SPECIAL FEATURE – ESSAY REVIEW
PLANT–SOIL INTERACTIONS AND THE CARBON CYCLE

The changing global carbon cycle: linking plant–soil carbon dynamics to global consequences

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Summary

1. Most current climate–carbon cycle models that include the terrestrial carbon (C) cycle are based on a model developed 40 years ago by Woodwell & Whittaker (1968) and omit advances in biogeochemical understanding since that time. Their model treats net C emissions from ecosystems as the balance between net primary production (NPP) and heterotrophic respiration (HR, i.e. primarily decomposition).

2. Under conditions near steady state, geographic patterns of decomposition closely match those of NPP, and net C emissions are adequately described as a simple balance of NPP and HR (the Woodwell-Whittaker model). This close coupling between NPP and HR occurs largely because of tight coupling between C and N (nitrogen) cycles and because NPP constrains the food available to heterotrophs.

3. Processes in addition to NPP and HR become important to understanding net C emissions from ecosystems under conditions of rapid changes in climate, hydrology, atmospheric CO_2, land cover, species composition and/or N deposition. Inclusion of these processes in climate–C cycle models would improve their capacity to simulate recent and future climatic change.

4. Processes that appear critical to soil C dynamics but warrant further research before incorporation into ecosystem models include below-ground C flux and its partitioning among roots, mycorrhizas and exudates; microbial community effects on C sequestration; and the effects of temperature and labile C on decomposition. The controls over and consequences of these processes are still unclear at the ecosystem scale.

5. Carbon fluxes in addition to NPP and HR exert strong influences over the climate system under conditions of rapid change. These fluxes include methane release, wildfire, and lateral transfers of food and fibre among ecosystems.

6. Water and energy exchanges are important complements to C cycle feedbacks to the climate system, particularly under non-steady-state conditions. An integrated understanding of multiple ecosystem–climate feedbacks provides a strong foundation for policies to mitigate climate change.

7. *Synthesis.* Current climate systems models that include only NPP and HR are inadequate under conditions of rapid change. Many of the recent advances in biogeochemical understanding are sufficiently mature to substantially improve representation of ecosystem C dynamics in these models.

Key-words: carbon cycle, climate change, decomposition, heterotrophic respiration, mycorrhizas, net ecosystem production, net primary production, roots, soil carbon

Introduction

Increases in atmospheric carbon dioxide (CO_2) since the early 19th Century reflect releases of CO_2 into the atmosphere from human activities and its uptake by land and oceans, which

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absorb approximately half of this anthropogenic CO_2 (Prentice *et al.* 2001; IPCC 2007). Recent declines in the fraction of anthropogenic emissions absorbed by the land and oceans suggest changes in the role of the biosphere in the global carbon (C) cycle (Canadell *et al.* 2007). An improved understanding of terrestrial C dynamics is therefore both scientifically and politically important. As the largest reservoir of terrestrial C, soils are particularly critical to our understanding of the changing global C cycle.

In recent years, there has been an explosion of insights into the genetic, ecological and biogeochemical dynamics of C-cycling processes in soils. These include plant and rhizosphere effects on soil respiration, the effects of microbial communities (e.g. mycorrhizas) on productivity and soil-C turnover, and interactions among element cycles (e.g. the role of organic nitrogen [N] as a C and N source to microbes). However, current models of the global C cycle seldom explicitly include these processes. The fundamental model of ecosystem C cycling embedded in these models has not changed in the last 40 years (Woodwell & Whittaker 1968):

$$NEP = GPP − ER = NPP − HR,$$

where NEP is the net ecosystem production, GPP is the gross primary production (= photosynthetic carbon gain), ER is the ecosystem respiration (the sum of autotrophic and heterotrophic respiration [AR + HR]), and NPP is the net primary production. Why have recent advances in soil C cycling not been incorporated into current climate–C cycle models? Are these soil processes unimportant to the large-scale C balance? Are they implicitly incorporated in the Woodwell-Whittaker model via their effects on photosynthesis and respiration? In this paper, we argue that understanding the controls over photosynthesis and respiration is sufficient to understand changes in C storage and therefore ecosystem feedbacks to the climate system, if

1. there is a tight linkage between NPP and decomposition, such that C inputs to soils control decomposition, and/or decomposer activity controls C inputs to vegetation,
2. biologically mediated CO_2 flux is the only large C flux in the ecosystem, and
3. C balance is the most important ecosystem feedback to the climate system.

We briefly summarize circumstances where these assumptions appear to be largely valid and provide an adequate approximation of ecosystem–climate feedbacks. We then review several key areas where recent research on soil biogeochemical dynamics shows that these assumptions are *not* met and therefore provide new insights that could improve our understanding of the global C cycle. Areas that warrant more consistent inclusion in ecosystem–climate coupled-system models include: (i) nutrient and other controls that couple photosynthetic C input to respiratory C outputs, (ii) non-CO_2 C fluxes that influence the climate system, and (iii) climate feedbacks in addition to C balance.

The NPP-decomposition balance

COUPLED BIOGEOCHEMICAL CYCLES

The central mechanism that links NPP with HR (or GPP with ER) is the coupling of C with N cycles (or with phosphorus (P) or other element cycles, where these elements strongly limit NPP and/or HR). Increased C inputs to ecosystems, due to changes in CO_2 or climate, are constrained by the supply of plant-available N, most of which is derived from decomposition of dead organic matter. If decomposition lags behind NPP, N supply declines, which constrains the capacity of plants to sequester more C. Conversely, if environmental changes speed up decomposition, the increased supply of N typically stimulates NPP, leading to enhanced C sequestration (a negative feedback to warming; Shaver *et al.* 2000).

In general, global-scale climate system models that incorporate the terrestrial C cycle largely rely on the Woodwell-Whitaker model of terrestrial C exchange with the atmosphere. The current generation of global climate system models generally does *not* consider linkages between the C and N cycles. However, this linkage and other ecological processes are increasingly included in ecological models that do not simulate climate dynamics (e.g. Thornton *et al.* 2007). In a recent evaluation of the responses of climate–C cycle models to future CO_2 emissions, all eleven models demonstrated a decline through time in the capacity of terrestrial ecosystems to absorb increases in atmospheric CO_2 (Friedlingstein *et al.* 2006). However, there was no consensus among the models as to whether NPP or ER was responsible for this response. Simulations that include C and N coupling constrain the stimulation of photosynthesis by atmospheric CO_2 fertilization and also determine whether CO_2 augments or diminishes terrestrial C storage (Sokolov *et al.* 2008). In simulations that do not consider C and N coupling, moderate surface warming significantly reduces C sequestration in both vegetation and soil by increasing ER (a positive feedback to warming). Thus, inclusion of biogeochemical coupling of C and N cycles through soil processes appears critical to understanding both the direction and magnitude of changes in ecosystem C cycles and their impacts on the climate system.

STEADY-STATE CONDITIONS

There is substantial variation among ecosystems in both NPP and decomposition, but the two processes remain surprisingly well-coupled across C cycling rates that vary by several orders of magnitude. One possible explanation is that climate and soil resources exert primary controls over NPP and that decomposition is "donor-controlled" by the transfer of dead organic C to soils and the coupling of C and N cycles. For example, NPP of vegetation near steady state (i.e. in stands where C inputs to and losses from ecosystems are approximately balanced) increases with temperature in the absence of water limitation and increases with precipitation (up to about 2000 mm) in the absence of temperature limitation (Lieth 1975; Schuur *et al.*

2003), suggesting a climatic control over C inputs to ecosystems. Climate controls NPP both directly and indirectly through its effects on soil resources (water and nutrients). Climate and soil resources together determine the distribution of plant functional types with characteristic leaf properties (leaf N, specific leaf area [SLA] and photosynthetic rate), allocation, growth and, therefore, NPP (Reich *et al.* 1997, 2006; Chapin 2003).

Many changes in environmental conditions have parallel effects on both NPP and decomposition. Both NPP and decomposition rate, for example, increase with temperature and soil moisture (up to some moisture optimum). Within a climatic regime, the same plant properties that govern species and habitat differences in photosynthesis and NPP (i.e. leaf N, SLA and plant functional type) also strongly influence decomposition rate, in part through variation in litter quality (Cornelissen 1996; De Deyn *et al.* 2008; Fornara *et al.* 2009). High-N plants decompose rapidly, release more N, and support greater NPP than low-N plants. Conversely, low-N plants decompose slowly and often have ericoid or ectomycorrhizal associations that enable them to absorb both organic and inorganic N (Chapman *et al.* 2006) (Fig. 1). In environments where NPP is limited more strongly by P than by N, P also influences decomposition (Hobbie & Vitousek 2000). These C–nutrient linkages explain in part why soil respiration correlates strongly with NPP, when major biomes of the world are compared (Raich & Schlesinger 1992).

Even ecosystems that are close to steady state show variations in NEP over all time scales, including day–night and summer–winter environmental cycles and successional cycles of vegetation renewal after disturbance. Over all these time scales, C:N feedbacks constrain the imbalance between NPP and decomposition, and the Woodwell-Whittaker NEP model, mediated by coupling of C and nutrient cycles, appears to provide an adequate description of steady-state ecosystem C balance. For example, mid-successional forest ecosystems show a tight linkage between NPP and NEP, providing a basis for predicting NEP based on measures of GPP and ER (Pregitzer & Euskirchen 2004).

In summary, under conditions close to steady state, decomposition appears to be largely donor-controlled by the C inputs from plants. Because of linkages among biogeochemical cycles, spatial variations in NPP, GPP and decomposition are similar to one another in their geographic patterns, and the Woodwell-Whittaker model provides a reasonable predictive approximation of the C dynamics of these ecosystems without explicitly invoking the underlying biogeochemical complexities.

CHANGES IN C-CYCLING DRIVERS

Recent rapid changes in climate, atmospheric CO_2, land cover, species composition and element inputs and losses fundamentally alter the relationship between climate drivers and ecosystem C dynamics (Clark *et al.* 2003). We argue that NPP and decomposition are likely to differ in their rate or pattern of response to these changes in conditions. We suggest a three-phased approach for deciding which biogeochemical complexi-
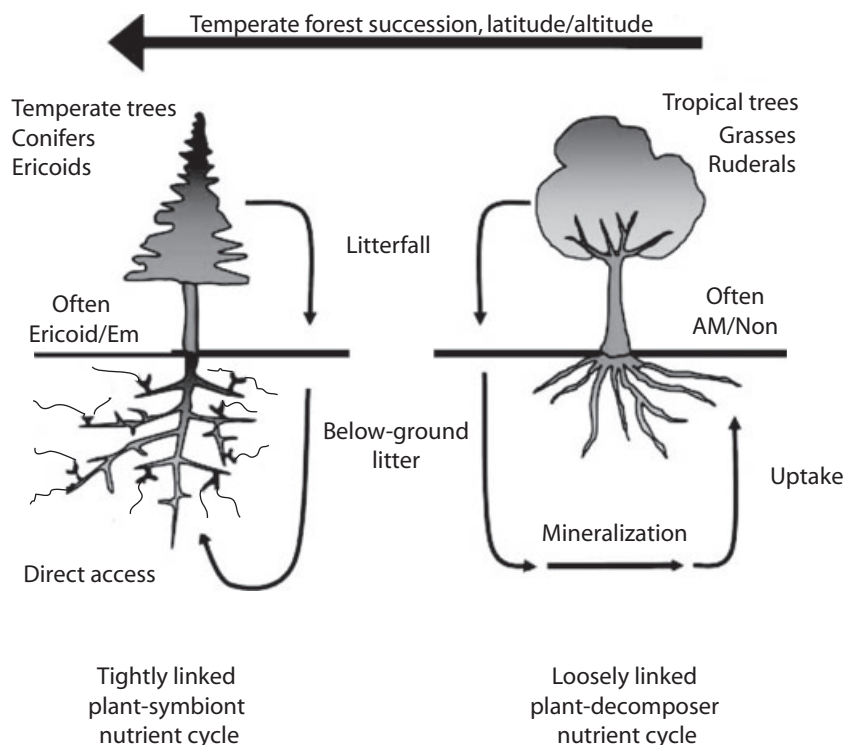
Fig. 1. Microbial impacts on nutrient cycling that cause a switch during succession or with change in environment from a loosely linked plant–decomposer N cycle that supports large C inputs to ecosystems to a more tightly linked plant–symbiont N cycle that supports smaller C inputs to ecosystems. EM and AM are ectomycorrhizas and arbuscular mycorrhizas, respectively. Modified from Chapman *et al.* (2006).

ties warrant inclusion in global-scale climate–C cycle models. (i) Ecologically important processes should initially be incorporated into stand-level ecological models, where results can be compared to whole-system C flux measurements. (ii) Those processes that substantially improve the fit between model and stand-level observations and might affect future stand-level C dynamics should then be incorporated into regional ecosystem models and compared with regional analyses of ground-based data (e.g. forest inventory analyses), remote-sensing data and atmospheric data (e.g. atmospheric inversion analyses). (iii) Finally, those processes (e.g. coupling of C and N cycles) that substantially affect the C dynamics of regional models over extensive areas warrant inclusion in climate–C cycle models.

Changes in climate or altered frequency of extreme events can trigger nonlinear changes in C balance, as new processes become important. Warming that triggers insect outbreaks, for example, radically reduces NPP relative to decomposition and often increases the probability of other avenues of C loss (e.g. wildfire or salvage logging) that are not readily predicted from a simple NEP formulation of ecosystem C balance. The inclusion of pest outbreaks substantially improves model performance in extensive areas where outbreaks occur (Kurz *et al.* 2008), indicating their potential value in regional models.

Hydrologic changes that substantially alter the balance between NPP and decomposition can radically alter C storage and therefore feedbacks to the climate system. This is particularly important when climatic or soil conditions produce such high soil moisture that low oxygen impedes decomposition. These conditions foster carbon sequestration in tropical soils with high (>2000 mm) annual precipitation (Schuur 2003), bogs and permafrost-dominated soils (Callaghan *et al.* 2005), and soils compacted by animals or machinery (Matson *et al.* 1997). Hydrologic changes that tip the balance between C sequestration and loss occur extensively in high latitude, temperate and tropical regions (Bunn *et al.* 2005; Chacón *et al.* 2005), have large effects on performance of stand-level (Yi *et al.* 2009) and regional (Zhuang *et al.* 2007; Govind *et al.* 2009) models and are therefore ready for inclusion in global climate–C cycle models.

Atmospheric CO₂ increases to 550 ppmv have been shown to increase NPP by about 23% across a range of temperate forest sites (Norby *et al.* 2005). Although the direct effects of elevated atmospheric CO_2 on photosynthesis are readily incorporated in simple C balance models, other indirect effects can shift ecosystem C dynamics in ways that require greater understanding of biogeochemical processes. For example, CO_2 stimulation of root exudation can speed rhizosphere decomposition, causing soil respiration to respond more strongly to photosynthetic rate than to soil temperature (Craine *et al.* 1999). Elevated CO_2 can also give rise to litter that has lower N concentration and is more resistant to microbial breakdown (McGuire *et al.* 1995; Norby 2001). CO_2 effects on litter quality and nutrient availability have proven important in stand- and regional-scale models (McGuire *et al.* 1997), but other indirect effects of CO_2 have yet to be tested in ecosystem-scale models.

Land-cover change has significantly altered vegetation structure and composition of about 80% of the terrestrial surface,

creating anthropogenic biomes that often differ functionally from "potential vegetation" (i.e. vegetation that would occur in absence of human activities; Ellis & Ramankutty 2008). Land use change has substantial effects on ecosystem feedbacks to the climate system. The C balance of Europe, for example, cannot be explained without including C imports and exports of food (Ciais *et al.* 2008). While extensive historical land use changes have been incorporated into global-scale ecosystem models (e.g. McGuire *et al.* 2001), they are not generally incorporated into coupled climate–C cycle models. Also, the *dynamics* of future land use change are not yet widely considered in ecosystem models at any scale because of the challenges of incorporating social processes in ecological models.

Changes in species composition can radically alter ecosystem C dynamics through changes in the functional types of plants, diseases, soil fauna (e.g. earthworms) and soil microbes (De Deyn *et al.* 2008). Slow-growing plants decompose slowly, supporting C sequestration through several mechanisms (De Deyn *et al.* 2008). Encroachment of N-fixing shrubs frequently increases ecosystem C turnover and sequestration (Baer *et al.* 2006; Hughes *et al.* 2006). Conversely, disease-mediated declines in native N fixers can reduce productivity, inducing disequilibrium in C cycling processes (Ruess *et al.* 2009). Fungi favour C sequestration through their higher growth efficiency than bacteria (Blagodatskaya & Anderson 1998) and through the recalcitrance of the compounds they produce (De Deyn *et al.* 2008). These are only a few of the many mechanisms by which species and traits exert predictable effects on C sequestration (Chapin 2003; De Deyn *et al.* 2008). Currently, species effects are inadequately represented in ecosystem models. These effects are implicitly included through C cycling parameters of different biomes or dominant plant functional types in dynamic vegetation models (e.g. Euskirchen *et al.* 2009), but are missing from climate–C cycle models.

Element inputs to and losses from active biogeochemical cycles can radically alter ecosystem C dynamics. N deposition, for example, both stimulates NPP and C storage (readily captured with C cycling models that are coupled to N cycling) and causes cation leaching that can reduce the productivity of forests and lakes (Driscoll *et al.* 2001). In high-N ecosystems, the maximum amount of C that can be decomposed may be less than in low-N ecosystems, resulting in greater C storage in high-N ecosystems (Berg & Meentemeyer 2002; De Deyn *et al.* 2008). Similarly, atmospheric deposition of N can retard rates of soil organic matter (SOM) decomposition by reducing the production of lignolytic and cellulolytic soil enzymes; however, the effect of enhanced soil fertility on decomposition processes may be ecosystem-specific (Waldrop *et al.* 2004). For example, long-term N addition in tundra caused C loss because of changes in rooting depth (and therefore decomposition environment) and N limitation of microbial activity (Mack *et al.* 2004). Differences in C sequestration responses to N addition may depend on whether the largest effect of N in soils is to increase non-biological formation of recalcitrant SOM (reducing decomposability) or to increase the growth and metabolism of soil decomposers (N stimulation of decomposition). Further

research on this topic would greatly improve our understanding of global C dynamics.

In summary, multiple processes influence the C dynamics of ecosystems undergoing rapid environmental, biological and social changes, if the changes differ in their effects or time lags on NPP vs. decomposition. These non-steady-state dynamics could occur, for example, in response to changes in disturbance regime, time lags in species migration, or balance between plants, microbial symbionts and diseases. Climate and species composition may also fail to predict C inputs in situations where species have large effects on soil resources, as with human impacts on agriculture or impacts of invasive N fixers on soil N.

COMPLEX DYNAMICS OF C CYCLING IN SOILS

Recent research has revealed many other dimensions of soil biology that strongly influence soil C dynamics, especially under non-steady-state conditions, but are insufficiently understood to provide the generalization that is easily incorporated into models of ecosystem feedbacks to the global C cycle. These are promising areas for further research (De Deyn *et al.* 2008).

Total below-ground C flux (TBCF), i.e. the plant C allocation below ground, is a critical determinant of soil C sequestration because (i) a large but variable proportion of GPP is allocated below-ground by plants, and (ii) this flux interacts with C and nutrient cycling processes in ways that differ from above-ground litter inputs. TBCF includes C flux to root-plus-mycorrhizal production and respiration and to root exudates and can be calculated as the soil CO_2 efflux (minus the C inputs that come from above-ground litter fall) plus any increases in C storage pools in litter, roots and SOM (Giardina & Ryan 2002; Litton *et al.* 2004). The proportion of C allocated to TBCF decreases with increasing GPP across a global data set of forests, whereas allocation to wood increases (Litton *et al.* 2007). Short-term partitioning to TBCF in individual stands in response to irrigation and fertilization also decreases with increasing GPP, but at a much steeper rate than would be predicted from global patterns (Litton *et al.* 2007). Allocation to TBCF also decreases with increasing stand age in most, but not in all forests (e.g. *Pinus contorta* [lodgepole pine] and *Eucalyptus saligna*) (Litton *et al.* 2004, 2007; Ryan *et al.* 2004). Together these results suggest that the proportion of GPP allocated below ground and potentially sequestered in soils decreases with increasing GPP and stand age, but that the strength of these relationships depends on time scale and stand type. These patterns are clearly important to understanding C cycling but are currently inadequate for modelling the short-term response of any given forest.

Similar complexities emerge with respect to temperature. Partitioning to TBCF increases with increasing mean annual temperature (MAT) for non-arid temperate and tropical forests, but decreases with MAT for boreal forests (Litton & Giardina 2008). TBCF also decreases with increasing annual soil temperature across a North American gradient of boreal *Picea mariana* (black spruce) forests (Vogel *et al.* 2008). The

near-constant GPP across the latter data set suggests a trade-off between above- and below-ground C partitioning that contrasts with the global forest relationship of increasing GPP with increasing MAT in temperate and tropical forests (Litton & Giardina 2008). Vogel *et al.* (2008) suggest that soil nutrient availability increases with annual average soil temperatures, as seen in some soil warming experiments (Rustad *et al.* 2001; Melillo *et al.* 2002). Understanding the interactions of soil moisture, nutrient availability and climate warming is critical for interpreting and predicting the partitioning of GPP to TBCF and therefore soil C sequestration, but these interactions are not yet sufficiently understood to incorporate them into global-scale C cycling models.

The partitioning of TBCF among fine roots, coarse roots, mycorrhizal growth, respiration and root and mycorrhizal exudates – soil C pools with very different residence times (Ruess *et al.* 2003; King *et al.* 2007) – is unknown for any ecosystem. This partitioning is critical to understanding the relationship between TBCF and C sequestration and remains perhaps the largest gap in our understanding of the response of terrestrial C cycles to environmental change. For example, although partitioning of TBCF to below-ground NPP, estimated from root production, appears to increase nonlinearly with MAT across global forests (Litton & Giardina 2008), this estimate excludes C partitioning to mycorrhizal growth, which could be inversely correlated with MAT. Although poorly quantified, C partitioning to ectomycorrhizas is widely recognized as a large component of TBCF that governs nutrient and C cycling dynamics in forested systems (Högberg & Högberg 2002; Read *et al.* 2004; Hobbie 2006).

The response of root and mycorrhizal respiration to climate warming could substantially influence the ecosystem C balance, because autotrophic respiration constitutes such a large percentage of soil CO_2 efflux (Ruess *et al.* 2003; Bond-Lamberty *et al.* 2004; Kuzyakov 2006). The long-term response of root respiration to soil warming will likely be less than the short-term responses due to a down-regulation of root metabolic activity at higher temperatures (Burton *et al.* 2008). However, ectomycorrhizal respiration may contribute more to soil CO_2 efflux than do fine roots. Due to its high sensitivity to substrate supply and soil moisture, ectomycorrhizal respiration may be less temperature-sensitive than fine-root respiration (particularly in the autumn when soils cool) (Heinemeyer *et al.* 2007; Moyano *et al.* 2008). Together, these patterns suggest that understanding mycorrhizal C dynamics will be critical for predicting changes in forest C cycling in response to warming as plants increase partitioning below-ground for increased nutrient acquisition.

Heterotrophic response to temperature is an important consideration when modelling ER under a warming climate. Microbial activity generally increases with increasing temperature, yet, this simple relationship is confounded by many co-varying factors (Davidson & Janssens 2006), including the temperature sensitivity of different SOM fractions (Fierer *et al.* 2005, Fang *et al.* 2005; Knorr *et al.* 2005), soil moisture and aeration (Davidson *et al.* 1998; Davidson & Janssens 2006),

and allocation of plant C below ground (Högberg *et al.* 2001). Several lines of evidence suggest that, at broad scales, temperature may be a weaker determinant of heterotrophic activity than is plant productivity. In European forest ecosystems, for example, much of the seasonal variation in soil respiration is explained by temperature, but GPP is a better predictor than temperature on an annual timescale (Janssens *et al.* 2001). Similarly, soil respiration in Norway spruce stands was initially stimulated by experimental warming but then declined, perhaps due to substrate depletion of labile C pools and down-regulation of heterotrophic activity (Eliasson *et al.* 2005). These studies highlight the need for more comprehensive studies of the interactive effects of temperature, moisture and C availability on heterotrophic activity and ecosystem C loss (Davidson & Janssens 2006).

Microbial community composition could substantially influence soil C sequestration, particularly if there are changes in plant litter quality (De Deyn *et al.* 2008). Soil organic matter has surprisingly similar chemical structure (Mahieu *et al.* 1999) and relative accumulation rate among ecosystems (Stevenson 1982) because the plant residues that enter soils have the same primary building blocks (cellulose, hemicellulose, protein, lignin and lipids) in all ecosystems. Although all microbial communities exhibit a core set of metabolic functions such as cellulose and protein degradation, the mineralization and immobilization of SOM is regulated largely by the metabolic demand of soil microbes and their capacity to decompose different substrates, which vary widely with the chemical complexity of SOM. The recognition that different functional groups (e.g. r- vs. K-strategists; bacteria vs. fungi) of microbes preferentially utilize different substrates for metabolism (De Deyn *et al.* 2008) raises the possibility that microbial community structure might substantially influence C storage and ecosystem C balance.

Most ecologists still use a 'black box' approach in attempting to link microbial diversity to function because of methodological limitations in partitioning C flux among the various biological components, e.g. roots, mycorrhizal associates and free-living heterotrophs subsisting on rhizodeposits and/or native SOM. Recent advances in molecular biology (Stres & Tiedje 2006) and the use of biomarkers (e.g. phospholipid fatty acids [PLFA] and nucleic acids [DNA, RNA]) in conjunction with traditional experimental approaches permit investigators to identify, with greater specificity, soil microbial groups responsible for C degradation. For example, use of ^{13}C-PLFA showed that microbial community structure and specific microbial activity varied with differences in SOM quality between oak and grassland soils (Waldrop & Firestone 2004). A functionally similar suite of microbes processed labile substrates in the two soil types, but the soils had quite different assemblages of soil microbes with different enzymatic capacities to decompose more complex substrates. Thus, microbial composition and plant effects on microbial community structure have important implications for C sequestration in soils and could warrant inclusion in C cycling models that address vegetation changes that alter litter quality.

Priming effect (PE), defined here as a stimulation of soil microbial activity in response to fresh inputs of labile substrate (generally of root origin), is a common response in soils that are otherwise limited by C or nutrient availability (Kuzyakov *et al.* 2000). The magnitude of PE determines whether changes in total belowground C flux, in response to elevated CO_2 or temperature, alter belowground C storage. The amount and source of C respired or sequestered in a soil depends on several factors, including soil fertility, the quality and quantity of the substrate added, and acidity (Mondini *et al.* 2006; Blagodatskaya *et al.* 2007). In the presence of adequate N, PE is diminished as microorganisms preferentially utilize C-rich substrate additions. However, when N availability is low, microorganisms 'mine' SOM for N, increasing the SOM-C respired. The end result is that increases in soil N may promote SOM conservation (Berg & Meentemeyer 2002; Craine *et al.* 2007), although this is only one of many factors that govern C sequestration.

Low-molecular-weight organic substrates (e.g. plant exudates and microbial turnover products) exert a strong effect on microbial community structure (Toljander *et al.* 2007; Broeckling *et al.* 2008) and nutrient cycling dynamics (Ekberg *et al.* 2007; Kuzyakov *et al.* 2007; Weintraub *et al.* 2007; Yuste *et al.* 2007), despite their low concentrations in soils. Amino acids in particular constitute an important source of nutrients supporting plant and microbial productivity in low-N ecosystems (Chapin 1995; Vitousek *et al.* 1997; Lipson & Näsholm 2001; van Breemen 2002). Both the composition and concentrations of soil amino acids are relatively similar among ecosystems (Kielland 1995; Jones *et al.* 2009; Werdin-Pfisterer *et al.* 2009). Amino acid turnover rate is closely related to gross production rates of NH_4^+ and CO_2 and may constitute up to 20% of total soil respiration in some ecosystems (Jones & Kielland 2002). The turnover rates of soil amino acids are remarkably similar across soils both within and across biomes, despite large variation in soil physico-chemical parameters (Kielland *et al.* 2007; Jones *et al.* 2009). Although some high-latitude soils have a high (70%) microbial yield (internal partitioning of amino acid-C into anabolic vs. catabolic processes), the survey by Jones *et al.* (2009) demonstrates that this process is very conservative over a broad range of microbial communities and apparently independent of geographic location. This supports the view that the conversion of high-molecular-weight organic matter to low-molecular-weight compounds is the rate-limiting step in organic matter breakdown in most ecosystems, thereby influencing patterns of soil C sequestration (Schimel & Bennett 2004).

In summary, the complexity of C cycling within soils raises questions as to whether the simple Woodwell-Whittaker model of ecosystem C balance can adequately predict ecosystem sequestration of C in response to environmental change. Recent research is uncovering new patterns and potential controls over C dynamics that warrant incorporation in stand-scale C cycle models, particularly under non-steady-state conditions of rapid global change. However, many fundamental questions require additional research to clarify the role of these processes in ecosystem C cycles.
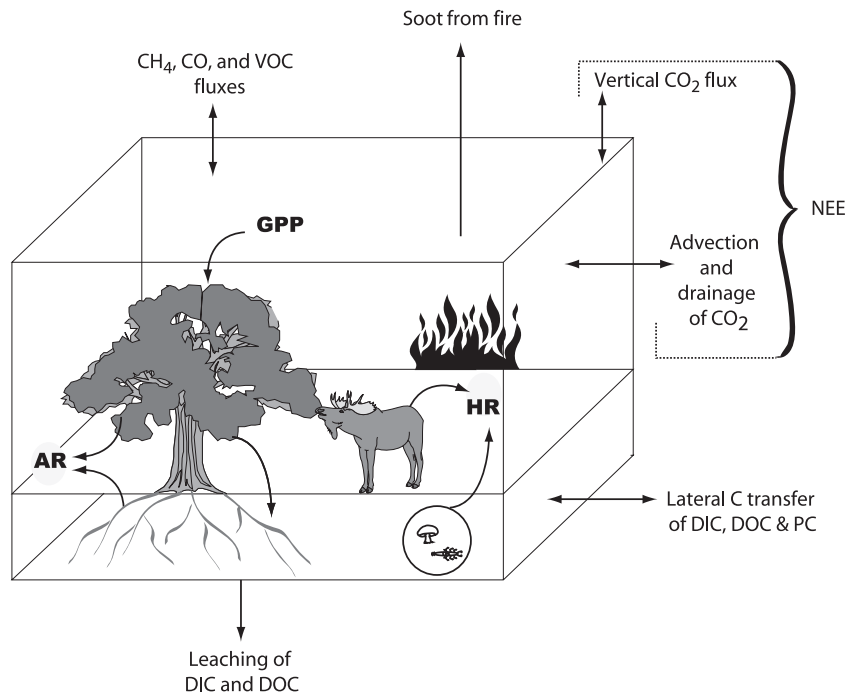
Fig. 2. Major components of net ecosystem carbon balance (NECB). The fluxes that determine Net Ecosystem Production (NEP) are shown in bold: autotrophic respiration (AR), gross primary production (GPP) and heterotrophic respiration (HR). The box represents the ecosystem. Fluxes contributing to NECB and NEP are defined in the text. Other abbreviations include VOC (volatile organic C), NEE (net ecosystem exchange), DIC (dissolved inorganic C) and DOC (dissolved organic C). Modified from Chapin *et al.* (2006).

Large C fluxes other than photosynthesis and respiration

Net ecosystem carbon balance (NECB), the change in C storage in the ecosystem, is the parameter that defines the net effect of ecosystems on C sequestration (Fig. 2):

$$NECB = dC/dt = -NEE + F_{CO} + F_{CH4} + F_{VOC} + F_{DIC} + F_{DOC} + F_{PC}$$

where NEE is net ecosystem exchange (CO_2 flux from ecosystems to the atmosphere), F_{CO} is carbon monoxide flux to the ecosystem, F_{CH4} is the methane flux to the ecosystem, F_{VOC} is the flux of volatile organic compounds to the ecosystem, F_{DIC} is the flux of dissolved inorganic C to the ecosystem, F_{DOC} is the flux of dissolved organic C to the ecosystem, and F_{PC} is the flux of particulate carbon to the ecosystem (Randerson *et al.* 2002; Chapin *et al.* 2006). NEE is used in the above equation instead of NEP because there is no consistent relationship between NEE and NEP since the relationship depends on the magnitude of F_{DIC}, which in some systems such as streams might dominate the inorganic C flux, and on non-respiratory sources of CO_2 (e.g. wildfire).

On short time scales, GPP and respiration (i.e. the components of NEP) are the processes that typically consume and produce, respectively, most of the inorganic C in an ecosystem and are therefore the fluxes that dominate NECB. During the day and during summer, for example, GPP typically exceeds respiration, resulting in a positive NEP. This reduces the concentration of CO_2 and/or DIC within the ecosystem and generates a diffusion gradient that causes CO_2 to enter the ecosystem from the free atmosphere (a negative NEE). Conversely, at night and during winter, respiration typically dominates CO_2 exchange, resulting in a negative NEP. This increases the concentration of CO_2 and/or DIC inside the ecosystem and generates a diffusion gradient that causes CO_2 to move from the ecosystem to the free atmosphere (a positive NEE). Thus, over short time scales and when ecosystems are close to steady state, GPP and respiration are two of the key processes that drive NECB, and [-NEE] often closely approximates both NEP and NECB in many ecosystems (Baldocchi 2003).

NEP fails to describe fully the effects of ecosystems on C exchange, when NECB diverges from NEP. This occurs when C fluxes other than C fixation and respiration occur or when inorganic C enters or leaves the ecosystem in dissolved form. These fluxes include leaching loss or lateral transfer of C from the ecosystem (e.g. from farms to cities); emission of volatile organic C, methane and carbon monoxide; and soot and CO_2 from non-respiratory sources such as wildfire. C fluxes in addition to NEP become significant components of NECB particularly over long time scales (e.g. landscape development), in ecosystems undergoing environmental or biological changes (e.g. climate or land use change), and in ecosystems with large lateral C transfers (e.g. streams, estuaries, wetlands and cities). For example, high-latitude warming has caused CH_4 flux from tundra ecosystems to increase substantially (Christensen *et al.* 2003; Walter *et al.* 2006) and wildfires to release substantial carbon through non-respiratory pathways (Kasischke &

Turetsky 2006). Similarly, forest clearing for agriculture and urban development has led to large changes in carbon exchanges that are only partly captured by changes in NEP.

In summary, photosynthesis, respiration and their balance (NEP) generally account for a large proportion of ecosystem C fluxes, particularly if they account for variation in these fluxes through cycles of disturbance and ecosystem renewal. This explains the effectiveness of NEP as a conceptual framework for describing geographic patterns of C exchange between ecosystems and the atmosphere. This conceptual framework requires expansion when fluxes other than those due to photosynthesis and respiration are large, which generally occurs during times of rapid change, as during agricultural expansion, thawing of permafrost, or with increased frequency or severity of wildfires.
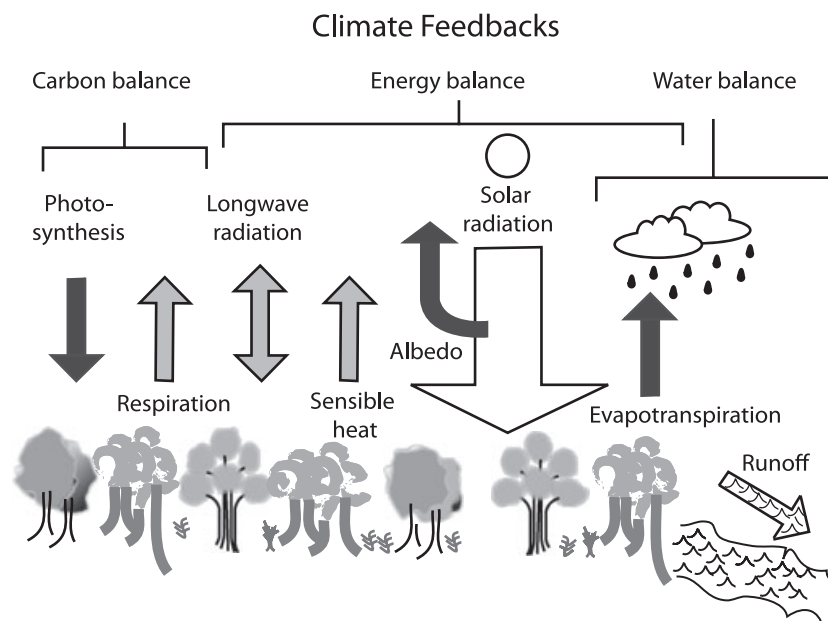
Multiple climate feedbacks

Linkages between plant and soil processes may influence the global climate system through more than uptake and release of CO_2 to the atmosphere. These include (i) emission or absorption of other greenhouse gases such as CH_4 and N_2O; (ii) altered albedo (the proportion of solar radiation that the Earth's surface reflects back to space), which influences the amount of heat transferred from ecosystems to the atmosphere; (iii) altered evapotranspiration (evaporation from the Earth's surface plus that from leaves), which cools the surface and provides moisture to form clouds and fuel atmospheric mixing; (iv) altered longwave radiation, which depends on surface temperature and cloudiness; (v) changes in production of aerosols (small particles that scatter and absorb light); and (vi)

changes in surface roughness, which determines the strength of coupling between the atmosphere and the surface and therefore the efficiency of water and energy exchange (Fig. 3) (Field *et al.* 2007; Chapin *et al.* 2008).

In some cases, a given ecosystem change can have both warming and cooling feedbacks to climate. Increases in forest cover, for example, generally lead to C sequestration (a cooling effect on climate) but cause an augmentation of energy absorption as albedo is reduced (a warming effect on climate). It has been suggested, for example, that afforestation is likely to slow climate warming in tropical forests, with marginal benefits in temperate forests, and could become counterproductive in boreal forests (Bala *et al.* 2007). This is because the effect of reduced albedo is particularly pronounced at high latitudes, where forests or shrublands have a much lower albedo than snow-covered tundra or a deforested landscape (Bala *et al.* 2007; Euskirchen *et al.* 2007; Chapin *et al.* 2008). Loss of vegetation cover in drylands associated with desertification can also alter the energy budget sufficiently to influence local to regional climate (Foley *et al.* 2003).

In summary, plant and soil processes may influence both greenhouse gas and energy balance feedbacks to the climate system. The direction of individual feedback pathways may be different and affect the climate system at different temporal and spatial scales. Climate system models are only beginning to consider how the interactions among these climate feedbacks influence the dynamics of the climate system (Bonan 2008). An improved understanding of these interactions is critical to policies aimed at mitigating climate warming. Currently trace gas fluxes are the only climate feedback being considered in the policy arena.

Climate Feedbacks

Fig. 3. Three major categories of climate feedbacks (each shown by the arrows beneath the bracket) between ecosystems and the climate system. Each of these ecosystem–atmosphere exchanges influences climate. Cooling effects on climate are shown by black arrows; warming effects by grey arrows. Arrows show the direction of the transfer; the magnitude of each transfer differs among ecosystems. The effects of aerosols and surface roughness are not shown. Redrawn from Chapin *et al.* (2008).

Conclusions

In summary, the balance between NPP and decomposition generally provides an adequate description of ecosystem C fluxes near steady state, for example geographic variation in C fluxes. However, understanding recent *changes* in the role of ecosystems in the global C cycle requires greater understanding of soil and microbial processes than is represented in most current climate–C cycling models. Critical gaps in the modelling of ecosystem-climate feedbacks include (i) nutrient and other controls that couple photosynthetic C input to respiratory C outputs, (ii) non-CO_2 C fluxes that influence the climate system, and (iii) climate feedbacks in addition to C balance. Improved understanding and representation in models of soil C dynamics has important implications for patterns and rates of climatic change and for informed choices that society must make about the future condition of our planet.

Acknowledgements

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