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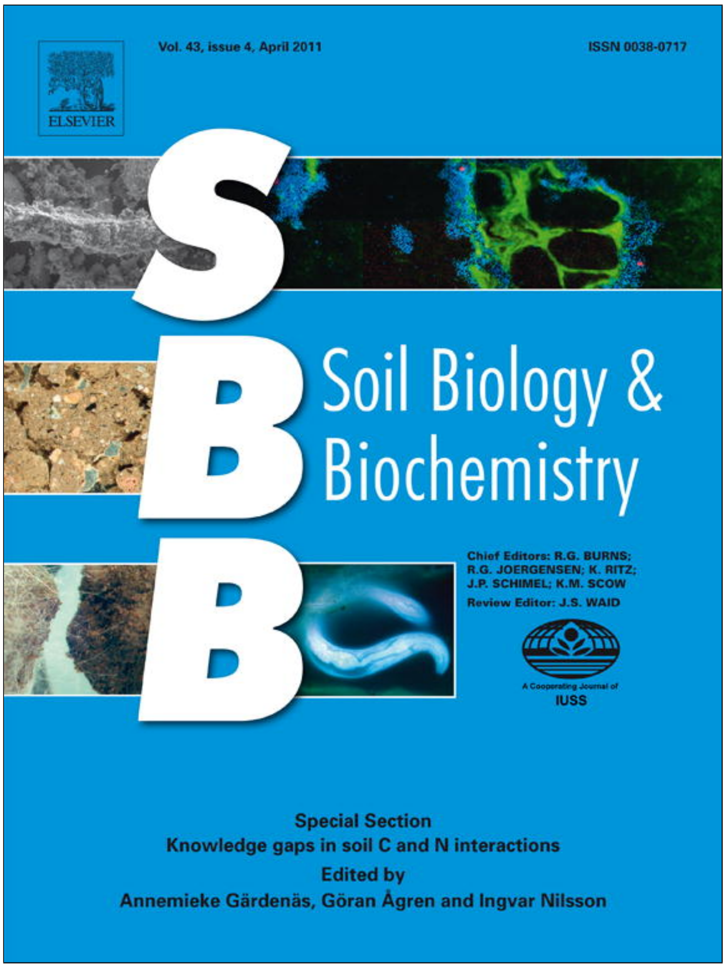
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Review

Knowledge gaps in soil carbon and nitrogen interactions – From molecular to global scale

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ABSTRACT

The objective of this review was to identify, address and rank knowledge gaps in our understanding of five major soil C and N interactions across a range of scales – from molecular to global. The studied five soil C and N interactions are: i) N controls on the soil emissions of greenhouse gases, ii) plant utilisation of organic N, iii) impact of rhizosphere priming on C and N cycling, iv) impact of black N on the stabilisation of soil organic matter (SOM) and v) representation of fractions of SOM in simulation models. We ranked the identified knowledge gaps according to the importance we attached to them for functional descriptions of soil–climate interactions at the global scale, for instance in general circulation models (GCMs). Both the direct and indirect influences on soil–climate interactions were included.

We found that the level of understanding declined as the scale increased from molecular to global for four of the five topics. By contrast, the knowledge level for SOM simulation models appeared to be highest when considered at the ecosystem scale. The largest discrepancy between knowledge level and importance was found at the global modelling scale. We concluded that a reliable quantification of greenhouse gas emissions at the ecosystem scale is of utmost importance for improving soil–climate representation in GCMs. We see as key questions the identification of the role of different N species for the temperature sensitivity of SOM decomposition rates and its consequences for plant available N.

1. Introduction

A large percentage of the Earth's active carbon (C) is found in soil organic matter (SOM) and its cycling rate is strongly linked to nitrogen (N) availability. It was recognised already in the 1990s, that N availability is the main governing factor controlling soil C response to climate change in N-limited ecosystems (Diaz et al., 1993; Ineson et al., 1996). This understanding has been emphasised through a number of research programmes studying interactions between the C and N balances in ecosystems, using both the present climate and simulated climate change conditions e.g. the Climex (Dise and Jenkins, 1995), Nitrex (Wright et al., 1995), Canif (Schulze, 2000) and Nitro-Europe (NitroEurope, 2006) programmes. Appreciation of the importance of soil C and N interactions for predicting the impacts of climate change has certainly increased, but we still lack a full understanding and quantification of the drivers (Hu et al., 2001; Hyvönen et al., 2007).

To date, the interactions between soil C and N are not adequately represented in general circulation models (GCMs) despite the

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importance attached to these interactions by the majority of soil and ecosystem scientists (Thornton et al., 2007). In 2000, some first attempts were made to incorporate soil feedback responses into GCMs (Cox et al., 2000) and these models are now considered too simplistic (Davidson and Janssens, 2006). It is possible that the influence of soil C and N interactions may to a certain extent be implicitly captured in the production and respiration predictions from GCMs for the recent past and present situations, assuming greenhouse gas fluxes are accurately quantified. However, this certainly does not mean that current representations are sufficient to accurately predict future greenhouse gas fluxes, together with their impact on the climate system. Future scenarios generated from GCMs may have significant biases if soil C and N interactions are being modified due to global change. Moreover, there is a growing body of literature suggesting that these interactions will change in response to a variety of factors, such as increased carbon dioxide (CO_2) fertilisation, land use and management as well as changing precipitation and temperature regimes. The challenge is to incorporate realistic aspects of the interactions between ecosystem/biome N status and trace gas emissions in coupled GCMs. Although the majority of basic knowledge is present in the literature, uncertainties still remain.

Bouma (2005) distinguished major kinds of knowledge gaps hampering progress in research: i) 'We know what we don't know', ii) 'We don't know what we know', and iii) 'We don't know what we don't know yet' (Bouma, 2005; pp. 73). The first kind is the most tractable one, and here we attempt to identify some of the key scientific issues falling under this heading since awareness of such knowledge gaps is a convenient starting point for progress in scientific understanding. The second type of knowledge gap is less tractable and may cause some degree of frustration. For example, there is still no standard way of measuring such a seemingly simple process as litter decomposition; even the results of the long-standing mesh bags techniques are difficult to interpret. So, for something even as seemingly straightforward as monitoring litter decomposition, we actually 'don't know what we know'. The third type of knowledge gap is the most problematic one. Science abounds with examples of falsely inherited wisdom or total ignorance of extremely important processes. For example, until the mid-1990s, the uptake of organic N by plants was assumed to be negligible. Consequently research focussed entirely on inorganic N and therefore, descriptions of N cycling in models often lack this entire pathway (Schimel and Bennett, 2004). We have identified five major knowledge gaps relating to soil C and N interactions relevant for soil–climate interactions.

i) *To what extent does N control the soil emissions of the greenhouse gases CO_2, CH_4 and N_2O?*
ii) *To what extent do plants utilise organic N?*
iii) *To what extent does rhizosphere priming affect C and N cycling?*
iv) *How does black N affect SOM stability?*
v) *How could different fractions of SOM be adequately represented in models at various scales?*

Several of these questions are hybrids of the first and second types of knowledge gaps. We know that processes, such as priming by roots, are potentially important; however, we cannot yet advise the GCM modellers whether these processes need to be represented in global models or how this could be achieved. We also know that N controls greenhouse gas emissions, but still, we cannot fully assess how strong these interactions are, and although there are studies quantifying these effects locally, it is difficult to generalise to a global scale.

The objective of this study was to identify, address and rank the knowledge gaps in the five topics on soil C and N interactions at molecular, organism, ecosystem and global scale. The ecosystem scale is here defined as field and forest stand scale. We ranked the knowledge gaps identified according to the importance we attached to them for functional description of soil–climate interactions at the global scale, for instance in GCMs. Both direct influences on soil–climate interactions and indirect influences through plant N availability were considered and how these influences might change with climate change.

An attempt was made to identify the governing factors at specific scales, i.e. what do we know, or what do we not know. We also discuss possible effects of climate change on the controlling factors, and what needs to be considered when moving between scales. Upscaling is an important and recurring issue throughout these discussions and, wherever possible, estimation has been made of where the uncertainties are, both regarding structural uncertainty due to lack of understanding of processes and uncertainty due to data quality and aggregation. For instance, what are the possible consequences of upscaling short-term experiments at microorganism scale to long-term global trends or those of aggregated data derived at different scales?

2. Knowledge gaps in five topics of soil C and N interactions

2.1. To what extent does N control the soil emissions of the greenhouse gases CO_2, CH_4 and N_2O?

There is a long-standing awareness of the importance of soil management as a central element in the sustainability or collapse of human societies at local and regional scales (Russell, 1973; Diamond, 2005). However, the full realisation of the importance of soils in maintaining atmospheric concentrations of greenhouse gases at the global scale first entered mainstream thinking as the 21st Century approached. The assessments of the Intergovernmental Panel on Climate Change (IPCC, 1995) and the incorporation of soil feedbacks into coupled GCMs (Cox et al., 2000) clearly demonstrated the developing concepts of the major role played by soils in climate feedback processes. Indeed, it is from soils that some of the greatest climate destabilising feedbacks can be expected (Heimann and Reichstein, 2008). The increases in atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) are of major importance when considering future climates. All three of these gases have a substantial part of their cycling, either production, consumption or storage, associated with soils and here we consider relevant knowledge across a number of scales and how N interacts with these transfers.

At the *molecular scale* there is considerable fundamental knowledge, gained largely from laboratory studies investigating the underlying reactions associated with the production and consumption of these three important trace gases. Undoubtedly, new pathways and reactions will be discovered. Of the three greenhouse gases mentioned above, CO_2 is one of the most frequently measured and more fully understood gas emitted from soils. Biological oxidation of energy-rich molecules in soils results in the uptake of oxygen, with a concomitant release of CO_2, a process termed soil respiration (Russell, 1905). The major components of this net flux are normally the combined respiratory activities of soil micro-organisms, such as bacteria and fungi, in the bulk soil (heterotrophic) and those from plant roots (autotrophic) (see Gloser and Tesarova, 1978; Högberg and Read, 2006; Heinemeyer et al., 2007). The contributions from heterotrophs and autotrophs to soil respiration are probably comparable in magnitude (Högberg et al., 2002). Behind the measured net CO_2 fluxes are numerous processes of CO_2 production and consumption, both biotic and abiotic.

Identifying, understanding and quantifying these processes is crucial, as we seek to find new ways to sequester increasing amounts of C from the atmosphere. The underlying biochemistry behind the biotic production of CO_2 in soils is highly conserved, and our understanding at the molecular scale is excellent. However, CO_2 production from abiotic sources in soils cannot be ignored and more sophisticated analytical techniques need to be applied to make the necessary distinctions (Biasi et al., 2008). Similarly, at the molecular level, we understand the mechanisms through which autotrophs can assimilate CO_2, but there are probably additional anapleurotic pathways active, potentially modified by starvation, the availability of oxygen and N, as demonstrated for yeast in laboratory studies (Wu et al., 2004) and for forest ecosystems *in situ* (Fleischer, 2003). The abiotic uptake of CO_2 by soils, resulting from reactions with, for instance Ca^{2+} and Mg^{2+} minerals to form carbonates, is proposed as a benign form of CO_2 sequestration (Parsons et al., 2004).

In order to manage C in soils, we need to know more about the quantities and turnover times of key organic soil constituents and their major controlling factors. The role of cutin in controlling responses of SOM to changes in temperature has recently been highlighted (Feng et al., 2008), and the sensitivity to temperature change of other components in soils is heavily debated (Fang et al., 2005; Knorr et al., 2005; Kirschbaum, 2006; Davidson and Janssens, 2006; Hartley and Ineson, 2008; Hartley et al., 2008; Bradford et al., 2008a; Gershenson et al., 2009). We do know that the availability of N has a profound effect on decomposition rates (Melillo et al., 1982).

Hypotheses addressing the question of why contrasting effects of N additions on decomposition of high and low quality litters had been observed, were first clearly formulated by Fog (1988). A reduction in the total activity of decomposers occurs in poor quality substrates, such as wood, when more readily available N is added; thus, the balance of chemically recalcitrant and available C and N should dictate whether CO_2 release from a substrate will increase or decrease on further N addition (Fog, 1988). Later research has shown that N enrichment can reduce microbial biomass and/or the activity of various enzymes, resulting in declines in CO_2 emissions (Treseder, 2008), and such declines do not appear to be closely coupled to changes in SOM chemistry, which was one of Fog's original hypotheses (Sjöberg et al., 2003, 2004).

Methane is another key greenhouse gas, the production of which is strongly influenced by soil C and N interactions. The molecular aspects of CH_4 production and consumption by micro-organisms are well studied and there is a comprehensive literature derived from research involving pure cultures of archaea and bacteria, ruminant animals, anaerobic digesters, entire wetlands and upland soils. CH_4 production occurs under anaerobic conditions and in systems with a relatively low redox potential, altering the competition for the major methanogenic substrates such as acetate (CH_3COO^-), formate ($HCOO^-$), H_2 and CO_2 (Fenchel et al., 1998). The role of available N in affecting rates of methanogenesis and methanotrophy (the oxidation of CH_4) is not straightforward, we know that at the molecular level, nitrate (NO_3^-) can act as an alternative electron acceptor (forming N_2O) and, consequently, exerting an obvious impact on methane production. According to a laboratory experiment reported by Yu and Patrick (2004), it should be possible to keep water-saturated paddy-rice soil within a certain redox potential window to minimise both CH_4 and N_2O emissions. For simplicity, all methanogens are normally assumed to use the same limited range of reactions and mechanisms for energy conservation, but this can be questioned. Thauer et al. (2008) showed that the presence of cytochromes appears to dictate whether the first and last steps in methanogenesis are coupled chemiosmotically or through cytoplasmic enzyme complexes. Similarly, the oxidation of CH_4 is not a single simple process, and the range of recognised reactions, and organisms involved, continues to grow (Raghoebarsing et al., 2006; Maxfield et al., 2006). Although work with single organisms has been crucial in revealing the nature of the fundamental reactions, this information only goes some way to revealing what is possible in nature.

The interactions between N supply and CH_4 oxidation were thoroughly discussed in an early review by Hanson and Hanson (1996). Numerous studies have shown a sensitivity of CH_4 oxidation to disturbances in the N cycle. Steudler et al. (1989) demonstrated that nitrogenous fertilisers inhibit CH_4 oxidation in forest soils. However, there are a series of conflicting studies. For example both the growth and activity of methanotrophs in the root zone of rice are stimulated by the addition of NH_4^+ fertilizer (Bodelier et al., 2000). Bykova et al. (2007) found that pre-incubation with NH_4^+ completely inhibited CH_4 oxidation in an arable soil and similar impacts have been found for NO_3^- additions to forest soils (Wang and Ineson, 2003; Reay and Nedwell, 2004). Noll et al. (2008) demonstrated, with stable isotope probing (Radajewski et al., 2000), that CH_4-oxidizing bacteria in soil are not only controlled by their main substrates, CH_4 and O_2, but also by N availability. Thus, availability of N is one of the major factors limiting CH_4 consumption in various types of soils.

Bodelier and Laanbroek (2004) attempted to resolve the conflicting results for N impacts on CH_4 emission. They argued that much of the confusion can be removed if a 'bottom-up' approach is used for comparing results from different studies and the role of mineral N availability for the micro-organisms involved is ignored. The authors question the paradigm that N fertilisers inhibit CH_4 oxidation. The priority is clearly to obtain solid empirical flux data from a wide range of ecosystems, climate zones, and biome types and relate these fluxes to associated changes in microbial populations and activities; a principal challenge thereby is to resolve scale differences that traditionally keep the work of microbial and ecosystem scientists apart. Demonstrable, only partial understanding is gained when treating CH_4 fluxes as a 'black box', and ignoring the identity of the organisms involved. For example, CH_4 oxidation rates in one particular rice field soil were increased seven-fold by N fertilisation, but the fertilisation only activated a small subset of the CH_4 oxidizing population present in the soil (Noll et al., 2008).

Of all the greenhouse gases, N_2O is the one most directly related to anthropogenic management of soils, with the main human-related sources of N_2O being agricultural land (Davidson, 2009). Moreover, N_2O is emitted from a variety of unfertilised soils, particularly forest soils in the humid tropics. Basic understanding of the biochemical pathways resulting in the production of N_2O is good and the 'leaky pipe' conceptual model proposed by Firestone and Davidson (1989) has stood the test of time and is still a useful starting point. N_2O is produced via two main routes and by two functional groups of micro-organisms. The anaerobic denitrifier pathway, mainly fuelled by available C sources, requires besides anaerobic conditions NO_3^- as a substrate. In contrast, the nitrifier route, in which N_2O is released as an intermediate product during nitrification, is an autotrophic process requiring aerobic conditions and NH_4^+ as a substrate. However, the chemodenitrification contributions to N_2O fluxes are still poorly quantified, these are the chemical reactions of NO_2^- with organic matter at low pH, resulting in the production of NO, HNO_3 and H_2O and the formation of N_2, N_2O and CH_3ONO (Van Cleemput and Samater, 1996). Chemodenitrification fluxes may be important in acid soils under certain specific conditions, such as after the addition of urine (Williams et al., 1999).

Heavy utilisation of N fertilisers in crop production, or the application of N-rich wastes to agricultural soils typically results in N_2O emissions through a number of identified biochemical routes. Crude representations of N_2O emissions, such as multiplying an emission factor by the amount of N applied in agricultural systems, along with a background emission rate from other land use systems may provide some realism. However, the accuracy of these approaches may diminish if the underlying physical and chemical conditions in soils are modified by climate change, including soil C and N interactions. This could well introduce bias into the prediction of N_2O emissions by GCMs if not more process-based representations are developed.

2.2. To what extent do plant utilise organic N?

Plant uptake of organic N compounds has been studied since the early 20th century (Hutchinson and Miller, 1911; Brigham, 1917), but it has only recently gained extensive attention. Over decades, the general concept of organic N utilisation being limited to plants forming ecto- and ericoid mycorrhiza, plants growing in cold climates or in low pH soils, still prevails despite several early studies showing that non-mycorrhizal plants utilise organic N. Organic N utilisation is a widespread capacity among plants and all plant species tested have been found to take up organic N, suggesting this to be a ubiquitous capacity of plants. Plant utilisation of organic N is demonstrated in arctic (Kielland, 1994, 1997; Schimel and Chapin, 1996; Henry and Jefferies, 2002; Nordin et al., 2004), boreal (Näsholm et al., 1998; Nordin et al., 2001; Persson and Näsholm, 2001a; McFarland et al., 2002; Bennett and Prescott, 2004), temperate (Falkengren-Grerup et al., 2000; Finzi and Berthrong, 2005), Mediterranean (Hawkins et al., 2005) and alpine ecosystems (Raab et al., 1996, 1999; Lipson et al., 1999; Miller and Bowman, 2002). Similarly, many agricultural species readily take up organic N (Yamagata and Ae, 1996; Näsholm et al., 2000, 2001; Okamoto et al., 2003). Thus, at a whole-plant scale, plants are able to take up at least some organic N compounds such as amino acids, amino sugars and small peptides (Näsholm et al., 2009).

We also have some knowledge of the molecular mechanisms enabling the process, and this knowledge is rapidly growing. In the model plant *Arabidopsis thaliana*, three transporters mediate root uptake of amino acids: the Lysine Histidine Transporter 1 (Hirner et al., 2006; Svennerstam et al., 2007), Amino Acid Permease 5 (Svennerstam et al., 2008) and Amino Acid Permease 1 (Lee et al., 2007). Lysine Histidine Transporter 1 and Amino Acid Permease 5 are probably the major transporters active in the concentration range of interest here, while Amino Acid Permease 1 may mediate uptake only at high (mM) concentrations. However, at the stand or ecosystem scale, there is little quantitative information on the importance of organic N utilisation by plants. It seems that climate and hydrology have a large influence on plant utilisation of organic and inorganic N. Organic N is more important in cool and wet environments than in hot and dry environments (Schmidt and Stewart, 1999; Warren, 2006).

The use of dual (^{13}C, ^{15}N) labelled amino acids has helped us to characterise uptake of various compounds in the field and to quantify the extent of short-term uptake of intact and mineralised amino acids. The detection of both ^{13}C and ^{15}N in plant tissues indicates uptake of intact amino acids. Uptake of ^{13}C and ^{15}N tracers can also occur from decomposition products of added dual-labelled amino acids, such as ^{13}C labelled organic acids or $H^{13}CO_3^-$ and $^{15}NH_4^+$. Plant uptake of intact amino acids can be verified with GC–MS (gas chromatography-mass spectrometry) analysis of tissue extracts of plants exposed to dual-labelled amino acids. Since the methodology for this verification was developed (Persson and Näsholm, 2001b), it has been applied in various field and pot experiments studies, and has confirmed that plants can acquire intact amino acids (Öhlund and Näsholm, 2001; Näsholm et al., 2001; Persson et al., 2003; Nordin et al., 2004). One short-coming of the dual labelling approach is that no information on the quantitative importance of organic N for plants is provided because plants gradually lose ^{13}C during the metabolism of absorbed organic N (Näsholm et al., 2009). The factors governing organic N utilisation by plants include production rates, fluxes and concentrations of organic N compounds in the soil, uptake capacities of plant roots and mycorrhizas, and competition between plants and non-symbiotic micro-organisms. Although the capacity for organic N uptake and utilisation may be ubiquitous for plants, it cannot be excluded that there are inter- and intra-species differences in the extent to which this capacity is developed and realised in the field. The few studies addressing this question reached different conclusions (McKane et al., 2002; Harrison et al., 2007, 2008). Therefore, we cannot forecast the extent to which altered climatic and edaphic conditions will alter plant organic N utilisation and how such changes alter the competitive ability of different plant types.

Soil N availability shows a wide variability. Many agricultural soils display concentrations of inorganic N in the mM range, but with concentrations of individual organic N compounds in the low μM range, suggesting plant N nutrition should be dominated by inorganic N in these systems. At the other end of the scale, many forest soils display low NO_3^- concentrations, NH_4^+ concentrations in the range 10–100 μM, and concentrations of individual organic N compounds in the range 1–10 μM (cf. Miller and Cramer, 2004). However, free amino acids may constitute less than 0.5% of the total soluble organic N pool, which is dominated by amino acids bound in proteins and peptides (Andersson and Berggren, 2005). In many soils of natural ecosystems, such as boreal forests, organic N dominates over inorganic N in the soil solution (Näsholm et al., 1998; Kielland et al., 2007; Kranabetter et al., 2007) and the turnover of organic N is rapid with half-lives of amino acids in the range of a few hours (Jones et al., 2005; Kielland et al., 2007). A critical choice is whether a relevant comparison between organic and inorganic N should be based on concentrations of individual compounds (e.g. NO_3^- vs. glycine) or groups of compounds (e.g. inorganic N vs. total amino acids). This choice is also critical when interpreting results from labelling studies. In such studies, dilution of added labelled compounds by pre-existing levels of unlabelled compounds are calculated and used to compare uptake rates of different compounds. Characterisation of the uptake mechanisms indicates that amino acid acquisition by the model plant *Arabidopsis* is governed mainly by two different transporters; one combined for acidic and neutral compounds, and one for basic compounds. If this pattern is valid for other non-mycorrhizal plant species, it means that from a plant-root perspective, all acidic and neutral species are part of one pool, while all basic species are part of another pool. Experimentalists and modellers should recognise and use this as a basis for comparisons. It is well documented that relatively low levels of NH_4^+ may inhibit uptake of NO_3^-. By contrast, interactions between inorganic and organic N compounds in plant N uptake are not well studied, but available data suggest that this interaction is small and may possibly favour uptake of organic N (Thornton and Robinson, 2005). This means that plants may not show "preference" for inorganic N when it is available, but may acquire N from organic and inorganic N simultaneously. Implicitly, the role of organic N for plant N nutrition may be dynamic in time and space.

Rates of production of simple (monomeric) organic N compounds in soil are found to be important determinants of plant organic N utilisation (Leadley et al., 1997; Schimel and Bennett, 2004). The competition between plants and micro-organisms for these substrates is usually suggested as a second major factor limiting the role of organic N for plants. Studies allowing for a full accounting of added ^{15}N labelled compounds indicate that plants are inferior competitors for both inorganic and organic N compared to micro-organisms and in the short-term only acquire a small fraction of the added N (Harrison et al., 2007, 2008; Kaye and Hart, 1997). Still, plant biomass and plant N are generally much higher than microbial biomass and microbial N, implying that short-term competition studies cannot accurately describe competition between these groups of organisms (Kaye and Hart, 1997). One problem with these studies is that plant symbiotic micro-organisms cannot be separated from the non-symbiotic ones, leading to underestimation of N acquired by plants (Eviner and Chapin, 1997).

Until now, no single experiment has been able to quantify to which extent plants utilise organic N in a specific ecosystem. We are thus left with speculations about the extent of organic N utilisation, although its very existence is well demonstrated by laboratory and field studies. A possible indicator of the importance of organic N is its contribution to the N pool in the soil solution. However, this approach is complicated by the slower diffusion rates of organic N than NO_3^- and by a lack of information on the extent to which other compounds, besides free amino acids, are directly accessible for plants. A large fraction of organic N in the soil solution consists of peptides and small proteins (Andersson and Berggren, 2005). Other sources of dissolved organic N are amino sugars, nucleotides, amides, and amines.

N has a pivotal role in regulating the global C cycle. An accurate estimation of all forms of plant available N is therefore crucial for the functioning of GCMs. There are several potential ramifications of a significant contribution of organic N to plant N nutrition, including the effects on growth, root-to-shoot ratio and soil pH.

2.3. To what extent does rhizosphere priming affect C and N cycling?

A critical and poorly understood link between vegetation and soil C and N cycling is how living roots alter or "prime" the decomposition rate of SOM. SOM priming was first described by Löhnis (1926) as the addition of fresh crop residues to soil, which accelerated the decomposition of SOM. Priming of SOM by living roots due to rhizodeposits, such as carbohydrates (including sugars), organic acids (including amino acids), hormones, vitamins, dead cells and other substances released from plant roots in small quantities is observed in various plant communities (Bottner et al., 1999; Dijkstra and Cheng, 2007a). The mechanisms to explain the wide range of responses reported are not yet established, despite that compelling hypotheses to address rhizosphere priming have been proposed (Kuzyakov, 2002). Consequently, current ecosystem- and global-scale models of terrestrial C cycling do not consider rhizosphere priming, even though it can be significant. Living roots both negatively (from 50% lower) and positively (up to 380% higher) affect existing soil C and N mineralisation rates and SOM loss can be as much as the amount of root C added to the soil (Cheng and Kuzyakov, 2005; Cheng, 2009). Hypotheses of the cause of SOM priming by living roots have focused on two interconnected areas: i) effects of root deposited C on microbial activity (Fontaine et al., 2003; Hamer and Marschner, 2005; Neill and Gignoux, 2006) and ii) N and/or water competition between plant roots and microbes (Liljeroth et al., 1994; Dijkstra and Cheng, 2007a). Questions related to the role of micro-organisms are whether priming is the result of a more general enzymatic activity of a broad microbial community or whether there are particular functional groups that stimulate SOM mineralisation to obtain N and P when supplied with C-rich, easily degradable substrates. The release of energy-rich rhizodeposits from roots increases microbial activity in general and enhances SOM decomposition rates (Kuzyakov et al., 2000). Faster microbial biomass turnover explained the rhizosphere-derived SOM priming under soybean and wheat (Cheng, 2009). This relationship between microbial turnover rate and enhanced SOM priming in the rhizosphere is sensitive to substrate utilisation efficiency, but not to microbial maintenance. However, we lack more fundamental understanding about the importance of the chemical composition of the substrate in relation to the recalcitrance of the SOM being primed.

The reactions of specific functional groups of micro-organisms to rhizodeposition have been studied (Fontaine and Barot, 2005). Fontaine et al. (2003) suggested that SOM priming events arise from the relative and competitive response of r-strategists and K-strategists among heterotrophic soil micro-organisms. The r-types are growing rapidly under conditions of high resource availability and the K-types exhibit lower growth rates, but higher substrate affinities. As micro-organisms are often energy limited in soils, rhizodeposits from roots may activate r- and/or K-strategists with labile, energy-rich root exudates (Jones et al., 2004). If K-strategists were competitive for rhizodeposits, SOM degradation would be enhanced – as these microbes are considered to produce a wide assortment of oxidative and hydrolytic enzymes that can degrade SOM (Fontaine and Barot, 2005). In contrast, a negative priming effect would occur when r-strategists out-compete K-strategists for exudates due to the suppression of enzyme production. The presence of an active rhizosphere increased SOM decomposition by 20% under oat and stimulated uptake of soil organic C by Gram (+) bacteria and actinobacteria, while Gram (–) bacteria and fungi assimilated significantly less soil organic C than in unplanted soils (Bird et al., 2011).

Competition for N and water between plant roots and microbes is the second hypotheses of the cause of SOM priming. The relationship between N availability and SOM priming has been observed in field studies (Bradford et al., 2008b) and a greenhouse experiment under oat and N fertilisation (Bird et al., 2011). If microbial activity is stimulated by rhizodeposits, an altered competition for N between plants and micro-organisms should occur in N-limited soils. Accordingly, DeAngelis et al. (2008) found higher N-cycling enzymatic activity (chitinases, proteases) and amounts of dissolved N in the rhizosphere of wild oat than in bulk soil without roots. This greater N-cycling activity in the rhizosphere was accompanied by an increase in bacterial density that may have been fuelled by rhizodeposits decreasing limitations on microbial growth and activity (DeAngelis et al., 2008). By contrast, Cheng (2009) showed that rhizosphere-primed C mineralisation was decoupled from net N mineralisation, negating the often assumed proportionality between soil C and N processes. Others have reported nitrification to be negatively affected in the rhizosphere (Philippot et al., 2009 and references therein) and to vary along the plant root due to rapid uptake of NH_4^+ by the older parts of the root (Herman et al., 2006). For example, gross nitrification rates in the soil near the root tip of *Avena barbata* were the same as those in bulk soil, whereas rates were lower in the soil near the older root sections. In addition to N, the effect of soil P availability on rhizosphere-related SOM priming may be significant and opposite to N (Bradford et al., 2008b). Plant uptake of water from the rhizosphere reduces soil moisture, which may limit microbial activity and the degree of SOM priming (Dijkstra and Cheng, 2007b). Alternatively, the more frequent wetting–drying cycles and more pronounced moisture ranges in the rhizosphere, compared to the root-free soil, may accelerate C cycling (Lundquist et al., 1999), which recently was identified as one of the main mechanisms of rhizosphere priming (Cheng, 2009).

The plant species and its phenological stage controls rhizosphere SOM priming (Cheng and Kuzyakov, 2005). However, information is limited on differences among plant species in the amount, composition and release patterns of root exudates and other root-derived C products. In early phenological stages and/or during the first half of the growing season, exudation is expected to be dominant, whereas, after maturing and/or during autumn and winter, deposition of root tissues may be increasingly important. One can speculate that seasonal dynamics may be more pronounced for annual species than for perennial species. Such dynamics would only be critical for larger scale modelling if the underlying species composition varies sufficiently with time and over a larger region to have a significant influence on the priming effect.

Rhizodeposits may also impact N cycling in other ways as discussed above. Analysis of the effect of root-derived organic compounds on the NO_3^- reducing- and denitrifying bacterial communities showed a stimulation of NO_3^- reduction and denitrification, but had little or no effect on the community composition (Henry et al., 2008; Mounier et al., 2004). Nevertheless, some studies have shown plant species to significantly influence denitrifier community composition (Bremer et al., 2007; Patra et al., 2005; Ruiz-Rueda et al., 2009), but if this is due to rhizodeposits or other plant-selective forces is not known. Archaeal *amoA* transcript levels and ammonia oxidizing archaea are prevalent at higher levels than the bacterial counterpart in the rhizosphere (Chen et al., 2008; Herrmann et al., 2008). This supports the hypothesis that ammonia oxidizing arcahea can be mixotrophs and/or heterotrophs (Hallam et al., 2006; Jia and Conrad, 2009; Tourna et al., 2008) and highlights the role of archaea in C and N interactions at the population level.

The following questions need to be addressed to adequately explain the mechanisms and main controllers driving rhizosphere effects on SOM cycling and better predict how plant roots affect C and N cycling at the ecosystem level:

i) Does the microbial community composition affect rhizosphere-related SOM priming? If so, at what taxonomic or functional level can that control bebest expressed for predictions?
ii) How does N or P limitation interact with rhizosphere-related SOM priming?
iii) Are rhizosphere-priming effects similar for soil organic C and N mineralisation?
iv) How can moisture changes by roots be linked to microbial SOM priming activity?
v) What are the links between plant species and rhizosphere effects on SOM decomposition?
vi) How will climate change effect rhizosphere priming?

Quantification and description of root exudates *in situ*, both among plant species and across time are crucial for improving basic understanding of the priming interactions in soil (Phillips et al., 2008). Studies on SOM priming have distinctly quantified C and N pool dynamics, often using isotopic tracers (^{13}C, ^{14}C), into separately existing SOM and plant-derived rhizodeposits (Kuzyakov et al., 2000; Cheng and Kuzyakov, 2005). We suggest that future research should focus on clarifying the links between C and N with the use of dual-isotopic tracers (^{13}C and ^{15}N). Cheng (2009) presented very different effects of roots on soil C and N mineralisation rates. We posit that research attempts to link SOM priming flows to ecosystem-level environmental variables, such as temperature, may be especially beneficial as Bader and Cheng (2007) reported much lower Q_{10} values (i.e. the increase in decomposition rate for 10° increase in temperature) for soil C cycling within the rhizosphere than in root-free soil. The effects of roots on soil C cycling are multiple, interactive, and include both physical and chemical metabolic limitations and triggers. The factors controlling the response of soil microbial communities need to be better understood to improve understanding of rhizosphere priming. This requires elucidation of specific enzyme dynamics, pathways and the interactions with N, P, and soil moisture on SOM decomposition. Rhizosphere priming may underlie some of the changes observed in soil C under simulated climate change conditions. For example, an increase in root exudates under elevated CO_2 concentrations (Pendall et al., 2004) may accelerate SOM decomposition, thereby, reducing soil C under future climates. Furthermore, root litter of plants grown under elevated CO_2 concentrations may decompose at a different rate than roots grown under ambient conditions (van Ginkel et al., 1996; Joffre and Ågren, 2001; Sindhøj et al., 2004). Elevated CO_2 concentrations may shift the rhizosphere to a state of enhanced surplus of C compared to available N for plants and micro-organisms (Kuzyakov, 2002). However, climate shifts may influence other major factors regulating root activity such as soil moisture and availability of other nutrients. Consequently, we suggest that future research on rhizosphere priming should address how several factors simultaneously affect soil microbial community response to living roots and thereby consider the impact of plant species, soil moisture, nutrient status, temperature, and chemical composition of root deposits and SOM.

2.4. How does black N affect SOM stability?

Charred organic N, here called black N, is an integral part of charcoal produced from vegetation, litter, and humic material subjected to fire. Nitrogen tends to be incorporated into molecules that are heat resistant. Wood, with a low N content, produces a char material with an atomic C-to-N ratio ranging from 440 to 630. Char from humic substances or N-rich vegetation, such as grass species, has a much lower ratio ranging from 7 to 14 (Almendros et al., 1990; Knicker, 2007). Black N might play an important role in the stabilisation of SOM in most fire-affected regions; however, in most black C models, black N is neglected. Considering the high frequency of vegetation fires on a global scale, black N could be equally important as black C for the function of char as a C sink.

Very little is known about the chemical structures and recalcitrance of black N compounds towards microbial and chemical degradation. This means that the persistence and turnover rates of black N in soils cannot be estimated at present. A chemical characterisation of alterations occurring during the formation of black N has been initiated (Knicker et al., 2008). Peptides and proteins are the major N-containing molecules in char sources such as vegetation, litter, and humic material (Knicker, 2004). Knicker et al. (2008) used the protein casein as a model substance, which was charred under controlled conditions. Approximately 62% of the initial C content and 46% of the initial N content remained after exposure to 350 °C for 8 minutes under aerobic conditions. When rye grass (*Lolium perenne* L.) was charred under the same conditions, 34% of the C and N content was recovered. Solid-state ^{13}C NMR (Nuclear Magnetic Resonance) and ^{15}N NMR revealed that N-containing pyrogenic structures mostly consisted of pyrrole/indole-type N, with minor contributions from pyridine N and possibly 2.5-diketopiperazines as well as pyrroline, and pyrrolidine (Fig. 1; Almendros et al., 2003; Knicker et al., 2008). Pyrolysis analyses indicate an increase of imidazole (González-Vila et al., 2001). Such heteroaromatic compounds are not observed in SOM decomposed by micro-organisms (Knicker et al., 1993, 1997; Knicker, 2000) and, consequently, these compounds are proposed as possible indicators of a fire history (Knicker et al., 2005).

The contributions of these heterocyclic chemical structures to the bulk char can be estimated by using their atomic C-to-N ratios. If C-to-N = 4, as found in pyrrole, is assumed, such structures could account for more than 50% of the black C in a grass char with a C-to-N ratio of 7.9, if the remainder consists of pure organic C compounds (Knicker et al., 2008). Alternatively, in a char produced from peat with a C-to-N ratio of 34 (Almendros et al., 2003), C in heterocyclic N compounds may have contributed to at least 12% of the total “black C” pool. Such simple calculations demonstrate that char models, assuming a graphite-like structure with no N, are strongly oversimplified. Only one structural concept for charcoal considers the black N component (Knicker et al., 2008). This concept describes chars as heterogeneous mixtures of thermally altered macromolecules with N and O (and probably S) substitutions as a common feature. These mixtures include remains of the lignin backbone and a significant contribution of pyrolysis products, such as furans and anhydrosugars from cellulose, and heteroaromatic N from peptides (Knicker, 2007). This concept suggests a lower biological and chemical stability of pyrogenic organic matter (PyOM) compared to the assumptions usually made in black C models. The proposed chemical composition is consistent with an observed and

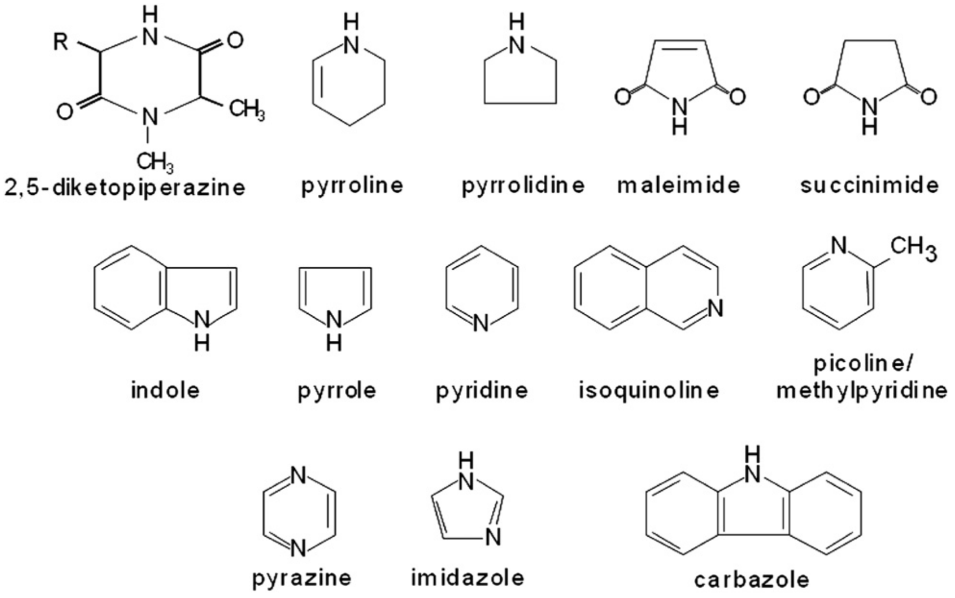

Fig. 1. Chemical structure of some black N compounds expected to be formed during charring of peptides and proteins.

unexpectedly high biodegradability of naturally occurring chars (Bird et al., 1999). However, most approaches to quantify black C are based on polyaromatic structures, which resist both thermal and chemical oxidation (Masiello, 2004). Therefore, new concepts could provide a much clearer picture of the analytical variability of black C obtained from the same reference materials, depending on the method used (Currie et al., 2002). New approaches are needed that consider the high heterogeneity and the presence of oxidizable functional groups in order to obtain a correct quantification of char in soils.

Although PyOM may not be as recalcitrant as assumed, N in a heterocyclic form should still be less accessible for micro-organisms than N in other chemical structures (Schnitzer and Spiteller, 1986). The incorporation of black N into SOM could have a long-term impact on soil biochemistry and N and C cycles. The assumption of a high biological stability of black N is supported by the identification of heterocyclic N in various fire-affected soils. In Neolithic paddy fields, almost all organic N occurred in N-heterocyclic species (Maie et al., 2006; Knicker, 2007). Although burning may increase the concentration of organic N in soils, the long-term N availability for plant production was found to decrease in some Australian soils (Knicker and Skjemstad, 2000), resulting in a lower litter production and, consequently, a decline of the input of fresh soil organic matter. Data collected so far highlight that black N needs further attention to obtain a better understanding of SOM stabilisation and the relationship between organic N and C sequestration.

Black N should be considered as an integral part of the char produced from vegetation, litter, and humic material during fires. The relatively high N content of the char indicates that black N is an important factor determining the chemistry and stability of black C. Thus, the properties of black N should be considered in models attempting to simulate C cycling in soils on the global scale. Whereas, black C is considered as a factor for increasing C sequestration, the N moiety may some extent have an opposite effect. Black N mainly consists of immobilised N that could serve as an N source stimulating new primary production. Conversely, the formation of heterocyclic black N may have an inhibitory effect on N mineralisation and primary production, and on the eventual formation of new litter material necessary for replacing losses of soil organic matter. N limitation introduced by N immobilisation may even support an acceleration of SOM decrease. Therefore, black N introduction to soil may contribute to a decline in C sequestration. On the other hand, the so-called “liming” effect (formation of alkaline plant ash during burning) and the function of newly formed unstable char as a fertiliser may to some extent compensate for these effects, at least after a fire of low intensity (Knicker, 2007).

From this short discussion it should be clear that a much deeper understanding of the black C and black N chemistry is necessary if the aim is to deliver reliable model predictions of C and N cycling in fire-affected soils. There are, however, some important technical obstacles to overcome, including a better understanding of the full range of structures forming black N and new methods for quantifying N compounds. Consequently, knowledge of the global abundance of black N is limited, and quantification of the importance of black N for SOM stabilisation on the global scale is in its infancy. The roles of fire frequency and intensity require a better understanding, particularly as the frequency of fires is expected to increase as the future climate unfolds.

2.5. How could different fractions of SOM be adequately represented in models at various scales?

The heterogeneity of SOM with respect to its stability is a central challenge in developing mechanistic and predictive models of SOM dynamics. SOM can rarely be satisfactorily represented as a single uniform entity. This was apparent already in the earliest mathematical modelling of SOM (Jenny et al., 1949). Hence, virtually all current models represent SOM heterogeneity as either: i) two or more ‘pools’ or fractions of SOM differing in their specific decay rates (and at least in some of their rate controlling factors) (Andrén and Kätterer, 1997; Coleman and Jenkinson, 1996; Parton et al., 1987) or ii) a continuous ‘quality’ spectrum, where the specific decay rate is a continuous function of the quality (Bosatta and Ågren, 1985; Ågren and Bosatta, 1998). The models explicitly represent SOM heterogeneity, but the question that arises is how these conceptualisations correspond to observable soil properties.

Some of the earliest multi-pool models (Jenkinson and Rayner, 1977; Van Veen And Paul, 1981; McGill et al., 1981) define SOM pools according to a classical chemical fractionation method for characterising SOM. However, these methods generally fail in isolating kinetically meaningful fractions that can be generalised across a range of different soils and SOM contents (Stevenson and Elliott, 1989; Bruun et al., 2010). Consequently, many of the SOM pools represented in models are operationally defined as 'conceptual' fractions that do not directly correspond to a specific measurable quantity of SOM. Explicitly defined, measurable pools would be advantageous, as initial conditions, i.e., the quantities of SOM across all pools (or a quality density distribution) could then be determined independently from direct measurements, negating the need for calibrations or model spin-up procedures for establishing the distribution of SOM between different fractions. This distribution is sensitive to land use history and previous management, which is often unknown and a major concern when applying models over large spatial scales. The existence of an extremely slowly reacting pool, of a so-called "inert" C pool such as black C, adds an additional dimension.

Most SOM models imply a catenary sequence of decomposition (*sensu* Swift et al., 1979), in which decomposition residues become progressively more recalcitrant. This pattern reflects old concepts of humification in which secondary decomposition products are assumed to successively form new complex molecules that are increasingly more difficult to decompose. However, increasing evidence suggests that so-called humic materials are mixtures of primary plant and microbial-derived molecules and metabolites rather than novel complex "humic substances" (Kelleher and Simpson, 2006; Sutton and Sposito, 2005; von Lützow et al., 2008).

Many SOM models have increasingly changed towards physically based OM fractions and greater consideration of organic matter–mineral interactions (see von Lützow et al., 2008 for an excellent discussion). Particulate organic matter (or light) fractions, representing relatively labile, partially decomposed plant fragments are explicitly included in some models (Sohi et al., 2005). However, most models include the effects of soil physical protection and mineral interactions in a simplistic manner, often as a function of soil texture (Paustian, 1994; Falloon and Smith, 2000).

A predominately physical basis (excluding processes involved in black C formation) for SOM stabilisation implies the potential for a finite space (e.g. mineral surface area) limitation – a saturation limit for SOM stabilisation (Hassink and Whitmore, 1997). Six et al. (2002) proposed a more general conceptual model of saturation and physical protection of SOM. This includes aggregated-protected organic matter and SOM protected on mineral surfaces, both of which could be subject to saturation of their protection capacities. A key implication of saturation is a departure from assuming first-order kinetics, which is the basis for nearly all ecosystem-level models of SOM dynamics (Paustian et al., 1997a). With saturation, the relative stabilisation efficiency of added organic matter decreases as a function of SOM content, whereas, under first-order kinetics, relative stabilisation efficiency is constant.

The dynamics of SOM with projected changes in CO_2, climate, land use, and management at the global scale is a major focus of current research. Of particular importance are questions about the potential feedback on SOM from changes in productivity, plant communities, and altered temperature and moisture regimes. Models directly coupling climate processes and C cycle processes address these questions. Many global C cycle models and coupled climate–carbon cycle models use model structures derived from existing ecosystem-level soil C models, although the level of detail varies considerably (Friedlingstein et al., 2006; Sitch et al., 2008). In an analysis of 11 coupled climate–carbon cycle models (Friedlingstein et al., 2006), the representation of soil and litter C stocks varied from a single pool for all SOM to as many as nine separate SOM and litter pools. All models used a discrete pool structure with decomposition based on first-order kinetics and included temperature and moisture limitations on decomposition rates. For temperature, most models assumed a Q_{10} type relationship (in most cases $Q_{10} = 2$), although one model assumed separate temperature response functions for pools with different mean residence time (MRT), such that the Q_{10} value decreased with increasing MRT. For climate feedback on C cycle processes, decomposition varied strongly, ranging from minimal response to a strong positive feedback, in which average SOM mean residence time decreased by one year for each 1 °C increase in global mean temperature (Friedlingstein et al., 2006).

A particular challenge for scientists is determining when explicit consideration of a microbial mechanism is needed to predict ecosystem-level cycles (Ågren, 2010). Rhizosphere effects on ecosystem C fluxes are important, but what information is needed about microbial community dynamics for predicting the direction (positive or negative) and the degree of SOM priming from living roots? Most ecosystem-level models rely on first-order kinetics to describe microbial mediated decomposition of SOM pools, despite microbial dynamics being better expressed with Monod kinetics. Improvements of SOM models should include explicitly microbiology, focus on community-level microbial dynamics and/or production of exoenzymes (Schimel and Weintraub, 2003; Allison et al., 2010). The prediction of rhizosphere-induced SOM priming events may require the understanding and consideration of both microbial substrate utilisation patterns and maintenance assumptions (Cheng, 2009). An effective microbial sub-model predicting priming effects has been constructed for use with SOM models (Neill and Gignoux, 2006). This model includes multiple microbial populations and substrate types (soluble and insoluble) and thresholds that alter both microbial growth (through substrate limitation) and the decay rates of SOM pools. Ultimately, ecosystem-scale SOM models may need to consider the activity of multiple microbial populations, substrates, and nutrient resources in order to express the complex interactions associated with rhizosphere-related SOM priming (McGill, 1996). Advances in microbial genomics may provide an effective approach to linking microbial community dynamics and activity in soil C cycling, and ultimately assess the functional capacity of soil microbial communities. Both ^{13}C stable isotope probing (SIP) and RNA/DNA functional arrays are potentially useful for explaining the roles of specific microbial groups important for the degradation of SOM in soils (Gentry et al., 2006; el Haichar et al., 2007).

There is an increasing awareness that the interactions of soil C and N need to be taken into account for modelling the impact of climate changes on N-limited ecosystems (Thornton et al., 2007). Some models directly describe the coupling between soil C and N, such as SOILN (Johnsson et al., 1987), CoupModel (Jansson and Karlberg, 2004), DNDC (Li et al. 2000), ROMUL (Chertov, 1990), CENTURY (Parton et al., 1987), Rothamsted Nitrogen Model (Bradbury et al., 1993), and Daisy (Bruun et al., 2003). Several models were originally developed for agricultural ecosystems, where plant available N is relatively high. The need to include a description of the plant uptake of organic N in symbiosis with mycorrhiza became apparent when these models were applied to N-limited ecosystems such as boreal forests (Eckersten and Beier, 1998; Gärdenäs et al. 2003; Svensson et al., 2008). However, the descriptions of the utilisation of organic N are incomplete and important knowledge gaps are that the accompanying energy costs and emissions of CO_2 are largely unknown.

Many existing SOM models focus on organic matter transformations in the near surface layers (e.g. top 20–30 cm) of soil. Modelling the full depth distribution and dynamics of SOM is still at a relatively early stage (Elzein and Balesdent, 1995; Jenkinson and Coleman, 2008). There is much less field data on SOM changes below the topsoil, as the majority of measurements in long-term trials and chrono-sequences are restricted to the plough layer.

Understanding of the processes of vertical movement, mobilisation and deposition of SOM within different soils – including root distributions and turnover, transport of Dissolved Organic Matter (DOM) and more diffuse movements of SOM to depth is scanty. SOM decomposition at depth is substantially different from SOM decomposition in surface soils (Rey et al., 2008). For example, a major mechanism is the rhizosphere priming of older SOM in the subsoil by fresh organic matter (Fontaine et al., 2007), with more spatial and temporal variation in the process than occurs in surface soils.

Several gaps in our understanding indicate important areas of continuing and new research for modelling soil C and N dynamics:

i) The interactions between soil C and N, especially of the utilisation of various sources of plant available N such as organic N, N made available by priming and black N.
ii) The interactions between secondary soil minerals and organic matter, accounting for stabilisation mechanisms involving clay and oxide surfaces as well as physical protection of organic matter within soil aggregates.
iii) The vertical variation in SOM and its decomposition rates in the whole profile,
iv) The stabilisation of black C and black N on SOM dynamics.
v) The interaction between soil C and N should go beyond fixed C-to-N ratios in different pools.

3. Comparison of knowledge levels and importance for soil–climate interactions

3.1. Comparison of knowledge level

A qualitative comparison of the current knowledge level of the five topics in relation to scale based on the preceding sections is given in Fig. 2a. For example, at the *molecular* scale, there is an excellent understanding of the chemical composition of the greenhouse gases emitted from the soil, whereas our understanding of black N compounds and their behaviour is rather poor. There is currently not even a standard method for determining black N content (Currie et al., 2002) and the lack of such a method is an obstacle for comparing the quantities of black N in different ecosystems, and rendering it difficult, if not impossible, to determine the importance of black N for soil–climate interactions at different scales. Consequently, the knowledge level of black N and its behaviour decline even more with increasing scale.

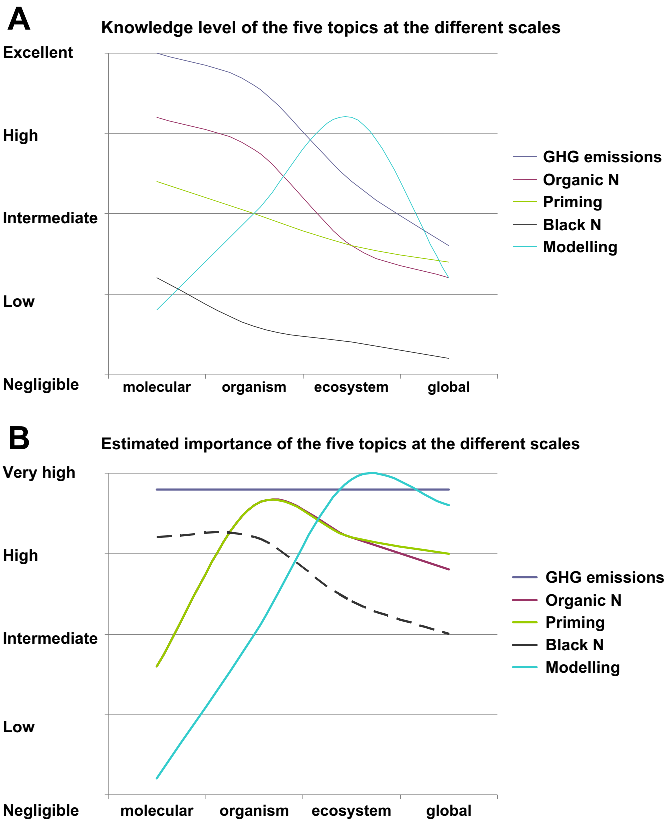

Fig. 2. (a) Knowledge level of the five topics at the different scales. (b) Estimated importance of the five topics at the different scales.

For greenhouse gas emissions, understanding at the ecosystem scale is intermediate. We have a fairly good qualitative understanding of which types of ecosystems that emit which greenhouse gases. Waterlogged ecosystems such as rice paddies in tropical and sub-tropical areas, and melting permafrost on the arctic tundra, emit large quantities of CH_4. Many agricultural systems, drained peat soils and humid tropical soils emit N_2O (Davidson, 2009) and boreal forest soils are a potentially large source of CO_2 (Raich and Schlesinger, 1992). Yet, we cannot quantify how these fluxes are affected by changes in climate, land use or management. Contradictory results have been presented, some of which are difficult to interpret. Among these are the regulation of CH_4 emissions by N fertilisation (Noll et al., 2008) and the huge coefficients of variation found for various soil C and N processes (i.e. 100–800%, Zak et al., 2000). Very little progress has been made in gas chamber methods despite that the systematic differences between static and dynamic chamber methods have been known for decades (Witkamp, 1969; Moore and Roulet, 1991). Thus, 'we don't know what we know' about greenhouse gas emissions at the ecosystem scale.

The knowledge level for uptake of organic N by plants is considered higher than that of priming by roots at both the molecular and the organism scale. The identification of the major transporters of organic N in the model plant *A. thaliana* is an important break-through for understanding uptake of organic N (Hirner et al., 2006; Svennerstam et al., 2008). Examples of the conceptualisation of plant uptake of organic N are found in the literature (Schimel and Bennett, 2004) and in some mathematical ecosystem models such as SOILN and CoupModel (Eckersten and Beier, 1998; Gärdenäs et al. 2003; Svensson et al., 2008). Despite these advances, quantification of the process is still hampered by i) the low stability of organic N compounds, ii) a lower diffusion rate of organic N compared to that of mineral N, and iii) inability to distinguish between uptake of organic N taken up by symbiotic from that by non-symbiotic micro-organisms.

In order to improve the basic understanding of the priming interactions in soil there is a need to quantify the variability of root exudates *in situ* among species and across time (Phillips et al., 2008). At the organism scale, the effects of N on the activity of those microbial groups being responsible for soil-priming events merit further investigation (Bird et al., 2011). Priming effects are highly variable across ecosystems (the literature cites examples ranging from −50% to more than +380%). We recommend that research efforts should focus on identifying the mechanisms responsible for such variability and unpredictability, since rhizosphere-priming effects may be large enough to influence C balances at both the ecosystem and the global scale. We are still unable to predict both the direction and degree of the effects despite the compelling concepts developed by Kuzyakov (2002). The knowledge gaps in priming and organic N uptake are substantially larger than those in greenhouse gas emissions from ecosystems. In terms of ecosystems and global scale, 'we know what we don't know'. Future research addressing these processes will require the use of dual-isotopic tracers (^{13}C and ^{15}N).

Unlike process-related topics, modelling is most advanced at the ecosystem scale. Manzoni and Porporato (2009) conducted an in-depth comparison of 250 biogeochemical models across different scales, with respect to their theory and mathematical structure. Models at the ecosystem scale were highest in number and had the highest median of phase-space dimension (PSD), which is a measure of model complexity in relation to scale. Manzoni and Porporato (2009) expressed concern that models developed for a certain scale are often used at other spatial and temporal scales and this might result in a bias between model formulation and application. Although the understanding at the ecosystem scale is good, understanding at the global scale is intermediate. At the global scale, Manzoni and Porporato (2009) found the lowest median PSD. Delire et al. (2003) evaluated how well the biosphere–atmosphere model CCM3-IBIS could simulate the present climate and global C cycle. The simulated climate did not reflect the African monsoon, which strongly affected the simulation of the local vegetation. The predicted increase in CO_2 concentration at the end of the 21th century varied from 20 to 200 ppm, with a median increase between 50 and 100 ppm in a comparison of 11 global climate–carbon cycle models (Friedlingstein et al., 2006). This reflects the need for improvement in knowledge levels and we suggest that by taking into account some of the major soil C and N interactions could lead to a considerable improvement in modelling climate change.

3.2. Importance for soil–climate interactions

Our third objective with this study was to rank the importance of each topic for soil–climate interactions (Fig. 2b). We used two criteria for ranking: i) direct influence on soil–climate interactions and ii) indirect influence on soil–climate interactions through plant available N and, thereby net ecosystem productivity (NEP). The direct effects of the greenhouse gases, CO_2, CH_4, and N_2O, on climate are known. CH_4 is known to have a 25 times stronger greenhouse gas forcing effect than CO_2 and N_2O has a 298 times stronger effect than CO_2 within a 100 years time frame. This high level of importance of the greenhouse gases at the molecular scale impinges on the other scales. The management of agricultural and forest ecosystems strongly influences global fluxes of greenhouse gases, with drainage and N fertilisation affecting whether C is emitted as CO_2 or CH_4 from wetlands. The net global rates of photosynthesis and respiration (both approximately 200 Pg year^{-1}; Schlesinger, 1997) have been relatively stable since the last glaciation, but they are currently being disrupted by anthropogenic CO_2 addition from fossil fuel combustion and land use change. Anthropogenic CO_2 emissions corresponds roughly to 10% of the annual global soil respiration and far-reaching consequences can be expected if global soil respiration is enhanced by climate change, and not balanced by a corresponding increase in photosynthesis. Variations in the concentration of global atmospheric CH_4 are attributed to climatically induced shifts in global distribution and activity of wetlands, which are the main natural sources. Similarly, variations in the atmospheric N_2O burden are considered as dominated by the production process, with two-thirds of the total N_2O sources coming from terrestrial ecosystems, and approximately one-third arising in the oceans since the last glaciations. At the heart of these globally significant changes lay the responses of soils.

The second criterion for ranking an identified knowledge gap is the importance of the process for plant available N or our understanding and capability to model plant available N. This criterion was included as several studies (e.g. Cramer et al., 2001; Thornton et al., 2007) have highlighted that the estimated change in NEP with climate change is much lower when plant available N is taken into account. In the comparison of 6 models by Cramer et al. (2001), the two models which included interactions between C and N cycles (Hybrid and SDGVM) showed only a small increase in NEP. The response of NEP to plant available N under climate change conditions is an essential soil–climate interaction. A lower response of NEP with climate change means a faster rate of climate change and implies that the global C sinks can be overestimated (Thornton et al., 2007).

Total plant available N is an example of a C and N interaction which requires further attention. The concept of N availability has widened from an emphasis on mineral N to include the formation and uptake of small molecular organic N compounds as well (Schimel and Bennett, 2004; Näsholm et al., 2009). Schimel and Bennett (2004) concluded that availability of N to plants and micro-organisms is primarily determined by i) de-polymerisation of N-containing organic molecules, ii) uptake of amino acids, small peptides and amino sugars by plant roots and micro-organisms (cf. Näsholm et al., 2009) and iii) N mineralisation/immobilisation, nitrification and root uptake of inorganic N. During recent years, there has been an increased insight that N availability is influenced by interactions between root exudates, root litter and rhizosphere micro-organisms (Herman et al., 2006; Dijkstra et al., 2009; Philippot et al., 2009). Therefore, appropriate investigations of potential plant available N in soil requires the use of plant–soil microcosms rather than the routine incubation tests of soil samples (Frank and Groffman, 2009).

Rhizosphere priming and uptake of organic N might be especially important in times of N shortage, as these processes imply a considerable energy demand on plants, but these costs must be seen in relation to costs for uptake of NO_3^- or NH_4^+. In barley, NO_3^- nutrition increased C costs for N nutrition by more than 60% compared to ammonium (Bloom et al., 1992). However, in many plants, NO_3^- reduction and assimilation takes place in the shoot, where energy, otherwise wasted, can be used (Andrews, 1986). The C costs of assimilating organic N are different from those for mineral N because organic C sources are absorbed together with N and at least for amino acids, metabolism is probably mainly through transamination reactions, which do not require energy input, in contrast to NO_3^- and NH_4^+ assimilation. On the other hand, the diffusion rate of NO_3^- ions in the soil is at least 1 order of magnitude higher than that of NH_4^+ ions, and 1–2 orders of magnitude higher than that of most organic N compounds. The C costs for organic N uptake might increase due to the low diffusion rates, because a considerable higher root or mycorrhizal area is needed to sustain a given rate of N absorption through uptake of organic N than that of NO_3^- ions and probably also that of NH_4^+ ions. The differences in energetic costs for the different N sources remain an unresolved question.

3.3. Impact of climate change on plant available N

A key question is how climate change will affect plant available N in different ecosystems and globally. Soil processes and interactions might fundamentally change with the future climate and create a different response to that revealed from the historical record. Such changes are not likely to be captured in a GCM with a simple implicit representation of soil processes. Moreover, other drivers of these processes such as N deposition may change simultaneously. For example, we can expect that the abundance of black N will increase with climate change in the current (semi-) arid areas due to an increased frequency and intensity of fires (Jones et al., 2009). Black N is assumed to reduce N availability to plants and microbes by its stabilising impact on SOM (Schnitzer and Spiteller, 1986).

The positive effect of elevated temperature on C and N mineralisation and emissions of greenhouse gases is well-known (Lloyd and Taylor, 1994). Studies on temperature effects are conducted since the early 1900s, when Arrhenius and van t' Hoff discussed temperature dependency of chemical reactions. Variations in temperature sensitivity of SOM and the interaction with N dynamics in soils influence both heterotrophic respiration and NEP. Therefore, the net flux of CO_2 between the biosphere and atmosphere will inevitably change under future climate change. Capturing this feedback is likely to be critical for accurate GCM predictions of future climatic conditions.

Zak et al. (2000) presented an excellent review of impacts of elevated CO_2 on microbes and microbial processes, recognising the impact of elevated CO_2 on N mineralisation as one of the major knowledge gaps. The coefficient of variation in gross N mineralisation of the 10 experiments included was as high as 800%, and that of the impact on net N mineralisation was almost 300%. In this case, 'we know what we don't know'. Zak et al. (2000) suggested that the key to unravelling this knowledge gap lies in the longevity and biochemistry of fine-roots, that is, in rhizosphere priming.

N losses such as N_2O emissions and N leaching from ecosystems in current cold-temperature regions might be further enhanced due to intensified freezing–thawing cycles (Goodroad et al., 1984; Dörsch and Bakken, 2004; Schimel and Clein, 1996; Joseph and Henry, 2008). Moreover, climate change will cause a shift in natural vegetation and in our selection of agricultural crops which, in turn, will lead to changes in litter quantity and quality and altered root-to-shoot ratios. Weintraub and Schimel (2005) observed a shift to more woody shrubs in arctic tundra ecosystems, which, among other things, means more litter with a high C-to-N ratio. Soil CO_2 emissions are related to both plant species composition and the amount of below-ground productivity (Craine et al., 2001). The effect of elevated atmospheric CO_2 concentrations on NEP is expected to be more pronounced than temperature, due to an increased water-use efficiency (Tyree and Alexander, 1993; Hungate et al., 2002) as well as an increased N-use efficiency (van Oijen et al., 2008).

The expected intensification of the hydrological cycle with climate change (Meehl et al., 2007) could potentially lower the amount of plant available N. For instance, in sub-tropical regions, lower N availability due to reduced mineralisation as a fold of intensified water stress, and sometimes even desertification, is to be expected, whereas in areas with a higher rainfall, N losses will increase due to enhanced N leaching (Kundzewicz et al., 2007; Eckersten et al., 2001). This latter effect could be somewhat moderated by a less dramatic snow-melt in boreal forest ecosystems, which is one of the important events for N leaching, especially in fertilised forests (Gärdenäs et al., 2003).

There have been only a limited number of multi-factor climate change experiments (Dukes et al., 2005; Craine et al., 2001; Edwards and Norby, 1998; Niinistö et al., 2004; Slaney et al., 2007), most of them presenting non-significant impacts, particularly when incorporating all the three major changing drivers, i.e. temperature, precipitation and CO_2 concentration (Luo et al., 2008). A number of critical questions arise from this; Firstly, can our understanding improve by comparing modelling results with non-significant results of experiments? Secondly, why do several factors so frequently cancel out each other, meaning the overall impact of climate change on the C balance is not as large as concluded from the results of single factor studies? Perhaps we are totally missing one or more important feedback mechanism, or to speak with Bouma 'We don't know yet what we don't know'. The challenge is to narrow these knowledge gaps. We identified one of the largest discrepancies between the level of knowledge and level of importance to be modelling at the global scale (Fig. 2a and b). We see here a huge potential for improvement, which is considered more in the next section.

4. C and N dynamics at the global scale and their representation in GCMs

Models are often limited to the number of spatio-temporal scales that are of direct interest for predictive capability, and therefore, do not explicitly represent processes and drivers at finer scales. Processes at larger or finer scales are represented either as a variable input to the model and/or crudely represented in the model algorithms or parameterisation. In turn, this creates uncertainty in the predictions due to errors in the input data or imperfections in the model structure. For example, if the influence of priming at the pedon scale varies linearly with climate, then it is probably not necessary to explicitly represent the processes occurring at the pedon scale. However, this may not be the case, and the underlying response may be due to interactions that can be explained by the processes at the finer scale. In turn, the larger scale model would need an appropriate input to capture these dynamics or explicitly represent the processes.

GCMs are coupled with ocean and terrestrial C models to simulate climate dynamics at a one-degree or larger gridded global resolution (Friedlingstein et al., 2006). The underlying heterogeneity occurring within the grid cells is often ignored under the assumption that its influence will not change the resulting exchange of CO_2 or the climate change trajectory. Many coupled GCM climate–carbon cycle models employ model structures derived from existing ecosystem-level soil C models (Friedlingstein et al., 2006; Sitch et al., 2008). However, many finer scale interactions between C and N in soils are not explicitly represented, or are crudely captured, as the spatial resolution is too large for distinguishing the underlying heterogeneity of for example soil texture or depth, topography, or microbial community structure. Where responses of SOM to such factors are nonlinear, the use of estimates from spatially averaged values as model inputs can lead to large aggregation errors (Paustian et al., 1997b).

For improving estimates of climate change impacts on C cycling at global scales, the question of temperature sensitivity as a function of SOM recalcitrance is important, as highlighted in the model comparison made by Friedlingstein et al. (2006). Although there is no consensus among modellers (Giardina and Ryan, 2000; Ågren and Bosatta, 2002; Knorr et al., 2005; Reichstein et al., 2005; Davidson and Janssens, 2006), empirical evidence supports the hypothesis that recalcitrant SOM has a higher temperature sensitivity (Conant et al., 2008; Hartley and Ineson, 2008). Indeed the question of temperature sensitivity of SOM recalcitrance is pivotal for research on the impact of climate change, but we would like to reformulate the question: Which roles do different N compounds play in SOM recalcitrance and what consequences have SOM recalcitrance for plant N availability?

Nested models or sub-spatial gridding could be used to incorporate some of the finer scale SOM controls, even in global-scale models. A useful first step is to conduct sensitivity testing to examine the effects of scale on the predicted soil C and N interactions. For example, to examine how much the finer scale soil processes would need to change before they significantly influenced the CO_2, N_2O, or CH_4 fluxes, as currently represented in the coupled GCM. A second approach is to develop empirical relationships between the processes and the underlying heterogeneity of the variable in question. This second approach would produce reasonable results if empirical data are collected from laboratory experiments, microcosm studies, or field experiments that adequately represent the future conditions. A third approach is to use nested models with a sub-spatial gridding of the coarser GCM grid. A sub-sample of the grid cells could be simulated that incorporates the influence of finer scale variables on plant production, litter, and SOM dynamics. The results could be used as an input to the coupled GCMs, after scaling the results to the coarser GCM grid. Uncertainty in predictions could be addressed by accounting for uncertainty with the variance of the responses, assuming the sub-sample of grid cells is selected at random.

These approaches require considerable effort, particularly the third approach. Soil and ecosystem models can be used to drive the processes and interactions, including representation of the heterogeneity of variables at scales finer than the GCM grids.

The question remains to what extent inclusion of soil processes at this level would elicit responses large enough to warrant inclusion in the coarser models.

5. Conclusions

The knowledge levels for different processes-related topics decline with increasing scale, while the knowledge level for simulation models is highest at the ecosystem scale. The largest discrepancy between knowledge level and importance appears at the scale of global modelling. We conclude that a reliable quantification of greenhouse gas emissions at the ecosystem scale is of paramount importance for improving soil–climate representation in GCMs. Key questions in climate change research are to identify the role of different N species for temperature sensitivity of SOM recalcitrance and what consequences SOM recalcitrance may have for plant N availability. The importance of priming and plant uptake of various N species at the ecosystem scale, including how these processes are affected by climate change, land use, management and N deposition needs to be quantified. An ability to quantify these processes would enable selection of which soil N processes need to be included into GCMs. Multi-method approaches, such as the use of dual-isotopes are developing tools necessary to narrow the existing knowledge gaps in soil C and N interactions.

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