respiration. Though little consistency has been identified, temperature could prove to be highly deterministic of microbial activity in

colder regions as Q₁₀ values are generally higher within depressed temperature ranges (Kirschbaum, 1995). Despite the clear impact of moisture and temperature on soil respiration, microbial communities are more frequently described as dependent not on gradients in environmental conditions, but rather gradients in available nutrients.

Surface soils, in comparison with their subsurface counterparts, are characterized by high rates of microbial activity and substantial organic matter input, leading to acceleration in rates of nutrient mineralization. As such, the quality of topsoil is considerably higher than that of deeper soils. Stimulated by the decomposition of surface litter, dead roots, and plant-root exudates, heterotrophic communities tend to thrive in these richer zones (van Veen et al., 1991). Within a vertical 2m-section of soil, only about 1/3 of the total microbial biomass was contained in the lower 1.75m of the sample (Fierer et al., 2003); limited most strongly by a reduction in the quantity and quality of organic matter (Richter and Markewitz, 1995; Trumbore, 2000), total microbial biomass decreased substantially with depth. It was suggested, however, that despite the noticeably lower biomass present in deeper soils, per-cell activity of microbes in topsoils might be matched or even exceeded by communities found at depth (Blume et al., 2002). Experiencing environmental conditions much more stable than communities at the surface, deep microbes may be able to sustain rates of respiration in the absence of ideal circumstances at shallower depths (Fierer et al., 2003).

Beyond direct relationships among soil moisture, temperature, nutrient content, and microbes, a network of other factors can affect soil community composition. Vegetation acts to alter not only the physical, but also the chemical structure of the environment. Though partially dictated by ambient growing conditions extraneous to the soil matrix,

vegetation is responsible for impacting soil CO₂ efflux rates. In areas of high root density, microbial activity is often accelerated as a result of higher concentrations of root exudates (van Veen et al., 1991). As these organic structures are simple to metabolize in comparison with ambient litter, the preferential use of exudates suggests root proximity is a favorable condition for microbes. This may also help to explain some of the differentiation that occurs between soil layers, as deep zones are less often exposed to these readily-utilized forms of carbon.

Vegetation

As with microorganisms, vegetation plays a dynamic part within the landscape and is capable of modifying environmental conditions. Within the soil, both physical and chemical alterations take place on account of the presence of vegetation and the nature of the biota themselves. Vegetation is especially important in affecting the seasonal variation in regional SCE. As the growing season progresses, plants construct more extensive rooting systems in order to maximize productivity as well as chances of survival (van Veen et al., 1991). In temperate forests, for instance, the AR component of SCE increases throughout the growing season; this is largely explainable as a combination of root biomass accumulation and elevated air temperatures, the latter of which necessitates higher maintenance costs, but may also be reflective of a general increase in translocation of photosynthetic production to roots later in the growing season (Lyr and Hoffman, 1967; van Veen et al., 1989; Andrews et al., 1999). Though highly fascinating and clearly valuable to the interpretation of system processes, physiological activities associated with individual species are often too distinctive to consider

independently; rather, a broader view of terrestrial vegetation must be taken in an effort to understand the larger functioning of the environment.

Canopy structure is a factor that shapes the soil environment heavily. The presence of foliage overlying a specific patch of ground can alter a number of characteristics of the soil. The two factors most directly impacted are soil temperature and soil moisture, not surprisingly the two most important factors associated with SCE. The presence or absence of a canopy can alter patterns of incoming radiation and thus change the thermal properties of the soil system. Direct radiation on bare soil can create a scenario of rapid drying in the topmost layers, and can dramatically impact the temperature at the surface as well as underlying depths as heat is transferred both vertically and laterally. Soil shielded by a canopy of some sort can display soil temperatures substantially less than bare soil counterparts during summer months. Canopy structure then becomes a factor in determining the degree of shielding; in forested ecosystems where an overstory and understory are found, the degree of cooling can be considerably greater. Cooler summer temperatures allow for a reduction in direct evaporation from the soil and may in fact promote higher rates of SCE throughout a growing season as compared to non-foliated terrain. Canopy structure also helps to insulate soils during winter months, thus elevating temperatures above those of exposed areas. This artifact of vegetation may allow for higher rates of SCE than would be expected in its absence.

Water regime represents the second direct impact imposed on soil by the presence of a canopy. As mentioned, covered soils can demonstrate temperatures significantly lower than uncovered soils and are thus capable of maintaining high soil moisture content. Nevertheless, it is important not only to consider retention of water, but also incidence.

Thus, rainfall events become significant points of consideration. In particular, canopy structure plays a major part in affecting interception. Leaves and stems are able to redirect the local flow of water and serve as forms of aboveground lateral redistribution of moisture. With preferential paths formed along the exteriors of plants, exemplified by stemflow in forested systems, water resources can be concentrated near the base of plants rather than being uniformly distributed as is the case with bare soils. This phenomenon allows for faster uptake by plant roots in the upper layers of soil. It is possible that this redistribution may in fact reduce total soil moisture shortly following the precipitation, but the presence of the canopy may also retard the drying out of the soils, thus promoting more consistent rates of soil respiration. Logically, the exact structure of the canopy is critical to the degree of impact seen. In subalpine forests, for example, limited water and nutrients allow for considerable space to form between each adjacent tree; this space ensures a largely undiminished amount of incident radiation at the soil surface (Battles and Fahey, 2000), though there is little doubt that preferential flow paths still dictate distribution of water.

Soil CO₂ efflux is affected not only by the presence of a canopy, it is also dependent on the type of vegetation that is present. It is safe to say that different ecosystem types are going to display characteristics unique unto themselves. Given the same climatic conditions, prairie grass plains with their shallow rooting depths and frequent water stress are going to have SCE values wildly different than those of old growth forests seasonally characterized by fog water inputs. What is more interesting to consider is the manner in which SCE changes within an ecosystem through time. In particular, understanding the effects of succession on the carbon budget of a system could provide a great wealth of

knowledge that may help predict future changes to the global budget. In terms of total soil CO₂ generation, mature plants demonstrate the highest rate of SCE, with progressive decreases in rates from building plants to pioneer plants, and finally to senescing plants (Brown and MacFayden, 1969). Larger quantities of root biomass are inherently responsible for larger values of AR. Thus, mature and building (or adolescent) plants have higher SCE than pioneer and senescing plants. It is often the case that microbial communities are more fully developed in systems that are characterized as mature; greater differentiation is able to occur with depth, likely due to the stability of the soil matrix in these situations. As such, values of HR may also be accelerated when compared to those of pioneer communities.

However, new evidence has been presented suggesting that, when applied to a larger scale, this generalization breaks down. In the case of secondary succession, Wang et al. (2010) found little variation in annual soil CO₂ efflux among sites of different successional stages. Though increases in root biomass as well as soil organic matter pools were observed with time since disturbance, the development of a canopy reduced soil temperatures; as temperature is considered to be the primary control on soil respiration rates, a decrease in soil temperatures roughly compensated for an increase in available substrate, thus generating a scenario of minimal change throughout ecosystem succession. Further studies on this topic are recommended, particularly in an effort to determine the carbon status (i.e. source or sink) and its variability in ecosystems in the time following disturbance. Understanding this shift in carbon storage within a region may prove fundamental to predicting environmental response to impending climate change.

Topography

Topography represents one of the final challenges that remain in understanding soil CO₂ efflux and even ecosystem processes as a whole. Within the scope of a watershed, variations in topography can become critical to developing predictive success. Small changes in slope or aspect can lead to significant alterations in the functioning of soil processes. By understanding how a landscape changes in response to topographic variation, a better picture of the environment in its entirety can be developed. Where SCE is concerned, a few main factors need to be considered to capture the dynamics of the system. Aspect, slope, and elevation, though broad in their classifications, are the essential elements of topography, which will be considered here. It is important to note that these factors are predominantly applicable to regions displaying substantial topographical variation, e.g. hillslopes and montane environments as will be addressed directly; however, variations on a much smaller scale than this can still produce substantial differences between sites. Nevertheless, understanding the influence of topography on soil conditions could improve estimates of soil respiration (Running et al., 1987).

The slope of the ground is a major factor determining both surface runoff and erosion rates. The greater the angle of the landscape, the more likely it will be for both soil and water to migrate down slope. Where water is concerned, an increase in the proportion of runoff requires a corresponding decrease in the proportion of water infiltrating the soil. A reduction in the water entering the soil, all other factors being held constant, will result in a reduction of soil moisture. This directly affects both autotrophic and heterotrophic life. For heterotrophs, limitations on water availability force higher instances of competitive

interaction, not only among heterotrophic biota, but also between hetero- and autotrophic biota. Soil water stress, therefore, limits the contribution of HR to total soil CO₂ efflux (Borken et al., 1999). In the case of autotrophs, the circumstances present a less straightforward argument. Possessing both aboveground and belowground components, plant life is dictated not only by soil conditions, but also by atmospheric conditions. Despite the fact that autotrophic respiration rates are controlled primarily by air temperature, reductions in water availability are expected to impact root functioning. In the case of severe stress, organic carbon exudates from roots increase in volume (Martin, 1977; van Veen et al., 1991). These exudates, prime sources of carbon for microbial communities, become an important jumpstart to SCE during future infiltration events and can lead to increases, if only short-term, in soil CO₂ production. When compared directly, autotrophic and heterotrophic responses to water limitation differ, particularly in the magnitude of the response. Heterotrophic respiration often sees more dramatic reductions than does autotrophic respiration (Goulden et al., 1996; Widen and Majdi, 2001). As autotrophic respiration is thought to be only about ¼ of annual respiration (Raich and Schlesinger, 1992), reductions in heterotrophic inputs could represent a huge shortfall in the balance of the global carbon budget and would increase the sink status of terrestrial systems.

In conjunction with increased runoff, erosion rates are elevated along hillslopes. The combination of gravity and higher surface flow following precipitation events generates a less stable soil environment and can lead to significant sediment transport to lower elevations. This can play a large role in determining nutrient conditions in surface and subsurface soils as material is displaced and relocated in stream beds or other reservoirs.

As with soil moisture, soil nutrients are a major point of contention between various forms of life. Removal of nitrogen and labile carbon through surface runoff, in addition to a number of other key minerals, can increase the level of competition on a hillslope. Such competition can then affect not only the type of biota that is able to thrive, but also the total biomass. Areas characterized by a dearth of nutrients are often sparsely vegetated and similarly possess reduced quantities of microbial biomass; in terms of C:N for hillslopes and their associated riparian zones, the former demonstrates ratios about two times greater (Pacific et al., 2008). As a result of both lowered nutrients and reduction in soil moisture, hillslope respiration rates are significantly less than those of nearby riparian zones (Pacific et al., 2008).

Beyond considerations of the slope angle of a terrain, the aspect, or facing of a landscape, is important in determining factors like soil temperature and soil moisture within an environment. In the northern hemisphere, due to the inherent solar azimuth, a system experiences greater incident solar radiation on slopes facing south. North-facing slopes are comparatively shielded by the topography. This shielding effect allows a differentiation in temperature and moisture to occur between north- and south-facing hillslopes. Soil moisture, in response to greater drying pressure imposed by more direct radiation, is significantly reduced in south-facing soils (Kang et al., 2003). This phenomenon is seen ubiquitously throughout temperate systems; the preferential positioning of moss and lichens on the north side of a substrate such as a tree or rock is indicative of the greater water availability in those locations. Soil temperature also exhibits some variation as a result of aspect, with warmer conditions typically occurring on south-facing slopes; however evidence has been presented suggesting that variation in

soil CO₂ efflux rates does not occur between differently oriented landscapes on account of soil temperature (Kang et al., 2003; Pacific et al., 2008). Rather, it appears that differences in soil moisture provide the most significant explanation for these results. As with all other elements of soil respiration, these factors do not operate in a vacuum. Soil moisture and temperature regimes give rise to unique autotrophic and heterotrophic communities, which in turn affect soil properties, such as turnover rates for carbon and nitrogen. This represents one of the great difficulties in modeling ecosystems; the nature and extent of feedbacks within a system become increasingly complicated as more detail is incorporated.

Elevation is a complex topic where soil CO₂ efflux is concerned, but its effects are not too dissimilar from those imposed by other topographic factors. Altitude within a watershed is often a determinant of many soil characteristics, primary among them being soil moisture. Soils located at elevation are more susceptible to dry-down than are soils closer to the bottom of a watershed, as vertical drainage dictates the flow of water downhill. Low soil water content can restrict rates of SCE, particularly in cases where soil water stress is severe (Borken et al., 1999). Soil temperature at the landscape-atmosphere interface is less strongly impacted by the effects of elevation than soil moisture; this concept does not apply, however, in cases of extreme elevation such as high mountain terrain. In these cases, significant variation in temperature is paired with soil drydown to depress rates of soil respiration. Often considered to be related in their nature and sensitivity to high latitude environments, high elevation areas are extremely responsive to alterations in temperature and moisture as a whole, as SCE in these areas is likewise dictated by altitudinal limitations on these two factors. Hillslope regions, for

example, often experience maximum rates of SCE shortly following snowmelt, when above-freezing soil temperatures and abundant water are available. Contrastingly, areas lower in the watershed tend to display peak SCE rates much later in the growing season (Pacific et al., 2008). In large part, elevation determines the factors that are the most significant controls on SCE for a given environment.

Topography exerts a control on soil carbon that will continue to require much investigation. Though a great deal of variability in the factors controlling SCE is directly related to changes in topography, it is unclear as to the exact importance of slope, aspect, and elevation. Hanson et al. (1993) found little correlation in the rates of SCE among topographically-unique sites, suggesting that heterogeneity on this scale can be largely ignored. A number of other findings seem to refute this point, suggesting that even small differences in elevation can impose dramatic changes in soil environments, which will inevitably feed back into soil respiration rates (Kang et al., 2003; Pacific et al., 2008). Disagreement within this field warrants further research as complex ecosystems have moved to the foreground of environmental concern in recent years.

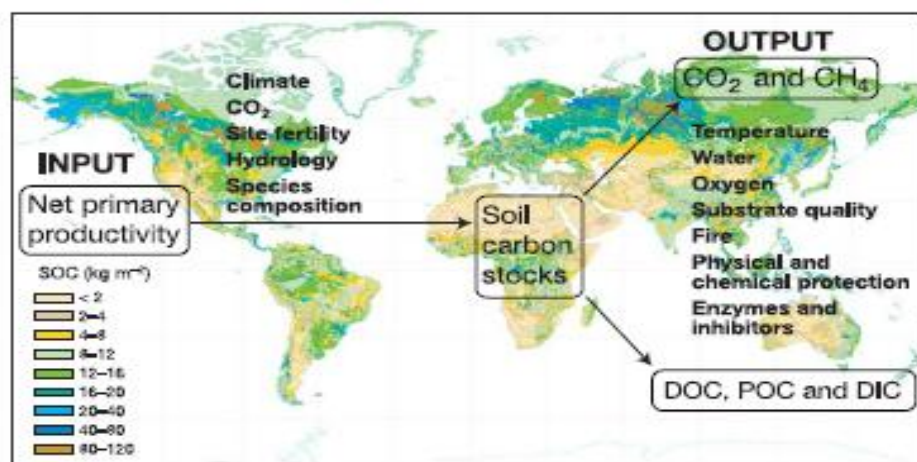


Figure 9: The major controls on soil carbon production and differentiation superimposed onto a map of soil carbon stocks (USDA-NRCS, 2000); Source: Davidson and Janssens (2006).

Soil CO₂ Efflux: The Need for a New Perspective

Understanding the dynamics associated with the carbon budget, and specifically those of the soil carbon pool, will continue to be a major focus of research as long as global climate change remains a dominant force within the field of environmental sciences. As soil CO₂ efflux (SCE) has the potential to provide significant feedbacks to the overall carbon budget, it will be important to monitor and assess the nature and size of this flux in order to soundly predict future environmental outcomes.

Climate warming will inevitably accelerate global rates of SCE, though the extent of this increase is unknown. Raich and Schlesinger (1992) suggest that even a moderate increase in temperature on the order of .3°C/decade could result in as much as 2 Pg C/yr increase in soil respiration output, equivalent to approximately 25% of current anthropogenic emissions. Such a significant annual increase in total atmospheric CO₂ is expected to exacerbate warming scenarios and serve as a gradually accelerating feedback mechanism when paired with soil respiration increases. Northern-latitude environments are of key interest, where soil warming impacts on SCE are concerned. The high sensitivity of soil activity to temperature increases coupled with large soil organic matter pools in these systems creates an incredible potential for CO₂ release from land surfaces (Bunn et al., 2007). Expected to see substantially greater warming than other latitudes, northern systems may be facing a significant shift in both NPP and soil CO₂ efflux in the coming years.

Microbial activity in soils, in particular, is poorly understood. Though the general relationships among soil respiration, temperature, and soil moisture are well established, the response of heterotrophic decomposition rates to climate change and shifting

contributions by temperature and moisture is still unclear. Rising global temperatures are expected to deepen the active zone of heterotrophic respiration due to increased heat propagation throughout the column of soil. With the potential for greater per-cell for activity (Blume et al., 2002; Jin et al., 2008) observed higher sensitivity to temperature increases in deep soil microbes, combined with the fact that non-surface soils may contain over one-third of total microbial biomass (Fierer et al., 2003) highlights rising soil temperature as a major source of ignition for global carbon feedbacks. Though temperature is considered the most influential control on soil respiration rates, microbial activity is also dependent on the quality and quantity of substrate available. Distributions of labile carbon versus recalcitrant carbon within a soil matrix may yield clues as to the extent to which SCE will increase in coming decades. Labile carbon, easily degraded by microorganisms, demonstrates rates of consumption significantly more responsive to warming than recalcitrant pools (Davidson and Janssens, 2006). Early acceleration in rates of heterotrophic respiration may introduce a large pulse of CO₂ into the atmosphere. However, rapid depletion of labile carbon within SOM pools may afford an acclimation of soils to increased temperatures and thus truncate the feedback mechanisms anticipated to compound global climate change. The exact outcome is unclear, though a change in both microbial activity and the composition of SOM is anticipated.

Issues of warming are not the only dilemma deserving attention where SCE is concerned; several models have suggested huge shifts in precipitation patterns as a result of climate change. These shifts, predicted to be on the order of a 7% increase in global annual total, will affect several of the fluxes associated with the carbon cycle (Weltzin et al., 2003). Exact influences imposed by precipitation are also poorly understood,

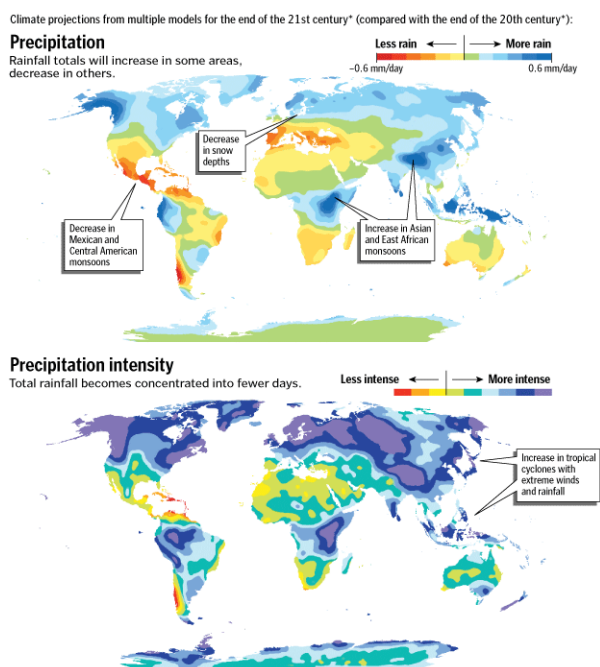


Figure 10: Changes in a) total annual precipitation and b) precipitation intensity between 2000-2100; Source: Washington Post – “A Future of Downpours and Droughts.”

especially within equilibrium climate models, which do not account for variability in rainfall totals (Weltzin et al., 2003). Soil CO₂ efflux will alter in response to increased precipitation, likely increasing in magnitude due to increased water availability (Riveros-Iregui et al., 2007); however, changes in both the frequency and severity of storm events, as well as the type of precipitation that impacts a landscape

(snow, rain, etc.), could produce scenarios in which total soil respiration declines (Weltzin et al., 2003). This divergence in predictions for global carbon balance merits considerable attention from the scientific community in order to more fully comprehend the outcomes of impending climate change.

NPP, correlated strongly with interannual variation in total precipitation (Hanson and Weltzin, 2000), is expected to respond not only to increases in water availability, but also to increases in total ambient CO₂. The extent of alteration expected from the biosphere is largely in question. Acclimation to higher carbon levels in the atmosphere by vegetation is predicted to occur as concentrations approach 800-1000ppm, a level that will likely be reached before 2100 (Houghton et al., 1996), but CO₂ saturation of global NPP could occur at levels below or beyond this range, particularly in light of rapid land-use change imposed on terrestrial systems by human use (Cox et al., 2000). What is clear is that the

biosphere will undergo many changes in the coming decades; predicting the speed and extent of these changes remains the biggest challenge in global climate modeling.

By increasing the wealth of studies aimed at understanding the controls of environmental and resource gradients on soil carbon pools, more discernible trends and patterns of response could be identified. This is of particular interest for individuals attempting to model ecosystem functioning and carbon cycle dynamics on a large scale. Where SCE is concerned, limited coverage of certain ecosystem types has been demonstrated in the literature; there is a dearth of information for arid and semi-arid environments, whereas temperate systems are grossly overrepresented (Raich and Schlesinger, 1992); terrains such as savannas, woodlands, drought-deciduous forests, and deserts are therefore poorly understood within global models despite accounting for approximately 33% of global land surface (Dregne, 1976). In contrast to this imbalance in soil CO₂ efflux observations, attempts to understand patterns of global precipitation demonstrated an underrepresentation of mesic sites as compared to arid and semi-arid ecosystems (Weltzin et al., 2003). Integrating new sites with unique characteristics will help to improve global coverage and further capture variability not already encompassed by past and present research. By doing so, the predictability of regional and global modeling schemes will improve and allow a more complete understanding of terrestrial systems.

Coupled with this concept of improving global coverage to better modeling attempts, incorporation of ecosystem complexity into the equation will be essential so as to portray the biosphere accurately. Components of the environment, such as topography, vegetation, and soil characteristics, are often considered to be homogeneous when

parameterized by models seeking to understand the aggregate response of functions within an environment. Though this simplification may prove legitimate in certain scenarios, it is the complexity of an ecosystem that produces unique associations among its biotic and abiotic components. Overlooking heterogeneity in complex environments risks losing sight of the lower-order processes that may in fact define a landscape and its soil efflux rate; local distributions of a tree species, for instance, could produce differences in microclimates that contribute significantly to patterns of water resource distribution and govern soil temperature conditions, both of which are responsible for moderating SCE. By ignoring such details, it becomes difficult to discern the intricacy and importance of biogeochemical pathways at scales smaller than entire systems.

Scale of Observation

Determining the resolution necessary to accurately represent the processes and functioning of an ecosystem is difficult; it often requires researchers to consider the dimensions of their investigative interests and on what level they are most relevant. In truth, each dimension provides a unique series of advantages, though a number of disadvantages are inherently associated with each scale as well. Four main levels are used to understand ecosystem dynamics within environmental sciences; here, a brief discussion on the utility of each is presented.

Plant-level Perspective

Small-scale studies are often designed to understand the intricate processes that take place within a highly specific system. In an effort to identify and observe the

individual mechanics of a plant, for example, it is not uncommon to consider the plant in isolation. A number of different experiments on the plant-level have provided information about the physiological characteristics of particular species, revealing the inner workings of processes such as carbon fixation, transpiration, and biomass accumulation. On this scale, experimentation is often focused on understanding the processes of and controls on photosynthesis, the nearly-ubiquitous method of carbon fixation on the surface of the Earth. Developing a more complete knowledge of this process can reveal the impact and significance of environmental controls on carbon fixation. In other cases, by observing the process of transpiration at the leaf level, water-use efficiency can be determined, which can then be scaled up to estimate total plant water use over a given period of time. Additionally, this measurement of transpiration can be converted to provide a good indication of the total carbon gain of an organism. Similar studies of physiological functioning associated with other plant processes can provide insights achievable only at this diminutive scale of observation.

Both of these techniques undoubtedly provide worthwhile insight into the functions of plants. Without understanding these processes, which form the foundations of ecology, it may never have been possible to develop methods and technologies that allow the scientific community to sample ecosystems on larger and more aggregate scales. However, each of the components to photosynthesis demonstrates a high degree of variability not only from one species to the next, but also from plant to plant within a given species. The unique growth patterns and microclimatic circumstances, both past and present, which collectively define an individual's environment, necessitate a highly specialized response. Furthermore, physiological differences and varying degrees of

phenotypic plasticity can produce unique responses among species despite identical growth conditions. As such, conclusions that can be drawn from experiments on this scale of observation are often not applicable to larger systems, especially in scenarios where a significant degree of heterogeneity may exist within the flora (e.g. high biodiversity). In addition, developing more comprehensive views of ecosystems requires understanding the actions of an individual as well as the interactions of that entity with its biotic and abiotic environment. Expanding the scope of observation beyond the plant-level will provide opportunities to assess these interactions.

Site-level Perspective

Site-level research demonstrates a small-scale approach to ecosystem functioning. Graduating beyond the level of plant-specific physiology, site-level studies seek to provide detailed information on characteristics ranging from soil properties to ecological distributions. Often, efforts on this scale attempt to describe individual sites as representative of a target environment (e.g. coastal salt marshes). In more homogenous ecosystems, dominated by a limited number of plant types and relatively few changes in topography, observations on this scale can be highly effective. Not only are they capable of analyzing the influences of climate and landscape on ecosystem functioning, they also serve as a foundation for the development of aggregate perspectives; by understanding the response of a site within a homogenous environment, conclusions derived from site-level studies can be scaled up to describe the response of continuous ecosystems.

Though site-level variability may be minimal in areas of high homogeneity, more complex landscapes cannot be as easily defined. In truth, even marginal variations in topography can produce drastic differences in observations. Local distributions of soil nutrients, for instance, can influence patterns of microbial biomass accumulation, which can lead to non-uniform rates of soil CO₂ efflux. In areas that demonstrate a high degree of topographical heterogeneity, such as montane ecosystems, characterized by considerable variability in elevation and aspect (and thus factors such as light availability and soil moisture), site-level studies present a limited view of the environment as a whole. Furthermore, highly complex environments can produce situations in which variability is greater within a series of closely related sites (i.e. similar elevation and plant type) than between distantly related sites. In the montane forest of Canaan Valley, WV, soil moisture fluctuates over time by as much as 16% when averaged for a series of similar elevation sites over time and as much as 25% within a single site, but only an average of ~7% across sites of different elevation (Richards et al., unpublished data). The inability to account for all instances of heterogeneity creates a large potential for error when attempting to extrapolate from site-level data to encompass the response of the larger environment. In order to account for a large range of variability to better approximate environmental functioning, a broader perspective than site-level research may be required.

Watershed-level Perspective

Expanding beyond plant-level and site-level studies, watershed-scale projects are able to incorporate a number of ecosystem-level processes not adequately considered by

narrower views. A watershed, delineated by the topographic boundaries that dictate patterns of surface water flow, operates as a discrete unit in which individual nutrient fluxes can be considered. Though interaction with the atmosphere is rarely restricted by the same boundaries that define the watershed, the generally accepted homogeneity of the atmosphere ensures limited variation due to air alone. As water is essential to the production of soil CO₂, understanding the movement and redistribution of water within a catchment can reveal aspects of nutrient flow within the system. Similarly, the movement of nutrients within a system, and the nature of plant and soil processes derived from this movement, is largely separable from adjacent watersheds, minimizing the occurrence of unknown loss from soil environments. Viewing processes at the watershed scale often represents the highest resolution at which large environmental fluxes like NPP and SCE can be considered; functioning as compartmentalized systems, carbon flux within watershed soils can be analyzed in virtual isolation from adjacent systems. Furthermore, utilizing watershed-scale studies is a powerful method of developing the components of a larger project. Acting as subunits within a global system, the integration of outcomes from catchments, whether empirical or modeled, can contribute to research aimed at viewing the biosphere as a continuous system while preserving heterogeneity in fluxes.

Watershed-level studies, despite possessing many of the benefits of both smaller and larger scale investigations, similarly can embody a number of the drawbacks associated with different perspectives. Many watershed studies, though attempting to consider ecological processes, rely heavily on site-based observations. As such, a general assumption must be made that the chosen sites are representative of the variability that can be expected within the catchment. In situations involving highly complex terrain, this

may prove to be a limiting factor in the reliability of results; however, this limitation may often be overcome by increasing the number of sites used to evaluate whole-watershed functions. The dilemma then becomes the feasibility of assessing all of the sites adequately given available resources and man-power. Watersheds are also sometimes criticized for their inability to encompass entire ecosystems. In order to accurately predict trends for the temperate deciduous forests of the eastern US, for example, a series of watershed studies must be conducted simultaneously and subsequently aggregated. Observations of an individual watershed cannot account for heterogeneity present throughout all other watersheds. Rather a larger global perspective considering the biome beyond distinct watersheds may be better equipped to estimate total ecosystem exchange.

Global Perspective

Dominated by modeling attempts, the global perspective seeks to understand the processes of the aggregate terrestrial (or aquatic) environment. At this level, specificity is at a premium and resolution is considerably lower than with any of the previous scales of observation. As such, a significant degree of ecosystem homogeneity must typically be assumed. Considering the Earth as a unified system also requires a great deal of interpolation. Despite empirical observations for individual landscapes, simple integration of available research leaves a number of gaps that must be filled, especially in undersampled biomes. Often this requires a detailed understanding of the variability in parameters involved in global models, both independently and in their interactions with other parameters. Mathematical approximations, process generalizations, and estimations are not uncommon features of research at this scale; that being said, any approximations

that are made are designed to address the needs of the model and provide the highest accuracy output possible. Global perspective is especially useful when considering large-scale circulations and terrestrial fluxes, such as the global carbon cycle, and may be most valuable for its ability to offer predictions of future atmospheric and biospheric change. In the wake of newly available satellite imagery and advanced computing technology, global models have gained favor in the scientific community and have demonstrated their utility effectively.

Gaining Perspective on Soil CO₂ Efflux

Many would argue that no single scale of observation is ideal, as each level of observation carries with it its own advantages and disadvantages. However, where soil CO₂ efflux is concerned, watershed-level studies may be the most beneficial. The highest structured scale of direct measurement, watershed studies offer the opportunity for both monitoring and manipulation of ecosystem fluxes, while still enabling both interpolation of heterogeneity within the system and extrapolation to larger scales or similar environments. Watershed studies also provide the greatest potential for understanding the impacts of complex terrains. Whether there is variation in topography, soil characteristics, or vegetation, this perspective provides insight into differentiation within catchments as well as the aggregate flux of carbon. Global perspective might eventually replace the watershed study as the most effective method of viewing SCE, but the current incompleteness in understanding of soil respiration patterns across the globe warrants research at a finer scale than global models can provide.

The variable nature of a landscape, in association with the numerous factors varying in conjunction, creates a complex mosaic of unique characteristics. Only through the integration of this mosaic into a larger perspective will predictive power of fluxes like soil CO₂ efflux become satisfactory. Observing complex environments remain a challenge for modern science, as is determining the appropriate scale at which to view the controls on ecosystem processes.. Efforts are being taken to incorporate many of the controls on SCE into regional and global modeling schemes, as well as into monitoring and research initiatives in the field, which will only serve to improve forecast capabilities in the future.

Modeling the Carbon Cycle

Interpreting changes in the carbon cycle requires knowledge of both past and present conditions as well as the processes that determined them. With a decent understanding of the variables that define an environment, it becomes possible to apply these interpretations in an effort to predict future dynamics. As previously mentioned, having adequate predictive capabilities will be crucial where soil CO₂ efflux is concerned. A number of attempts are currently being made to develop accurate and reliable models that encompass a wide array of elements associated with global climate change. Incorporating detail into these modeling efforts, though often complicated, ensures a greater degree of precision in the implications generated. In general, modeling allows researchers to make educated guesses as to the fate of the environment, ranging in scale from watersheds to the entire globe, and from decades to centuries. The predictive power offered by models helps to target areas of particular interest and demonstrate the

value in understanding specific ecosystem processes. Additionally, they may be capable of impacting policy and conservation strategies in light of the outcomes they forecast (Cramer et al., 2001). As such, the importance of modeling cannot be overstressed; however, careful consideration must be used at all times when evaluating results lest the assumptions implicit in these models be taken for granted. In the case of climate change, a number of model types have been presented to assess the fate of terrestrial systems. Two particular types, general circulation models (GCMs) and dynamic global vegetation models (DGVMs), have gained favor in recent years. Each provides a different method by which changes to the carbon budget can be assessed.

GCMs are utilized to model the circulation of the atmosphere or ocean and operate centrally around the Navier-Stokes equation, which defines patterns of fluid motion (e.g. air or water). Independently, GCMs may not be relevant to the specific assessment of the global carbon fluxes; however, their value lies in their coupling with other component models. Partnerships of GCMs with vegetation and oceanic models increase their significance dramatically. In general, GCMs are limited in their understanding of scenarios involving more rapid climate change (Cramer et al., 2001). GCMs are also poorly adapted to understanding the dynamics associated with physiological processes; where SCE is involved, direct estimations of fluxes of carbon are rarely provided from the model, though they may be implied from the overall outcome. As such, GCMs are more often utilized in tandem with more biogeochemically-centered models that can pair flux estimations with atmospheric circulation predictions.

Dynamic global vegetation models (DGVMs) represent another side of the carbon budget that is often not considered fully by GCMs. DGVMs are designed to include

detailed information on vegetation and their sensitivity to climate change and elevated CO₂ concentrations. Though the resolution of these models is still fairly low, the classification of vegetation into five main plant functional types (PFTs) enables some differentiation in the response values of different categories (Woodward and Cramer, 1996; Cramer, 1997). These types (broadleaf and needleleaf trees, C₃ and C₄ grasses, and shrubs) are limited in their ability to describe all autotrophic life (Cox et al., 2000). At the same time, division into PFTs enables a greater deal of flexibility within the model itself and allows for independent variation in each of the groups. By doing so, a better overall picture of net primary productivity can be achieved than if a single set of variables were assigned to all forms of terrestrial vegetation. In addition, DGVMs can also be designed to incorporate dynamics associated with soils, such as SCE, and can chart predicted responses by these components in relation to climate change; TRIFFID (top-down representation of interactive foliage and flora including dynamics) is one such model that considers both autotrophic- and soil-based pools of carbon (Cox et al., 2000). This tool considers a range of plant physiological features as well as soil characteristics that determine microbial respiration rates. Integration of this degree provides a detailed prediction of carbon fluxes and can be scaled to a variety of dimensions to consider regional or global dynamics.

The true value of these models appears to be in their ability to be combined and function in tandem. By combining a GCM with a DGVM, and additionally, with an OCC (ocean carbon-cycle) model, many features tightly coupled to the global dynamics of carbon are simulated jointly. Cox et al. (2000) utilized this approach to understand the impact of climate change and atmospheric CO₂ enrichment on terrestrial systems. In their

findings, it was demonstrated that the biosphere will ultimately saturate with carbon prior to the apex of climate change effects. Despite increasing in total vegetation biomass and soil carbon initially, the terrestrial systems are expected to see reductions of ~170 Pg C between 2000-2100. This agrees with predictions by Smith and Shugart (1993), who also predicted a significant release of CO₂ in conjunction with atmospheric temperature increases. A large proportion of this loss is thought to be a direct result of climatic warming; higher air and soil temperatures trigger increases in microbial and plant metabolic rates. Though a large portion of carbon is anticipated to undergo burial in ocean sediments (400 Pg C), the rate of burial declines over time in response to exceedingly higher concentrations of CO₂ in the atmosphere.

Overall, these models are adept at providing information on large-scale dynamics and global change. A broader understanding of the future awaiting terrestrial systems will be significant in defining both the responses and controls of the biosphere to environmental variability. Models of this nature are limited in their ability to represent individual processes and ecosystem-specific functions. As such, the resolution of information provided by GCM-DGVM couplings may not yield conclusions on the fate of independent ecosystems. Lost in the aggregate, more sensitive landscapes critical to the interpretation of regional and global trends may be overlooked.

Future Considerations

Determining the direction this field must go in order to better understand carbon cycle processes within terrestrial ecosystems is challenging. At one level, higher resolution models provide regional views on landscape functions, but do not offer the same

longevity that larger scale models can (Weltzin et al., 2003). Broadening the scope to include global processes enables an encompassing view that avoids the magnification of local variability (Jones, Jr. and Mulholland, 1998), but often it is this variability that provides indications of environmental change. It seems that, in order to overcome the difficulties presented by considering one scale of observation over another, an integration of scales is necessary to achieve more accurate results. Integration of components into a single schema will provide at the very least two separate levels of data, one associated with the larger region and another indicative of localized processes. In generating these types of integrated systems, a number of previously overlooked aspects responsible for inducing environmental variation can be incorporated. In terms of soil carbon studies, unknown quantities of inorganic carbon are lost through abiotic reactions and leaching as a direct result of lateral redistribution of water. While some speculate that such losses are inconsequential to the overall interpretation of carbon flux (Schlesinger and Melack, 1981; Schlesinger, 1985), thus justifying their absence from modeling attempts, others suggest that such losses are sizeable, especially in regions characterized by human-induced change (Schimel et al., 1997). An integration of scales would allow for variation in stream effluent carbon concentrations in areas more heavily impacted by leaching rates and may provide insight into interregional variability. Regardless, adding complexity to models, despite increasing the potential for error propagation, is expected to increase predictability; in the case of SCE, adding soil moisture and precipitation parameters improved the reliability of results (Raich and Schlesinger, 1992; Hanson et al., 1993). At the same time, consideration must be given to the need for additional computing power required to introduce new components. It may be that significant and affordable

advancements in processing technology must first be achieved before total assimilation of ecosystem processes into modeling efforts can occur.

Integration of scales is one method of improving overall analysis of the global carbon budget. The integration of information through the development of extensive networks, on the other hand, can provide a major boon to global models. PrecipNet, a system of worldwide sites collaboratively generating data on annual precipitation patterns, is intended to improve the communication and exchange of information associated with ecosystem processes (Weltzin et al., 2003). Utilizing a large network of synchronized data points such as that provided by PrecipNet or AmeriFlux (a similar network of eddy covariance stations gathering CO₂ exchange data) into a model will not only simplify the access and manipulation of information for researchers, but it will also increase the applicability of the results produced, as empirical measurements from many different environmental types are incorporated into the model itself. Such networks create

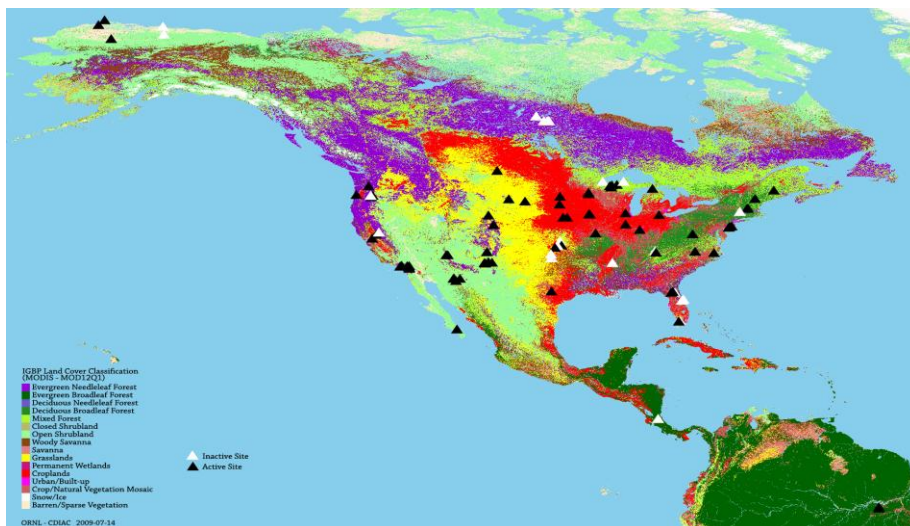


Figure 11: Map of AmeriFlux sites superimposed on a vegetation map; Source: <http://public.ornl.gov>

the possibility
for independent
variation on a
local scale rather
than relying
entirely on a
mathematical
approximation

of climate and vegetation trends. Improving the connectivity between empirical research methods and modeling efforts will undoubtedly affect the reliability of results.

Just as PrecipNet and AmeriFlux are designed to monitor values of mean annual precipitation and ecosystem CO₂ exchange continuously, a similar network, perhaps termed SoilNet, could be established to provide continuous measurements of soil CO₂ efflux. By including empirical data from a series of ecosystem types representative of the global terrestrial environment, developing a more detailed picture of SCE and the carbon budget as a whole becomes significantly more feasible. Unlike with precipitation and eddy covariance observations, field methods that allows for continuous measurements of SCE have not been implemented widely; rather, instantaneous measurements are more common. As SCE rates are highly responsive over relatively short time scales to diurnal and seasonal variability, as well as fluctuations in environmental and resource gradients, it is difficult to ensure the reliability of these data for long-term modeling efforts.

Beyond the steps necessary to integrate both scale and information availability, some vital aspects have yet to enter the mainstream as significant factors in light of climate change. Although research into the dynamics of the carbon cycle is extensive already, there are a few areas that are frequently overlooked by investigations into terrestrial systems. Ocean sediment burial is the dominant means by which carbon is removed from direct interaction in the carbon cycle. Ocean carbon stocks are on the order of 38,000 Pg C (Raich and Schlesinger, 1992), and the large majority of this carbon is held inactive due to low productivity at the ocean floor. Increases in atmospheric CO₂ in the future may be partially counterbalanced by burial in sediments; however, consideration for such a burial flux is often absent where terrestrial-atmosphere interactions are involved. Another element of the carbon budget that is frequently neglected despite its particular importance in the modern environment is the role of

changing land-use. With rapid conversion of some landscapes from natural settings to agriculture, the act of biomass destruction inhibits carbon fixation while simultaneously enhancing carbon release to the atmosphere. Disturbances of this type are responsible for massive releases of CO₂ and represent land area that is comparatively less able to store carbon in vegetation or soil. In the case of terrestrial models, few seem to incorporate information concerning land-use change unless that is their primary directive (Houghton et al., 1983; King et al., 1995). As this initial input of carbon is frequently absent from consideration, so too is the feedback within the biosphere to such pulses of CO₂ in the atmosphere (King et al., 1995). By not accounting for response of the system to events such as ocean sediment burial and land-use change, modeling attempts might be overestimating or underestimating the rate of change that will be seen over the next century.

Conclusion

Though the field of environmental sciences has come far in its understanding of the global carbon budget, there are now as many new questions awaiting researchers as there are answers. The dynamic nature of this cycle warrants diligent monitoring and detailed analysis of the interactions among the various carbon pools. Where soil carbon stocks are concerned, response to both biotic and abiotic factors determines the rate of production and transport of CO₂. Variations in soil temperature demonstrate the largest impact on rates of soil efflux over short time periods, while soil moisture, nutrient status, and vegetation play larger roles over seasonal and interannual extents. A number of gaps persist in our conceptualization of the carbon cycle, particularly in terms of modeling

future climates and landscapes. Through the development of more effective technology capable of monitoring evolution of CO₂ from soils on a continuous basis, as well as the establishment and maintenance of systems integrated both in scale and across ecosystems, the fate of the biosphere in the face of climate change can become clearer.

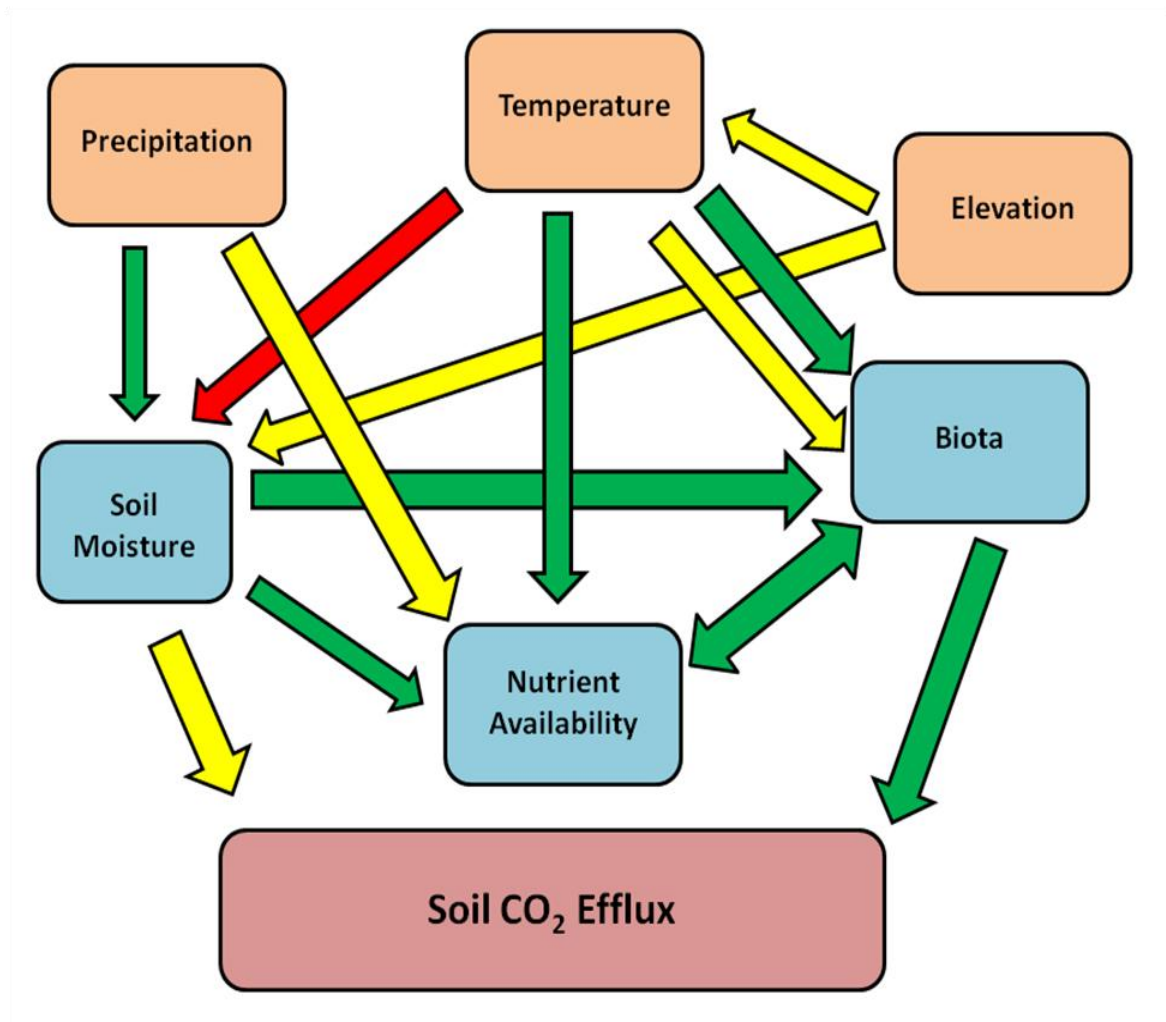


Figure 12: Flow chart of simple interactions among environmental factors; green arrows denote positive interactions (increases), red arrows denote negative interactions (decreases), and yellow arrows denote interactions where relationships are significant, but not clearly defined as either positive or negative.

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