

## SPECIAL FEATURE – ESSAY REVIEW

## PLANT–SOIL INTERACTIONS AND THE CARBON CYCLE

# Integrating plant–soil interactions into global carbon cycle models

Nicholas J. Ostle<sup>1\*</sup>, Pete Smith<sup>2</sup>, Rosie Fisher<sup>3</sup>, F. Ian Woodward<sup>3</sup>, Joshua B. Fisher<sup>4</sup>, Jo U. Smith<sup>2</sup>, David Galbraith<sup>5,6</sup>, Peter Levy<sup>5</sup>, Patrick Meir<sup>6</sup>, Niall P. McNamara<sup>1</sup> and Richard D. Bardgett<sup>7</sup>

<sup>1</sup>Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK; <sup>2</sup>Institute of Biological and Environmental Sciences, University of Aberdeen, St Machar Drive, Aberdeen AB24 3UU, UK; <sup>3</sup>Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK; <sup>4</sup>Environmental Change Institute, School of Geography & the Environment, University of Oxford, Oxford OX1 3QY, UK; <sup>5</sup>Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, Edinburgh EH26 0QB, UK; <sup>6</sup>School of Geosciences, Edinburgh University, Drummond Street, Edinburgh EH8 9XP, UK; and <sup>7</sup>Soil and Ecosystem Ecology Group, Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

## Summary

1. Plant–soil interactions play a central role in the biogeochemical carbon (C), nitrogen (N) and hydrological cycles. In the context of global environmental change, they are important both in modulating the impact of climate change and in regulating the feedback of greenhouse gas emissions (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O) to the climate system.

2. Dynamic global vegetation models (DGVMs) represent the most advanced tools available to predict the impacts of global change on terrestrial ecosystem functions and to examine their feedbacks to climate change. The accurate representation of plant–soil interactions in these models is crucial to improving predictions of the effects of climate change on a global scale.

3. In this paper, we describe the general structure of DGVMs that use plant functional types (PFTs) classifications as a means to integrate plant–soil interactions and illustrate how models have been developed to improve the simulation of: (a) soil carbon dynamics, (b) nitrogen cycling, (c) drought impacts and (d) vegetation dynamics. For each of these, we discuss some recent advances and identify knowledge gaps.

4. We identify three ongoing challenges, requiring collaboration between the global modelling community and process ecologists. First, the need for a critical evaluation of the representation of plant–soil processes in global models; second, the need to supply and integrate knowledge into global models; third, the testing of global model simulations against large-scale multifactor experiments and data from observatory gradients.

5. *Synthesis.* This paper reviews how plant–soil interactions are represented in DGVMs that use PFTs and illustrates some model developments. We also identify areas of ecological understanding and experimentation needed to reduce uncertainty in future carbon coupled climate change predictions.

**Key-words:** carbon, climate change, DGVM, feedbacks, GCM, models, PFT, plant, soil

## Introduction

The severity of the influence of human activity on global ecosystem resources and services is raising concern among scientists and politicians alike (Stern 2006; IPCC 2007). Rapid and long-term changes in environmental conditions, due

directly or indirectly to human activities, are occurring simultaneously across a range of spatial and temporal scales and, in some instances, threaten the existence of valued terrestrial ecological resources (Millennium Ecosystem Assessment 2005). A key challenge in the coming years will be to provide a scientific basis for the sustainable use and development of Earth's biosphere. One area in which ecology has an important role to play is in the development of predictive models that couple the

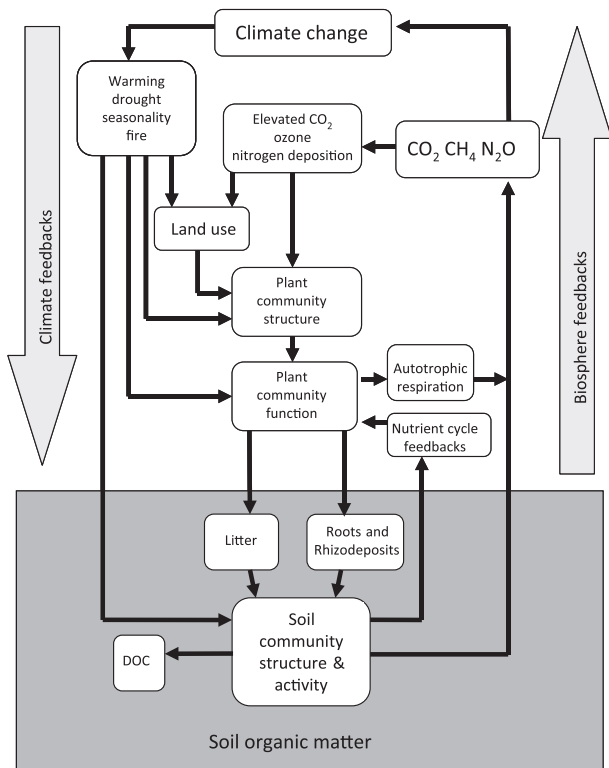
\*Correspondence author. E-mail: no@ceh.ac.uk

global terrestrial carbon (C) cycle with atmospheric circulation models.

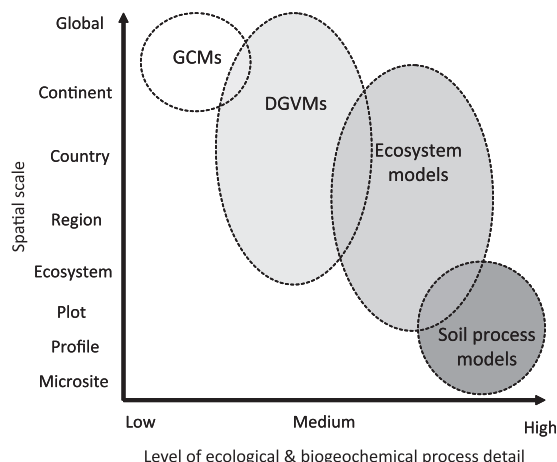
Plant–soil interactions lie at the heart of global biogeochemical and hydrological cycles, with climate change and land use having considerable potential to influence their role in feedbacks of greenhouse gases between the biosphere and atmosphere (Fig. 1). Climate change can affect plant–soil interactions directly as a result of atmospheric warming, alterations in precipitation patterns (IPCC 2001) and lengthening of plant growing seasons (Sherry *et al.* 2007) and indirectly as a result of longer-term changes in the distribution, productivity and composition of vegetation (Heimann & Reichstein 2008; Sitch *et al.* 2008). These changes then influence the size, composition and activity of soil biological communities that determine the magnitude of the soil C store and the emission of greenhouse gases at the ecosystem scale (e.g. CO<sub>2</sub>, N<sub>2</sub>O and CH<sub>4</sub>) (Bardgett, Freeman & Ostle 2008). There is also evidence that non-climatic global changes due to land use changes (Smith *et al.* 2008), nitrogen (N) enrichment (Magnani *et al.* 2007; Galloway *et al.* 2008), sulphur deposition (Monteith *et al.* 2007), CO<sub>2</sub> fertilization (Woodward 2002; Norby *et al.* 2005) and changes in atmospheric ozone concentration (Sitch *et al.* 2007) are having a significant effect on ecosystem functioning including emissions of greenhouse gases (Meir, Cox & Grace

2006). Improving predictions of the impacts of these multiple stressors on ecosystem biodiversity and biogeochemistry poses a significant challenge in the development of protection, mitigation and adaptation strategies.

Mathematical models offer one means to make predictions and to test hypotheses regarding the effects of changes on responses of ecosystem functioning to global changes. A number of modelling approaches exist spanning a broad range of dynamic and spatial dimensions from global circulation models (GCMs) that operate at the 2° global grid cell scale to soil carbon process models that can be parameterized at the plot, core or microsite scale (Fig. 2). Linking between these are dynamic global vegetation models (DGVMs) of varying degrees of complexity that represent the state-of-the-art for studying the impacts of change on plant–soil interactions and their feedbacks to the climate system, e.g. CLM-CN, IGSM, LPJ, BIOME-BGC, CENTURY, DNDC, HYBRID, SDGVM, TRIFFID, ORCHIDEE (Schimel *et al.* 1996; Friend *et al.* 1997; Woodward, Lomas & Betts 1998; Cox 2001; Sitch *et al.* 2003; Krinner *et al.* 2005; Thornton & Rosenbloom 2005; Miehle *et al.* 2006; Thornton *et al.* 2007, 2009; Sokolov *et al.* 2008; Xu-Ri & Prentice 2008). These DGVMs can be operated whilst coupled to global atmospheric circulation models (GCMs) to enable explicit simulation of the feedbacks between the biosphere and atmosphere (Friedlingstein *et al.* 2006). As well as simulating the instantaneous biogeochemical processes of photosynthesis and plant respiration, DGVMs can also simulate longer-term impacts of climate change on vegetation cover and soil carbon storage (Cox *et al.* 2000; Sitch *et al.* 2003; Levy, Cannell & Friend 2004; Woodward & Lomas 2004; Sato, Itoh & Kohyama 2007). Most DGVMs typically utilize the concept of ‘plant functional types’ (PFTs; numbering between 3 and 20) to classify global vegetation diversity and its reactivity to climate (Table 1). Each PFT represents a broad class of vegetation



**Fig. 1.** Global change and land use effects on plant–soil biogeochemical C and N feedbacks. Showing how climate change, elevated CO<sub>2</sub>, N deposition, atmospheric ozone and land use can have direct and indirect effects on the composition and function of plant primary producer communities or crop cultures, soil biological activity and resultant greenhouse gas feedbacks to the atmosphere.



**Fig. 2.** Multiscale carbon models, i.e. soil, ecosystem, dynamic global vegetation models (DGVMs) and general circulation models (GCMs): scales of prediction and process resolution. Showing that the level of detail in process resolution generally diminishes as the predictive scale (spatial and temporal) of the model increases.

**Table 1.** Plant–soil PFTs within five commonly used DGVMs (HYLAND, LPJ, ORCHIDEE, SDGVM and TRIFFID)

HYLAND	LPJ	ORCHIDEE	SDGVM	TRIFFID
Broadleaf evergreen	Tropical evergreen	Tropical broadleaf evergreen	Broadleaf evergreen	Broadleaf
Needleleaf evergreen	Temperate broadleaf evergreen	Temperate broadleaf evergreen	Needleleaf evergreen	Needleleaf
C3 grasses	Temperate needleleaf evergreen	Temperate needleleaf evergreen	Broadleaf deciduous	Shrubs
	Boreal needleleaf evergreen	Boreal needleleaf evergreen	Needleleaf deciduous	C3 grasses
	Tropical raingreen	Tropical broadleaf raingreen	C3 grasses	C4 grasses
	Temperate summergreen	Temperate broadleaf summergreen	C4 grasses	
	Boreal summergreen	Boreal broadleaf summergreen		
	C3 grasses	Boreal needleleaf summergreen		
	C4 grasses	C3 grasses		
		C4 grasses		

type such as deciduous forest or grassland and is parameterized for a core set of physiological processes and ecological phenomena. These physiological processes are represented by different mathematical means in each DGVM and include photosynthesis (i.e. Farquhar, Caemmerer & Berry 1980; Collatz *et al.* 1991; Collatz, Ribas-Carbo & Berry 1992) C and N allocation using allometric and qualitative relationships (Friedlingstein *et al.* 1998) stomatal conductance (Jarvis 1976; Ball, Woodrow & Berry 1987; Stewart 1988; Leuning 1995; Haxeltine & Prentice 1996; Cox, Huntingford & Harding 1998), sapwood and/or fine root respiration (Lloyd & Taylor 1994; Gifford 1995) and evapotranspiration (Monteith 1995; Monteith & Unsworth 1990; Ducoudre, Laval & Perrier 1993). Ecological vegetation phenomena that are addressed include the phenological responsiveness of plants, their competition and mortality. Other approaches to the representation of plant functionality propose the use of plant biogeochemical or ecological traits that cover a gradient of overlapping characteristics (Wright *et al.* 2004). All of these models draw on established ecological understanding and field measurements to develop, parameterize and test their predictive certainty. Table 1 provides information on the range of PFTs simulated by five commonly-used DGVMs: HYLAND, LPJ, ORCHIDEE, SDGVM and TRIFFID (see Sitch *et al.* 2008 for a detailed breakdown of model compositions).

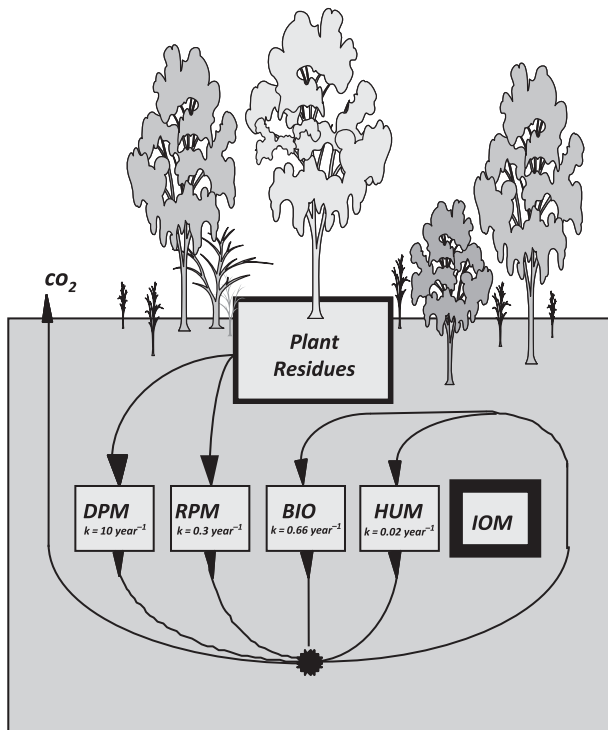
Accurate representation of plant–soil interactions is crucial to improving predictions of climate change on global ecosystems and the feedbacks between them. The overall aim of this paper is to review the integration of plant–soil interactions and their role in C and N cycling into global DGVMs. To achieve this aim, we illustrate four component model processes: (i) soil carbon dynamics, (ii) nitrogen cycling, (iii) drought impacts on vegetation, and (iv) vegetation dynamics. We also discuss the challenges faced by global vegetation modellers and ecologists to reduce uncertainty in their predictions.

#### SOIL CARBON DYNAMICS

The balance between photosynthetic assimilation of CO<sub>2</sub> and soil organic matter decomposition is critical to the global C balance (Davidson & Janssens 2006), with most terrestrial C

being held below-ground in the soil (Lal 2004). Changes in environmental conditions, including land use change, ecosystem degradation and climate change, are having strong impacts on both the ecology and biogeochemistry of soils and vegetation across the globe (Millennium Ecosystem Assessment 2005; IPCC 2007). Plant–soil carbon models have been developed over the past 50 years to maximize soil C turnover for agricultural productivity and to predict land use and global change effects on ecosystem nutrient dynamics. Early soil models simulated soil organic C (SOC) as one homogeneous compartment (Jenny 1941), then two-compartment models were proposed (Beek & Frissel 1973; Jenkinson 1977) and later multi-compartment models were developed (McGill 1996; Molina & Smith 1998). Of the 33 SOC models currently represented within the Global Change and Terrestrial Ecosystems Soil Organic Matter Network (SOMNET) database (Smith, Bradbury & Addiscott 1996; Smith *et al.* 2001, 2002), 30 are multi-compartment, process-based models. Each SOC pool is characterized by its position in the model's structure and its decay or 'turnover' rate (Fig. 3). Decay rates are usually expressed by first-order kinetics with respect to the C in the pool, i.e.  $[dC/dt = -kC]$  where  $t$  is time and the rate constant  $k$  is related to its half-life [ $h = (\ln 2)/k$ ], time required to halve the C content without inputs, or turnover time ( $\tau = 1/k$ ). Generally, the lower the decay rate constant, the higher the half-life, the turnover time and the stability of the organic pool. Using this approach the complexity and variability of SOC observed in the field is condensed into a mathematical representation of hypothetical pools that are parameterized individually, giving the resultant process based model considerable transferability between soils, ecosystems and land uses. A thorough review of the structure and underlying assumptions of different process-based SOC models is available (Molina & Smith 1998).

Currently, the most widely applied soil C models employ multiple SOC pools to simulate soil organic matter dynamics (e.g. DNDC; Li, Frohling & Harriss 1994; CENTURY Del Grosso *et al.* 2006; ROTHC Coleman & Jenkinson 1996; SUNDIAL Bradbury *et al.* 1993). They generally include key soil biogeochemical processes and have been used to determine soil C and N turnover in a range of ecosystems from arable croplands to grasslands, forests and peatlands (McGill 1996;



**Fig. 3.** The multi-pool RothC soil carbon model with the four active compartments and their decay rates ( $k$ ): decomposable plant material (DPM), resistant plant material (RPM), microbial biomass (BIO) and humified organic matter (HUM) and the inert organic matter (IOM) fraction.

Smith *et al.* 1998; Smith 2001, 2002; Peltoniemi *et al.* 2007). Most soil models have adopted the representation of soil C in multiple pools of organic matter decomposing using first-order rate kinetics (Paustian 1994), but others have attempted to include more detailed understanding of soil ecology in the form of food webs that predict the energy and nutrient flows between organisms (Hunt *et al.* 1984; Hunt, Coleman & Ingham 1987; Hunt, Trlica & Redente 1991; de Ruiter *et al.* 1993; de Ruiter & Van Faassen 1994; de Ruiter, Neutel & Moore 1995). All current DGVMs use process based descriptions of soil C dynamics (Smith *et al.* 2009a), some with a single C soil pool (e.g. Cox *et al.* 2000), others with multiple SOC pools similar to those found in soil models (e.g. Parton, Stewart & Cole 1988; Comins & McMurtrie 1993; Jones *et al.* 2005a,b).

Major uncertainties and areas for research and development of representations of soil C in DGVMs relate to their inability to represent potentially important ecological phenomena including priming of soil C decomposition at depth (Fontaine *et al.* 2007), the 'gadkil' effect and non-equilibrium dynamics (Schimel & Weintraub 2003; Fontaine & Barot 2005; Neill & Gignoux 2006; Wutzler & Reichstein 2007) and for assumptions about the temperature sensitivity of different soil carbon pools (Davidson & Janssens 2006). Other challenges include understanding the nature of impacts of land management change on the stability of different pools of soil carbon (e.g. the physical protection of organic matter; Deneff *et al.* 2004, 2007) and the inclusion of microbial feedbacks of decomposition that

are not captured by first-order assumptions (e.g. soil methanogenesis and methanotrophy).

#### NITROGEN CYCLING

Nitrogen is crucial for plant growth and productivity in all terrestrial ecosystems (Vitousek & Howarth 1991; LeBauer & Treseder 2008). The availability of N is determined by the balance between inputs from biological N fixation, anthropogenic inputs and atmospheric N deposition, the recycling of plant residues and losses in gaseous ( $\text{N}_2\text{O}$  and  $\text{N}_2$ ), inorganic ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) and dissolved organic matter forms (Vitousek *et al.* 2002). Ecosystem N limitation is common and the rate of plant N demand often exceeds the rate of soil N supply (Luo *et al.* 2004). The N cycle is, therefore, tightly coupled with soil–plant C dynamics so that N supply and limitation also affect the structure and function of ecosystems with important feedbacks to the global C cycle (Lloyd 1999). Land surface models and DGVMs used in the IPCC assessments have, historically, not included the plant–soil N cycle, and thus predict C sequestration rates far greater than that which expected N limitation would allow (Cramer *et al.* 2001; Hungate *et al.* 2003; Sitch *et al.* 2008). Here we review recent developments in DGVM modelling to introduce the N cycle to constrain C cycling (Zaehle & Friend 2006; Thornton *et al.* 2007, 2009; Sokolov *et al.* 2008; Xu-Ri & Prentice 2008).

Plants can acquire N from the soil via four pathways: advection (passive uptake), retranslocation (resorption), active uptake and biological N fixation (Ourry, Gordon & Macduff 1997; Hopmans & Bristow 2002; Wright & Westoby 2003). Well-established general ecosystem and DGVM models initially included plant N uptake simply as proceeding at the rate of demand until depleted from the soil (e.g. BIOME-BGC, CENTURY, DNDC, HYBRID, SDGVM) (Schimel *et al.* 1996; Friend *et al.* 1997; Woodward, Lomas & Betts 1998; Thornton & Rosenbloom 2005; Miehle *et al.* 2006). More recently energetics-based models have been developed that couple soil–plant C and N cycles by prescribing a vegetation C cost for N acquisition (Vitousek & Field 1999; Rastetter *et al.* 2001; Dickinson *et al.* 2002; Vitousek *et al.* 2002; Wang, Houlton & Field 2007). This latter set of models is particularly important for modelling plant C dynamics because it represents a second pathway for C expenditure other than growth and respiration making the link between C and N cycles explicit (Chapman *et al.* 2006).

The importance of incorporating both the plant–soil C and N cycles in these coupled DGVMs and climate models was demonstrated by Thornton *et al.* (2007) when the biophysical framework of the Community Land Model (CLM 3.0; Bonan & Levis 2006; Dickinson *et al.* 2006; Oleson *et al.* 2004) was coupled to the terrestrial biogeochemistry model (Biome-BGC 4.1.2.; Thornton *et al.* 2002; Thornton & Rosenbloom 2005) resulting in a new model, the Community Land Model (CLM-CN; Thornton *et al.* 2007). The simulated change in global terrestrial C uptake in response to increasing atmospheric  $\text{CO}_2$  concentration was reduced in CLM-CN by 74%, relative to the C-only counterpart model when N limitation was included.



The importance of including N was further demonstrated when Sokolov *et al.* (2008) compared terrestrial C uptake in response to increased surface temperatures as simulated by the MIT Integrated Global Systems Model (IGSM2; Sokolov *et al.* 2005) coupled to the Terrestrial Ecosystem Model (TEM; Melillo *et al.* 1993; Felzer *et al.* 2004) either with or without C–N interactions. TEM includes two carbon pools (vegetation and soil detritus), heterotrophic respiration being dependent on C:N ratio, temperature and moisture. A change in terrestrial C uptake with increased surface temperatures was observed when N was included, resulting in a net sequestration of C in the soil–plant system and a reduced CO<sub>2</sub> feedback to the climate system. Similarly, Xu-Ri & Prentice (2008) have coupled DyN, a comprehensive process-based model of the C and N cycling in terrestrial ecosystems, into the Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ). The DyN model represents the uptake, allocation and turnover of N in plants, and soil N transformations including mineralization, N<sub>2</sub> fixation, nitrification and denitrification, NH<sub>3</sub> volatilization, N leaching, and N<sub>2</sub>, N<sub>2</sub>O and NO emissions.

Although the C–N cycle models within CLM-CN, IGSM and LPJ (Thornton *et al.* 2007, 2009; Sokolov *et al.* 2008; Xu-Ri & Prentice 2008) all represent state-of-the-art N cycling models, none of them have applied the energetics-based plant N uptake theory developed by Vitousek, Rastetter and colleagues (Vitousek & Field 1999; Rastetter *et al.* 2001; Dickinson *et al.* 2002; Vitousek *et al.* 2002; Wang, Houlton & Field 2007). Currently, these models allow for plant N uptake to proceed at the rate of demand, and unmet demand results in a proportional downscaling of vegetation productivity. As part of the UK-based model development project, QUEST, a new energetics-based plant N uptake model (Fixation and Uptake of Nitrogen – FUN), has been developed (Fisher *et al.*, unpublished data) within the JULES land surface model (JULES 2009) and that is coupled to the soil C and N model ECOSSE (Smith *et al.* 2007; Smith *et al.* 2009a). ECOSSE uses a five SOC pool approach (two plant debris and three soil organic matter pools) derived from the ROTHC (Coleman & Jenkinson 1996) and SUNDIAL (Bradbury *et al.* 1993) models (Fig. 4a), and with the incorporation of the FUN model allows plant N acquisition from all four major pathways: passive uptake through transpiration, re-translocation of N from senescing leaves, active uptake from the soil, and biological N fixation (Fig. 4b). All pathways except for passive uptake require C expenditure for N uptake based on the energetics theory (Vitousek & Field 1999). The model selects the least energetically costly N uptake routes, C is then allocated to optimize growth until N demand is met. Under N limitation, increasing C is expended on a decreasing soil N supply, resulting in less photosynthate C being allocated to growth.

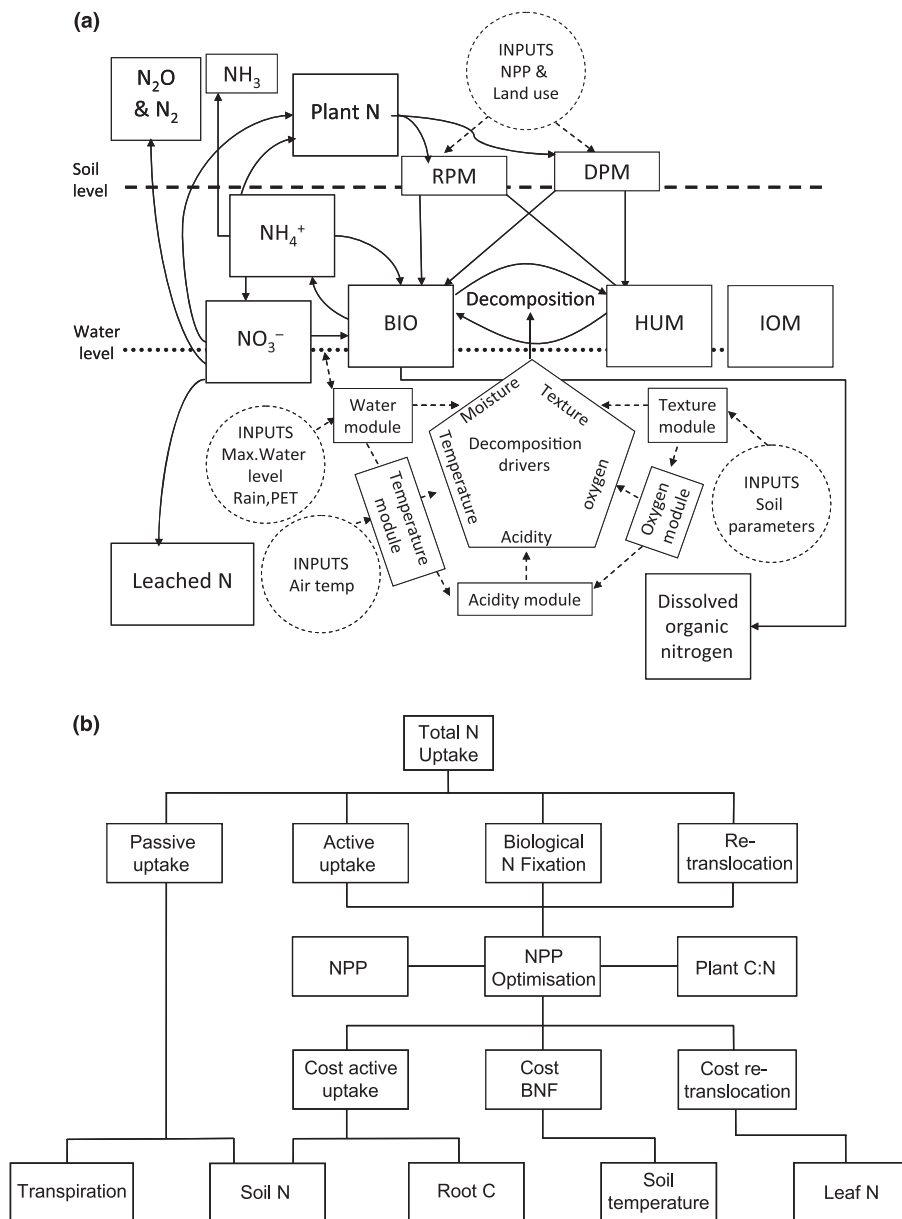
There are a number of uncertainties in our understanding and modelling of soil N and plant N uptake that require further research. First, the impact of physical protection on soil organic matter decomposition is poorly understood and so introduces uncertainty into simulations of N supply especially following land use change (Oades & Waters 1991; Beare, Hendrix & Coleman 1994; Six, Elliott & Paustian 1999, 2000;

Six *et al.* 2002; Del Galdo *et al.* 2003; Deneff *et al.* 2004, 2007; Jiao, Whalen & Hendershot 2006). Second, the various N uptake processes operate across a range of time scales whereas they are confined to prescribed time steps in mathematical models. Third, existing PFT categorizations are based on C function, growth and competition that may not necessarily reflect their N cycling characteristics (i.e. assumptions with respect to the C:N ratios for different plant compartments may propagate uncertainty due to PFT definitions). Fourth, it is unclear under what circumstances plants favour NH<sub>4</sub><sup>+</sup> versus NO<sub>3</sub><sup>-</sup> versus organic N uptake (Marschner, Haussling & George 1991; Falkengren-erup 1995; Nordin, Hogberg & Nasholm 2001; Jones *et al.* 2005a,b; Weigelt, Bol & Bardgett 2005). Fifth, there is considerable evidence that other limiting nutrients including phosphorous (P) have an important regulatory function in terrestrial ecosystems (Lambers *et al.* 2008; Wardle *et al.* 2009). Finally, there is no unifying mathematical framework with which to accurately model and/or predict the amount of N supplied to the plant through mycorrhizal symbioses in exchange for plant C, despite the evident importance of this interaction (Allen *et al.* 2003; Smith *et al.* 2009b).

#### DROUGHT IMPACTS ON VEGETATION

As climate change progresses, rainfall is expected to reduce in several regions of the world with extreme scenarios, such as that predicted by some climate models, leading to a large-scale loss of forest cover across the Tropical biomes (Cox *et al.* 2000; Salazar, Nobre & Oyama 2007; Sitch *et al.* 2008). DGVMs vary widely in their simulation of the impacts of reduced rainfall on forest productivity and carbon storage (Galbraith *et al.*, personal communication). This is due both to differences in their parameters and in process descriptions between models. Here, we review some current approaches to the simulation of drought impacts on forest productivity, using Amazonia as a regional case study.

The sensitivity of ecosystems to drought depends on factors that determine both the *onset* of drought stress and factors that modulate the *rate* at which declines in productivity proceed once hydraulic stress has become established. Plant available water (PAW) is dependent on rainfall, soil physical properties and on the availability of soil water to plant roots. Key soil parameters that influence PAW include soil water holding capacity, soil hydraulic conductivity and soil water retention, a measure of the relationship between soil moisture content and soil water potential. The characteristics of the root system, including rooting depth and the distribution of roots at different depths, are also important determinants of PAW. The simulation of PAW in DGVMs is generally simple with soil divided into discrete layers or horizons and water percolating between them (e.g. Prentice *et al.* 2007). Often entire model grid cells (3.75° longitude by 2.5° latitude) are assumed to have a uniform soil texture, uniform soil water holding capacity and the same soil hydraulic characteristics. Values for key parameters determining PAW are presented in Table 2 for several DGVMs. Differences in parameterization can lead to large differences in the amount of water accessible to the vegetation in



**Fig. 4.** (a) ECOSSE ecosystem soil N model structure showing integration of plant–soil N cycle with multi-pool soil organic matter model and, (b) the Fixation and Uptake of Nitrogen (FUN) model flowchart with four pathways of plant N uptake (passive uptake, active uptake, biological N fixation and re-translocation).

different models. For example, Harris *et al.* (2004) found that calibration of the soil hydraulics parameters in MOSES (precursor of JULES) with data from an Amazonian forest site resulted in a considerable reduction in PAW and an increased sensitivity to soil moisture stress in the model. The uncertainty in the representation of PAW will inevitably result in poor predictions of climate change effects on plant and ecosystem productivity and CO<sub>2</sub> feedbacks to the atmosphere.

The below-ground treatment of roots in DGVMs has been given considerably less attention than the above-ground vegetation (Woodward & Osborne 2000). At their most basic representation, such as in the HYLAND DGVM, roots are bypassed completely when simulating the effects of drought on vegetation. The amount of available water from a particular

soil layer is usually weighted by the fraction of roots in that layer to determine total available water (e.g. as in the LPJ and JULES models). Rooting depth in most DGVMs is usually a PFT-specific parameter and tends to be not greater than 3 m (Poulter, Heyder & Cramer 2009), whereas in reality much deeper rooting depths have been observed in Amazonia (Nepstad *et al.* 1994; Bruno *et al.* 2006). The root distribution in most models is assumed to be constant, often declining exponentially with depth (e.g. JULES model). A number of root adaptation mechanisms have been proposed under drought conditions, including increased root production and root:shoot ratios (Joslin, Wolfe & Hanson 2000), vertical plasticity of the rooting profile (Schymanski *et al.* 2008) and increases in the surface-area-to-mass ratios of fine roots (Metcalf *et al.* 2008). However, due

**Table 2.** Summary of root system descriptions in a selection of large-scale vegetation models including dynamic global vegetation models. Data represent default parameter settings for a broadleaf, evergreen tropical tree

Model (Ref.)	Rooting depth (m)	Root distribution	Leaf:Root allocation
CLM-DGVM (Levy, Cannell & Friend 2004)	10.0	Fixed fraction in each of 10 layers.	Allocation to roots increases under drought
CTEM (Arora & Boer 2003)	Varies according to root biomass, up to 2.0	Varies with root biomass	Allocation to roots increases under drought
HYLAND (Levy, Cannell & Friend 2004)	Not explicitly considered	Not explicitly considered	Fixed
IBIS (Foley <i>et al.</i> 1996)	4.0	Exponential decline, following Jackson <i>et al.</i> 1996	Fixed
JULES (Cox 2001)	3.0	Exponentially declining	Fixed
LPJ (Sitch <i>et al.</i> 2003)	1.5	Fixed fraction in each of two soil layers	Allocation to roots increases under drought
MC1 (Bachelet <i>et al.</i> 2001, Daly <i>et al.</i> 2000)	1.5	Fixed fraction in each of 10 soil layers	Fixed
ORCHIDEE (Krinner <i>et al.</i> 2005)	1.25	Exponentially declining	Allocation to roots increases under drought
SDGVM (Woodward & Lomas 2004)	1.0	Not explicitly simulated	Allocation to roots determined by transpiration
SEIB-DGVM (Sato, Itoh & Kohyama 2007)	Not explicitly considered	Not explicitly considered	Fixed
SIB3 (Baker <i>et al.</i> 2008)	3.5	Exponential decline, following Jackson <i>et al.</i> 1996	Not explicitly considered

to limited data availability, these are generally not addressed in DGVMs. The phenomenon of hydraulic redistribution, or vertical movement of soil moisture by plant roots from deeper layers to more superficial layers, may also confer additional advantage to plants under drought conditions (Horton & Hart 1998; Oliveira *et al.* 2005) and has recently been incorporated into some ecosystem models (Baker *et al.* 2008; Lee *et al.* 2006).

A common strategy for simulating the effect of soil moisture stress on plant productivity in DGVMs is to use a dimensionless soil moisture stress factor, ( $\beta$ ), which directly scales photosynthesis or stomatal conductance. For example, in JULES, the  $\beta$  scalar is defined mathematically as:

$$\beta = \frac{\theta - \theta_w}{\theta_c - \theta_w} \quad \text{eqn 1}$$

where  $\beta$  is equal to 1 when the actual soil moisture content ( $\theta$ ) ( $\text{m}^3 \text{H}_2\text{O m}^{-3}$  soil) is greater than the *critical soil moisture* ( $\theta_c$ ), equal to zero at soil moistures below the *wilting soil moisture* ( $\theta_w$ ) and decreases linearly between  $\theta_c$  and  $\theta_w$ . JULES assumes a direct effect of  $\beta$  on net leaf photosynthesis,  $A$  (Cox, Huntingford & Harding 1998):

$$A = A_p \beta \quad \text{eqn 2}$$

where  $A_p$  is the potential rate of net photosynthesis ( $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ), without water stress. The parameters  $\theta_c$  and  $\theta_w$  are soil texture-specific and correspond to the soil moisture content at suction pressures of  $-0.033$  and  $-1.5$  MPa, respectively. More detailed formulations of the effect of drought on productivity exist, including optimality approaches (Cowan & Farquhar 1977a,b; Williams *et al.* 1996) and more detailed mechanistic models of stomatal behaviour (Buckley, Mott & Farquhar 2003). The former

approach has been used successfully to simulate changes in vegetation water fluxes in a throughfall exclusion experiment in an Amazonian rainforest (Fisher *et al.* 2007). Such detailed formulations, however, have generally been absent from DGVMs, although Hickler *et al.* (2004) recently implemented a more detailed description of plant hydraulic architecture in the LPJ DGVM.

DGVM simulations of drought impacts on ecosystems could be improved in several ways. First, data on root and soil properties influencing PAW are still scarce for many regions of the world, especially the tropics. For example, only a small number of studies have provided data on soil hydraulic properties (Hodnett & Tomasella 1997; Belk *et al.* 2007; Fisher *et al.* 2008) and on root properties (Trumbore *et al.* 2006; Metcalfe *et al.* 2008) in Amazonia. Second, root water uptake is still poorly understood in many natural ecosystems. For example, the relationship between amount of roots available and the uptake of water from different soil layers is unclear, as soil depths with low root density have been shown to contribute significantly to evapotranspiration (Bruno *et al.* 2006). This misunderstanding is partly due to poor measurement of root activity, or the fraction of roots that are actively taking up moisture from the soil, although recent methodological advances are beginning to address this (Čermák *et al.* 2006). Third, work is needed to translate plant species differences in sensitivity to drought (e.g. Engelbrecht *et al.* 2007) into an optimal set of PFTs that best captures this variability. Current DGVM approaches to simulate competition for water between plant functional types (e.g. differences in rooting distribution) lack strong empirical support. Recently, differences in stomatal control strategies have been implicated as the cause of differential species mortality under prolonged drought in the

United States (McDowell *et al.* 2008). Finally, more research into the relative importance of below-ground and above-ground processes and interactions in determining species responses to drought is ultimately required if uncertainty in C and N cycle predictions is to be reduced.

#### VEGETATION DYNAMICS

Typically, the distribution of PFTs and vegetation in DGVMs is controlled to a large extent by 'climate envelopes' defined as the range of temperature and rainfall conditions under which a particular vegetation type can establish with changes in vegetation occurring in response to shifts in these conditions (e.g. Smith *et al.* 2001; Bonan *et al.* 2003; Sitch *et al.* 2003; Woodward & Lomas 2004; Krinner *et al.* 2005; Sato, Itoh & Kohyama 2007). The use of climate envelopes limits the extent to which other factors, including soil and nutrients such as N, and disturbance can potentially affect vegetation. Most DGVMs are 'area-based' models in which grid cell fractions occupied by homogeneous populations of PFTs exist without any real age or size structure and do not mechanistically simulate the process of vegetation succession or competition for light resources between PFTs. In recent years, however, several advances have been made towards addressing these deficiencies. For example, the LPJ-GUESS (Smith *et al.* 2001) and SEIB-DGVM (Sato, Itoh & Kohyama 2007) DGVMs are based on individual-based forest gap models. These models can simulate vertical competition for light among individual trees in small patches within each modelled grid cell. Similarly, the Ecosystem Demography (ED) model (Moorcroft, Hurtt & Pacala 2001), recently coupled to JULES (Huntingford *et al.* 2008), simulates vegetation succession following disturbance on patches of land characterized by 'time since last disturbance'. In this model, different cohorts of PFTs, each corresponding to a particular height and plant functional type, vertically compete for light by occupying different canopy layers. These approaches have allowed for vegetation dynamics to be represented in a much more ecologically realistic manner and will contribute to resolving long-standing DGVM weaknesses, such as inadequate simulation of tropical savannas. For example, Scheiter & Higgins (unpublished data) recently developed a DGVM to simulate the effect of fire on individual trees, as a function of height, resulting in improved simulations of current African vegetation. On the other hand, current PFTs do not account for functional groups such as bryophytes which are clearly important in C cycling in high latitude and temperate systems with globally significant C stocks below-ground (Beringer *et al.* 2001; Cornelissen *et al.* 2007a,b).

The opportunities and challenges that inevitably come from the development of new, more complex DGVM models are many. The absence of a model of vegetation disturbance and recovery impedes our ability to: (i) represent the time scales associated with vegetation change and succession; (ii) represent vegetation co-existence caused by vertical and spatial ecosystem heterogeneity; (iii) represent the mechanisms by which fire disturbance affects vegetation

and *vice versa* (Grigulis *et al.* 2005); (iv) have an interactive soil N model; and (v) operate at the scale of ecological observations (i.e. individual trees) (Purves & Pacala 2008). However, the more complex the models become the more data and information they require, making them difficult to parameterize and leading to co-dependence of parameters on input variables. This can, in turn, lead to multiple stable equilibria in soil and vegetation status, as small perturbations of the initial equilibrium lock the system into a high- or low-nutrient status. Other multiple stable equilibria are likely to occur in fire-dominated ecosystems (Bond, Woodward & Midgley 2004), and in systems with strong biosphere-atmosphere feedbacks (Betts *et al.* 2004). This problem illustrates that the challenge of representing the natural world as a single general mathematical description is not necessarily made easier by the development of such complex models, but only by bringing our models closer to the real world, to real observations and experimental findings will we improve our chances of correctly predicting the role of the biosphere in future climate change.

#### Discussion

It is important to consider that the outputs of DGVMs vary substantially, on account of their differing assumptions about the functioning of the biosphere resulting in considerable divergences in their predictions (e.g. Friedlingstein *et al.* 2006; Sitch *et al.* 2008). There are a number of means to increase confidence in their function: a) a critical evaluation of plant-soil processes in global models, b) use of parameters that are both mechanistically important and measurable, c) making direct comparisons of model outcomes against data from large-scale manipulation experiments, gradients and ecological observatories.

There are significant gaps in current DGVMs including the lack of a bryophyte or cryptogram PFT class despite their strong influence of soil and ecosystem biogeochemistry in boreal and tundra biomes (Cornelissen *et al.* 2007b). An inevitable feature of global vegetation models is that 'average' parameter values are assumed for PFTs or soils covering broad geographical ranges. This simplification obscures the large variability commonly observed in ecological measurements on the ground, in the field. Increased field measurements of model parameters, therefore, are necessary to ensure that the 'average' values used in DGVMs are representative of reality. Data on some parameters (e.g. leaf morphological properties) are often much more readily available than data on other parameters (e.g. photosynthate allocation) (White *et al.* 2000). Similarly, more data are available from temperate zones than tropical regions with some geographical regions, such as Africa, being particularly understudied (e.g. Meir *et al.* 2008). This deficiency can result in the application of unsuitable or approximate parameter values to certain regions of the world, such as the afore-mentioned discrepancy between rooting depth in several models and observed rooting depths in Amazonia. A further complication lies in the fact that some parameters are very difficult to measure. For example, the



notion of distinct soil organic matter pools, each with a unique decay rate, has historically been difficult to relate to field measurements. However, such challenges are being addressed with the aid of *in situ* tracer approaches. For example, Zimmermann *et al.* (2007) recently developed a fractionation procedure that yielded distinct SOC pools, which showed close correspondence with pools simulated by the Roth C model. Nonetheless, the links between plant trait functions and soil biological processes are still poorly developed and work is needed to remedy this gap.

DGVMs need to strike a balance between accurate process representation at large spatial scales whilst constraining model complexity. This can be achieved by robust evaluation of plant–soil interaction process representations across a range of different climatic conditions. Identifying which processes are important at a local level and which are important for global predictions is central to this goal. For example, global change can influence feedbacks between plant and soil biological communities. Changes in productivity and composition of plant communities could alter the quantity and quality of organic matter entering soil as litter and root exudates (Wardle *et al.* 2004; Cornelissen *et al.* 2007a,b). In turn, such changes could elicit further shifts in the composition and activities of soil biological communities (Wardle 2002), with significant consequences for C cycling and C-cycle feedbacks to climate change. These indirect effects of climate change on plant–soil interactions operate via a variety of mechanisms, including short-term changes in the transfer of photosynthate C to fine roots, mycorrhizal fungi and heterotrophic microbes, and long-term shifts in the functional composition and diversity of vegetation, which alter the supply of organic matter to soil over time scales from decades to centuries (Högberg & Read 2006; Bardgett, Freeman & Ostle 2008; De Deyn, Cornelissen & Bardgett 2008). More work is needed, however, on understanding the relative importance of these mechanisms and the role of soil biodiversity and activity, both in a local and global context.

Finally, there is an urgent need to validate DGVM predictions against data from longer-term manipulation experiments conducted in natural ecosystems. Large-scale studies on ecosystem response to enhanced carbon dioxide (Norby *et al.* 2005), drought (Fisher *et al.* 2007; Nepstad *et al.* 2007; Meir *et al.* 2008), experimental warming (Wan *et al.* 2005) and fire (Balch *et al.* 2008) have all been established, but as yet, comparison of these results with DGVM predictions has been limited. Most of these studies, however, have been single-factor studies, examining ecosystem response to one particular global change variable (e.g. Finzi *et al.* 2007). However, the interactive effects (additive, synergistic or antagonistic) of different drivers could be very important under global change (Mikkelsen *et al.* 2008; Tylianakis *et al.* 2008; Wookey *et al.* 2009). For instance, the combined and positive effect of elevated temperature and atmospheric CO<sub>2</sub> on microbial decomposition of peat was found to be greater than when these factors operated in isolation (Fenner *et al.* 2007), creating an even stronger positive feedback on C loss from soil as DOC and respiration (Freeman *et al.* 2004). As recently highlighted by Tylianakis *et al.* (2008) the unanticipated effects of multiple drivers acting

simultaneously create major challenges in predicting future responses to global environmental change. It is clear, therefore, that data is needed from *in situ* multifactor experiments designed to unravel the effects of concurrent global change drivers, such as climate change, N deposition and land use on ecosystem functioning. Distributed large-scale experiments that reflect simultaneous global change factors can also provide valuable insights and data to attribute the drivers of change in plant–soil functions. Such studies can benefit model developments by constraining the uncertainties and feedback to ecological studies by providing a strengthened theoretical framework on which to base future experiments, measurements and modelling. At the same time these data sets provide evidence of the impacts of global changes on ecosystems that can be used to inform future mitigation and adaptation strategies.

## Conclusion

Global scale mathematical models that integrate the effects of plant–soil interactions on biogeochemical and hydrological cycles offer two valuable functions. First, they provide a means to test specific hypotheses about individual and interactive drivers of change, including the direct and indirect effects of climate, on ecosystem form and function and resultant ecological feedbacks. Second, they offer a mechanism to identify gaps in current knowledge that need to be addressed through ecological measurement, experimentation and the development of testable ecological theory that can be used to predict the effects of possible global change scenarios.

There are demonstrably considerable gaps between the detailed process studies that biologist and ecologists undertake in the field and the ways that this understanding is represented within global-scale models. Ecological and biological research clearly has a crucial role to play in the development of these models. First, in a critical evaluation of the current representation of plant–soil processes to ensure that key feedbacks are simulated; second, by supplying the theory and data to structure and parameterize global models; and third, to validate global model simulations against large-scale multifactor experiments specifically designed to study the interactive effects of simultaneous global change drivers and through the provision of data from across global gradients.

## Acknowledgements

Thanks to anonymous referees for their constructive comments. All authors were funded through the Natural Environment Research Council UK, Quantifying Earth Systems (QUEST) programme and the Quantifying and Understanding the Ecosystem Role in Carbon Cycling (QUERCC) project.

## References

- Allen, M.F., Swenson, W., Querejeta, J.I., Egerton-Warburton, L.M. & Treseder, K.K. (2003) Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. *Annual Review of Phytopathology*, **41**, 271–303.
- Arora, V. & Boer, G.J. (2003) A representation of variable root distribution in dynamic global vegetation models. *Earth Interactions*, **7**, Paper 6.

- Bachelet, D., Neilson, R.P., Lenihan, J.M. & Drapek, R.J. (2001) Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems*, **4**, 164–185.
- Baker, I.T., Prihodko, L., Denning, A.S., Goulden, M., Miller, S. & da Rocha, H.R. (2008) Seasonal drought stress in the Amazon: Reconciling models and observations. *Journal of Geophysical Research*, **113**, D20, G00B01.
- Balch, J.K., Nepstad, D.C., Brando, P.M., Curran, L.M., Portela, O., de Carvalho, O. & Lefebvre, P. (2008) Negative fire feedback in a transitional forest of southeastern Amazonia. *Global Change Biology*, **14**, 2276–2287.
- Ball, J.T., Woodrow, I.E. & Berry, J.A. (1987) A model predicting stomatal conductance and its control of photosynthesis under different environmental conditions. *Progress in Photosynthesis* (ed. I. Biggins), pp. 221–224, Martinus Nijhoff Publishers, the Netherlands.
- Bardgett, R.D., Freeman, C. & Ostle, N.J. (2008) Microbial contributions to climate change through carbon cycle feedbacks. *The ISME Journal*, **2**, 805–814.
- Beare, M.H., Hendrix, P.F. & Coleman, D.C. (1994) Water-stable aggregates and organic-matter fractions in conventional-tillage and no tillage soils. *Soil Science Society of America Journal*, **58**, 777–786.
- Beek, J. & Frissel, M.J. (1973) *Simulation of Nitrogen Behaviour in Soils*. Pudoc, Wageningen, The Netherlands.
- Belk, E.L., Markewitz, D., Rasmussen, T.C., Carvalho, E.J.M., Nepstad, D.C. & Davidson, E.A. (2007) Modeling the effects of throughfall reduction on soil water content in a Brazilian Oxisol under a moist tropical forest. *Water Resources Research*, **43**, W08432. doi:10.1029/2006WR005493.
- Beringer, J., Lynch, A.H., Chapin, F.S., Mack, M. & Bonan, G.B. (2001) The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate*, **14**, 3324–3335.
- Betts, R.A., Cox, P.M., Collins, M., Harris, P.P., Huntingford, C. & Jones, C.D. (2004) The role of ecosystem–atmosphere interactions in simulated Amazonian precipitation decrease and forest die-back under global climate warming. *Theoretical and Applied Climatology*, **78**, 157–175.
- Bonan, G.B. & Levis, S. (2006) Evaluating aspects of the Community Land and Atmosphere Models (CLM3 and CAM3) using a dynamic global vegetation model. *Journal of Climate*, **19**, 2290–2301.
- Bonan, G.B., Levis, S., Sitch, S., Vertenstein, M. & Oleson, K.W. (2003) A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Global Change Biology*, **9**, 1543–1566.
- Bond, W.J., Woodward, F.I. & Midgley, G.F. (2004) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
- Bradbury, N.J., Whitmore, A.P., Hart, P.B.S. & Jenkinson, D.S. (1993) Modelling the fate of nitrogen in crop and soil in the years following application of <sup>15</sup>N-labelled fertilizer to winter wheat. *Journal of Agricultural Science (Cambridge)*, **121**, 363–379.
- Bruno, R.D., da Rocha, H.R., de Freitas, H.C., Goulden, M.L. & Miller, S.D. (2006) Soil moisture dynamics in an eastern Amazonian tropical forest. *Hydrological Processes*, **20**, 2477–2489.
- Buckley, T.N., Mott, K.A. & Farquhar, G.D. (2003) A hydromechanical and biochemical model of stomatal conductance. *Plant Cell and Environment*, **26**, 1767–1785.
- Čermák, J., Ulrich, R., Staněk, Z., Koller, J. & Aubrecht, L. (2006) Electrical measurement of tree root absorbing surfaces by the earth impedance method: 2. Verification based on allometric relationships and root severing experiments. *Tree Physiology*, **26**, 1113–1121.
- Chapman, S.K., Langley, J.A., Hart, S.C. & Koch, G.W. (2006) Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist*, **169**, 27–34.
- Coleman, K. & Jenkinson, D.S. (1996) RothC-26.3- A Model for the turnover of carbon in soil. *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets*, NATO ASI Series I, Vol.38 (eds D.S. Powlson, P. Smith & J.U. Smith), pp. 237–246. Springer-Verlag, Heidelberg, Germany.
- Collatz, G.J., Ribas-Carbo, M. & Berry, J.A. (1992) Coupled photosynthesis-stomatal conductance model for leaves of C4 plants. *Australian Journal of Plant Physiology*, **19**, 519–538.
- Collatz, G.J., Ball, J.T., Griivet, C. & Berry, J.A. (1991) Physiological and environmental-regulation of stomatal conductance, photosynthesis and transpiration - a model that includes a laminar boundary-layer. *Agricultural and Forest Meteorology*, **54**, 107–136.
- Comins, H.N. & McMurtrie, R.E. (1993) Long-term response of nutrient-limited forests to CO<sub>2</sub> enrichment - equilibrium behavior of plant-soil models. *Ecological Applications*, **3**, 666–681.
- Cornelissen, J.H.C., Van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J. et al. (2007a) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, **10**, 619–627.
- Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & Daring, H.J. (2007b) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987–1001.
- Cowan, I.R. & Farquhar, G.D. (1977a) Stomatal function in relation to leaf metabolism and environment. *Integration of Activity in Higher Plants* (ed. D.H. Jennings), pp. 471–505, Cambridge University Press, Cambridge.
- Cowan, I.R. & Farquhar, G.D. (1977b) Stomatal function in relation to leaf metabolism and environment. *Integration of Activity in Higher Plants* (ed. D.H. Jennings), pp. 471–505, Cambridge University Press, Cambridge.
- Cox, P.M. (2001) Description of the 'TRIFFID' dynamic global vegetation model. Hadley Centre Technical Note 24.
- Cox, P.M., Huntingford, C. & Harding, R.J. (1998) A canopy conductance and photosynthesis model for use in a GCM land surface scheme. *Journal of Hydrology*, **213**, 79–94.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.
- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V. et al. (2001) Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Daly, C., Bachelet, D., Lenihan, J.M., Neilson, R.P., Parton, W. & Ojima, D. (2000) Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*, **10**, 449–469.
- Davidson, E.A. & Janssens, I.A. (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.
- De Deyn, G.B., Cornelissen, H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.
- Del Galdo, I., Six, J., Peressotti, A. & Cotrufo, M.F. (2003) Assessing the impact of land-use change on soil C sequestration in agricultural soils by means of organic matter fractionation and stable isotopes. *Global Change Biology*, **9**, 1204–1213.
- Del Grosso, S.J., Parton, W.J., Mosier, A.R., Walsh, M.K., Ojima, D.S. & Thornton, P.E. (2006) DAYCENT national-scale simulations of nitrous oxide emissions from cropped soils in the United States. *Journal of Environmental Quality*, **35**, 1451–1460.
- Denef, K., Six, J., Merckx, R. & Paustian, K. (2004) Carbon sequestration in microaggregates of no-tillage soils with different clay mineralogy. *Soil Science Society of America Journal*, **68**, 1935–1944.
- Denef, K., Zotarellia, L., Boddey, R.M. & Six, J. (2007) Microaggregate-associated carbon as a diagnostic fraction for management-induced changes in soil organic carbon in two Oxisols. *Soil Biology & Biochemistry*, **39**, 1165–1172.
- Dickinson, R.E., Berry, J.A., Bonan, G.B., Collatz, G.J., Field, C.B., Fung, I.Y., Goulden, M., Hoffmann, W.A., Jackson, R.B., Myneni, R., Sellers, P.J. & Shaikh, M. (2002) Nitrogen controls on climate model evapotranspiration. *Journal of Climate*, **15**, 278–295.
- Dickinson, R.E., Oleson, K.W., Bonan, G.B., Hoffman, F.M., Thornton, P., Vertenstein, M., Yang, Z.-L. & Zeng, X. (2006) The Community Land Model and its climate statistics as a component of the Community Climate System Model. *Journal of Climate*, **19**, 2302–2324.
- Ducoudre, N.I., Laval, K. & Perrier, A. (1993) SECHIBA, a new set of parameterizations of the hydrologic exchanges at the land atmosphere interface within the LMD atmospheric general-circulation model. *Journal of Climate*, **6**, 248–273.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.
- Falkengrengrerup, U. (1995) Interspecific differences in the preference of ammonium and nitrate in vascular plants. *Oecologia*, **102**, 305–311.
- Farquhar, G.D., Caemmerer, S.V. & Berry, J.A. (1980) A biochemical-model of photosynthetic CO<sub>2</sub> assimilation in leaves of C-3 species. *Planta*, **149**, 78–90.
- Felzer, B., Kicklighter, D.W., Melillo, J.M., Wang, C., Zhuang, Q. & Prinn, R. (2004) Effects of ozone on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model. *Tellus*, **56B**, 230–248.
- Fenner, N., Ostle, N.J., McNamara, N., Sparks, T., Harmens, H., Reynolds, B. & Freeman, C. (2007) Elevated CO<sub>2</sub> effects on peatland plant community carbon dynamics and DOC production. *Ecosystems*, **10**, 635–647.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E. et al. (2007) Increases in nitrogen uptake rather than nitro-

- gen-use efficiency support higher rates of temperate forest productivity under elevated CO<sub>2</sub>. *Proceedings of the National Academy of Sciences*, **104**, 14014–14019.
- Fisher, R.A., Williams, M., Da Costa, A.L., Malhi, Y., Da Costa, R.F., Almeida, S. & Meir, P. (2007) The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Global Change Biology*, **13**, 2361–2378.
- Fisher, R.A., Williams, M., Ruivo, M.D., de Costa, A.L. & Meira, P. (2008) Evaluating climatic and soil water controls on evapotranspiration at two Amazonian rainforest sites. *Agricultural and Forest Meteorology*, **148**, 850–861.
- Foley, J.A., Prentice, I.C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S. & Haxeltine, A. (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles*, **10**, 603–628.
- Fontaine, S. & Barot, S. (2005) Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecology Letters*, **8**, 1075–1087.
- Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B. & Rumpel, C. (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, **450**, 277–U10.
- Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D., Hughes, S. & Hudson, J. (2004) Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. *Nature*, **430**, 195–198.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V. *et al.* (2006) Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *Journal of Climate*, **19**, 3337–3353.
- Friend, A.D., Stevens, A.K., Knox, R.G. & Cannell, M.G.R. (1997) A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling*, **77**, 233–255.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z.C., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. & Sutton, M.A. (2008) Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, **320**, 889–892.
- Gifford, R.M. (1995) Whole plant respiration and photosynthesis of wheat under increased CO<sub>2</sub> concentration and temperature: Long-term vs short-term distinctions for modelling. *Global Change Biology*, **1**, 385–396.
- Grigulis, K., Lavorel, S., Davies, I.D., Dossantos, A., Lloret, F. & Vila, M. (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica* in Catalan shrublands. *Global Change Biology*, **11**, 1042–1053.
- Harris, P.P., Huntingford, C., Gash, J.H.C., Hodnett, M.G., Cox, P.M., Maihi, Y. & Araujo, A.C. (2004) Calibration of a land-surface model using data from primary forest sites in Amazonia. *Theoretical and Applied Climatology*, **78**, 27–45.
- Haxeltine, A. & Prentice, I.C. (1996) BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochemical Cycles*, **10**, 693–709.
- Heimann, M. & Reichstein, M. (2008) Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, **45**, 289–292.
- Hickler, T., Smith, B., Sykes, M.T., Davis, M.B., Sugita, S. & Walker, K. (2004) Using a generalized vegetation model to simulate vegetation dynamics in Northeastern USA. *Ecology*, **85**, 519–530.
- Hodnett, M.G. & Tomasella, J. (1997) Estimating unsaturated hydraulic conductivity of Brazilian soils using soil-water retention data. *Soil Science*, **162**, 703–712.
- Högberg, P. & Read, D.J. (2006) Towards a more plant physiological perspective on soil ecology. *Trends in Ecology & Evolution*, **21**, 548–554.
- Hopmans, J.W. & Bristow, K.L. (2002) Current capabilities and future needs of root water and nutrient uptake modeling. *Advances in Agronomy*, **77**, 103–183.
- Horton, J.L. & Hart, S.C. (1998) Hydraulic lift: a potentially important ecosystem process. *Trends in Ecology & Evolution*, **13**, 232–235.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y. & Field, C.B. (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.
- Hunt, H.W., Coleman, D.C. & Ingham, R.E. (1987) The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils*, **3**, 57–68.
- Hunt, H.W., Trlica, M.J. & Redente, E.F. (1991) Simulation model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling*, **53**, 205–246.
- Hunt, H.W., Coleman, D.C., Cole, C.V., Ingham, R.E., Elliott, E.T. & Woods, L.E. (1984) Simulation model of a food web with bacteria, amoebae, and nematodes in soil. *Current Perspectives in Microbial Ecology* (eds M.J. Klug & C.A. Reddy), pp. 346–352, American Society for Microbiology, Washington DC.
- Huntingford, C., Fisher, R.A., Mercado, L., Booth, B.B.B., Sitch, S., Harris, P.P. *et al.* (2008) Towards quantifying uncertainty in predictions of Amazon 'dieback'. *Philosophical Transactions of the Royal Society (B)*, **363**, 1857–1864.
- IPCC (2001) *Climate Change: Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- IPCC (2007) *Climate Change: Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.
- Jarvis, P.G. (1976) Interpretation of variations in leaf water potential and stomatal conductance found in canopies in field. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **273**, 593–610.
- Jenkinson, D.S. (1977) Studies on the decomposition of plant material in soil. V. *Journal of Soil Science*, **28**, 424–434.
- Jenny, H. (1941) *Factors of Soil Formation. A System of Quantitative Pedology*. McGraw-Hill, New York, N.Y.
- Jiao, Y., Whalen, J.K. & Hendershot, W.H. (2006) No-tillage and manure applications increase aggregation and improve nutrient retention in a sandy-loam soil. *Geoderma*, **134**, 24–33.
- Jones, C., McConnell, C., Coleman, K., Cox, P., Falloon, P., Jenkinson, D. & Powlson, D. (2005a) Global climate change and soil carbon stocks; predictions from two contrasting models for the turnover of organic carbon in soil. *Global Change Biology*, **11**, 154–166.
- Jones, D.L., Healey, J.R., Willett, V.B., Farrar, J.F. & Hodge, A. (2005b) Dissolved organic nitrogen uptake by plants—an important N uptake pathway? *Soil Biology and Biochemistry*, **37**, 413–423.
- Joslin, J.D., Wolfe, M.H. & Hanson, P.J. (2000) Effects of altered water regimes on forest root systems. *New Phytologist*, **147**, 117–129.
- JULES (2009) <http://www.jchmr.org/jules/> (accessed on 06.02.09).
- Krinner, G., Viovy, N., de Noblet-Ducoudre, N., Ogee, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S. & Prentice, I.C. (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*, **19**, GB1015 doi:10.1029/2003GB002199.
- Lal, R. (2004) Soil carbon sequestration impacts on global climate change and food security. *Science*, **304**, 1623–1627.
- Lambers, H., Raven, J.A., Shaver, G.R. & Smith, S.E. (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology and Evolution*, **23**, 95–103.
- LeBauer, D.S. & Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, **89**, 371–379.
- Lee, J.-E., Oliveira, R.S., Dawson, T.E. & Fung, I. (2005) Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 17576–17581.
- Leuning, R. (1995) A critical appraisal of a combined stomatal-photosynthesis model for C-3 plants. *Plant Cell and Environment*, **18**, 339–355.
- Levy, P.E., Cannell, M.G.R. & Friend, A.D. (2004) Modelling the impact of future changes in climate, CO<sub>2</sub> concentration and land use on natural ecosystems and the terrestrial carbon sink. *Global Environmental Change-Human and Policy Dimensions*, **14**, 21–30.
- Li, C., Frolking, S. & Harriss, R. (1994) Modelling carbon biogeochemistry in agricultural soils. *Global Biogeochemical Cycles*, **8**, 237–254.
- Lloyd, J. (1999) Current perspectives on the terrestrial carbon cycle. *Tellus B*, **51**, 336–342.
- Lloyd, J. & Taylor, J.A. (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Luo, Y., Su, B.O., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U. *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.
- Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S. *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–850.
- Marschner, H., Haussling, M. & George, E. (1991) Ammonium and Nitrate Uptake Rates and Rhizosphere Ph in Nonmycorrhizal Roots of Norway Spruce [*Picea-Abies* (L) Karst]. *Trees-Structure and Function*, **5**, 14–21.



- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G. & Yezzer, E.A. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.
- McGill, W.B. (1996) Review and classification of ten soil organic matter (SOM) models. *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds D.S. Powlson, P. Smith & J.U. Smith), NATO ASI Series I, Vol.38, pp. 111–133. Springer-Verlag, Heidelberg, Germany.
- Meir, P., Cox, P. & Grace, J. (2006) The influence of terrestrial ecosystems on climate. *Trends in Ecology & Evolution*, **21**, 254–260.
- Meir, P., Metcalfe, D.B., Costa, A.C.L. & Fisher, R.A. (2008) The fate of assimilated carbon during drought: impacts on respiration in Amazon rainforests. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 1849–1855.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore III, B., Vorosmarty, C.J. & Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.
- Metcalfe, D.B., Meir, P., Aragao, L.E.O.C., da Costa, A.C.L., Braga, A.P., Gonçalves, P.H.L., Silva, J.D., de Almeida, S.S., Dawson, L.A., Malhi, Y. & Williams, M. (2008) The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, **311**, 189–199.
- Miehle, P., Livesley, S.J., Li, C., Feikema, P.M., Adams, M.A. & Arndt, S.K. (2006) Quantifying uncertainty from large-scale model predictions of forest carbon dynamics. *Global Change Biology*, **12**, 1421–1434.
- Mikkelsen, T.N., Beier, C., Jonasson, S., Holmstrup, M., Schmidt, I.K., Ambus, P., et al. (2008) Experimental design of multifactor climate change experiments with elevated CO<sub>2</sub> warming and drought: the CLIMAITE project. *Functional Ecology*, **22**, 185–195.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- Molina, J.A.E. & Smith, P. (1998) Modeling carbon and nitrogen processes in soil. *Advances in Agronomy*, **62**, 253–298.
- Monteith, J.L. (1995) Accommodation between transpiring vegetation and the convective boundary-layer. *Journal of Hydrology*, **166**, 251–263.
- Monteith, J.L. & Unsworth, M. (1990) *Principles of Environmental Physics*. Edward Arnold, London.
- Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Hogasen, T. et al. (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, **450**, 537.
- Moorcroft, P.R., Hurtt, G.C. & Pacala, S.W. (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–586.
- Neill, C. & Gignoux, J. (2006) Soil organic matter decomposition driven by microbial growth: A simple model for a complex network of interactions. *Soil Biology & Biochemistry*, **38**, 803–811.
- Nepstad, D.C., De Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., Da Silva, E.D., Stone, T.A., Trumbore, S.E. & Vieira, S. (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, **372**, 666–669.
- Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. & Cardinot, G. (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**, 2259–2269.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S. et al. (2005) Forest response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 18052–18056.
- Nordin, A., Hogberg, P. & Nasholm, T. (2001) Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. *Oecologia*, **129**, 125–132.
- Oades, J.M. & Waters, A.G. (1991) Aggregate hierarchy in soils. *Australian Journal of Soil Research*, **29**, 815–828.
- Oleson, K.W. et al. (2004) *Technical Description of the Community Land Model (CLM)*. NCAR Tech. Note, NCAR-TN-461 + STR, Natl. Cent. for Atmos. Res., Boulder, Colorado, 174 pp.
- Oliveira, R.S., Dawson, T.E., Burgess, S.S.O. & Nepstad, D.C. (2005) Hydraulic redistribution in three Amazonian trees. *Oecologia*, **145**, 354–363.
- Ourry, A., Gordon, A.J. & Macduff, J.H. (1997) Nitrogen uptake and assimilation in roots and root nodules. *A Molecular Approach to Primary Metabolism in Higher Plants* (eds C.H. Foyer & W.P. Quick). pp. 237–254. Taylor and Francis, New York.
- Parton, W.J., Stewart, J.W.B. & Cole, C.V. (1988) Dynamics of C, N, P and S in grassland soils – a model. *Biogeochemistry*, **5**, 109–131.
- Paustian, K. (1994) Modelling soil biology and biochemical processes for sustainable agricultural research. *Soil Biota. Management in Sustainable Farming Systems* (eds C.E. Pankhurst, B.M. Doube, V.V.S.R. Gupta & P.R. Grace). pp. 182–193, CSIRO Information Services: Melbourne, Australia.
- Peltoniemi, M., Thürig, E., Ogle, S., Palosuo, T., Shrumph, M., Wützler, T. et al. (2007) Models in country scale carbon accounting of forest soils. *Silva Fennica*, **41**, 575–602.
- Poulter, B., Heyder, U. & Cramer, W. (2009) Modelling the sensitivity of the seasonal cycle of GPP to dynamic LAI and rooting depths in tropical rainforests. *Ecosystems*, **12**, 517–533.
- Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S.P., Hickler, T., Lucht, W., Sitch, S., Smith, B. & Sykes, M.T. (2007) Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. in *The IGBP Series: Terrestrial Ecosystems in a Changing World* (eds P. Canadell, E. Pataki & L.F. Pitelka). pp. 175–192, Springer-Verlag, Berlin.
- Purves, D.W. & Pacala, S.W. (2008) Predictive Models of Forest Dynamics. *Science*, **320**, 1452–1453.
- Rastetter, E.B., Vitousek, P.M., Field, C., Shaver, G.R., Herbert, D. & Ågren, G.I. (2001) Resource optimization and symbiotic nitrogen fixation. *Ecosystems*, **4**, 369–388.
- de Ruiter, P.C., Neutel, A.-M. & Moore, J.C. (1995) Energetics and stability in belowground food webs. *Food Webs, Integration of Patterns and Dynamics* (eds G.A. Polis & K.O. Winemiller). pp. 201–210, Chapman and Hall, New York.
- de Ruiter, P.C. & Van Faassen, H.G. (1994) A comparison between an organic matter dynamics model and a food web model simulating nitrogen mineralization in agro-ecosystems. *European Journal of Agronomy*, **3**, 347–354.
- de Ruiter, P.C., Van Veen, J.A., Moore, J.C., Brussaard, L. & Hunt, H.W. (1993) Calculation of nitrogen mineralization in soil food webs. *Plant and Soil*, **157**, 263–273.
- Salazar, L.F., Nobre, C.A. & Oyama, M.D. (2007) Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, **34**, L09708 doi:10.1029/2007GL029695.
- Sato, H., Itoh, A. & Kohyama, T. (2007) SEIB-DGVM: A new Dynamic Global Vegetation Model using a spatially explicit individual-based approach. *Ecological Modelling*, **200**, 279–307.
- Schimel, J.P. & Weintraub, M.N. (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biology and Biochemistry*, **35**, 549–563.
- Schimel, D.S., Braswell, B.H., McKeown, R., Ojima, D.S., Parton, W.J. & PULLIAM, W. (1996) Climate and nitrogen controls on the geography and time-scales of terrestrial biogeochemical cycling. *Global Biogeochemical Cycles*, **10**, 677–692.
- Schymanski, S., Sivapalan, M., Roderick, M.L. & Beringer, J. (2008) An optimality based model of coupled soil moisture and root dynamics. *Hydrology and Earth System Science*, **12**, 913–932.
- Sherry, R.A., Zhou, X.H., Gu, S.L., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L. & Luo, Y.Q. (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of America*, **104**, 198–202.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.
- Sitch, S., Cox, P.M., Collins, W.J. & Huntingford, C. (2007) Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature*, **448**, 791–794.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L. et al. (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon feedbacks using 5 Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, **14**, 2015–2039.
- Six, J., Elliott, E.T. & Paustian, K. (1999) Aggregate and soil organic matter dynamics under conventional and no-tillage systems. *Soil Science Society of America Journal*, **63**, 1350–1358.
- Six, J., Elliott, E.T. & Paustian, K. (2000) Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no tillage agriculture. *Soil Biology & Biochemistry*, **32**, 2099–2103.
- Six, J., Callewaert, P., Lenders, S., De Gryze, S., Morris, S.J., Gregorich, E.G., Paul, E.A. & Paustian, K. (2002) Measuring and understanding carbon storage in afforested soils by physical fractionation. *Soil Science Society of America Journal*, **66**, 1981–1987.
- Smith, P. (2001) Soil organic matter modeling. *Encyclopedia of Soil Science* (ed. R. Lal). Marcel Dekker Inc, NY.



- Smith, P. (2002) Soil and the environment: Role of soil in models for climate change. *Encyclopedia of Soils in the Environment* (eds D. Hillel, C. Rosenzweig, D. Powlson, K. Scow, M. Singer & D. Sparks). Academic Press, London.
- Smith, J.U., Bradbury, N.J. & Addiscott, T.M. (1996) SUNDIAL: A PC-based system for simulating nitrogen dynamics in arable land. *Agronomy Journal*, **88**, 38–43.
- Smith, F.A., Grace, E.J. & Smith, S.E. (2009b) More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. *New Phytologist*, **182**, 347–358.
- Smith, P., Powlson, D.S. & Glendinning, M.J. (1996). Establishing a European soil organic matter network (SOMNET). *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds D.S. Powlson, P. Smith & J.U. Smith), NATO ASI Series I, Vol. 38. pp. 81–98. Springer-Verlag, Berlin.
- Smith, B., Prentice, I.C. & Sykes, M.T. (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, **10**, 621–638.
- Smith, P., Andr en, O., Brussaard, L., Dangerfield, M., Ekschmitt, K., Lavelle, P. & Tate, K. (1998) Soil biota and global change at the ecosystem level: describing soil biota in mathematical models. *Global Change Biology*, **4**, 773–784.
- Smith, P., Falloon, P., Smith, J.U. & Powlson, D.S. (Eds) (2001) *Soil Organic Matter Network (SOMNET): 2001 Model and Experimental Metadata*. GCTE Report 7 (2nd Edition), GCTE Focus 3 Office, Wallingford, Oxon, 224 pp.
- Smith, P., Falloon, P.D., K rschens, M., Shevtsova, L.K., Franko, U., Romanenkova, V., Coleman, K., Rodionova, V., Smith, J.U. & Schramm, G. (2002) EuroSOMNET - a European database of long-term experiments on soil organic matter: the WWW metadatabase. *Journal of Agricultural Science (Cambridge)*, **138**, 123–134.
- Smith, P., Smith, J.U., Flynn, H., Killham, K., Rangel-Castro, I., Foeroid, B. *et al.* (2007) ECOSSE: Estimating Carbon in Organic Soils - Sequestration and Emissions. Final Report. SEERAD Report. ISBN 978 0 7559 1498 2. 166 pp.
- Smith, P., Fang, C., Dawson, J.J.C. & Moncreiff, J.B. (2008) Impact of global warming on soil organic carbon. *Advances in Agronomy*, **97**, 1–43.
- Smith, J.U., Chapman, S.J., Bell, J.S., Bellarby, J., Gottschalk, P., Hudson, G., Lilly, A., Smith, P. & Towers, W. (2009a) Developing a methodology to improve soil carbon stock estimates for Scotland and use of initial results from a resampling of the national soil inventory of Scotland to improve the ECOSSE model. *RERAD Report*, in press.
- Sokolov, A.P., Schlosser, C.A., Dutkiewicz, S., Paltsev, S., Kicklighter, D.W., Jacoby, H.D. *et al.* (2005) The MIT Integrated Global System Model (IGSM) Version 2: Model Description and Baseline Evaluation. *MIT JP Report*, **124**.
- Sokolov, A.P., Kicklighter, D.W., Melillo, J.M., Felzer, B.S., Schlosser, C.A. & Cronin, T.W. (2008) Consequences of considering carbon–nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. *Journal of Climate*, **21**, 3776–3796.
- Stern, N. (2006) *The Economics of Climate Change: The Stern Review*. HM Treasury, Cambridge University Press, Cambridge, UK.
- Stewart, J.B. (1988) Modeling surface conductance of pine forest. *Agricultural and Forest Meteorology*, **43**, 19–35.
- Thornton, P.E. & Rosenbloom, N.A. (2005) Ecosystem model spin-up: estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecological Modelling*, **189**, 25–48.
- Thornton, P.E. *et al.* (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural Forest Meteorology*, **113**, 185–222.
- Thornton, P.E., Lamarque, J.-F., Rosenbloom, N.A. & Mahowald, N.M. (2007) Influence of carbon-nitrogen cycle coupling on land model response to CO<sub>2</sub> fertilization and climate variability. *Global Biogeochemical Cycles*, **21**, 1–15.
- Thornton, P.E., Doney, S.C., Lindsay, K., Moore, J.K., Mahowald, N., Randerson, J.T., Fung, I., Lamarque, J.-F., Feddes, J.J. & Lee, Y.-H. (2009) Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences Discussions*, **6**, 3303–3354.
- Trumbore, S., Da Costa, E.S., Nepstad, D.C., De Camargo, P.B., Martinelli, L.I.Z.A., Ray, D., Restom, T. & Silver, W. (2006) Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology*, **12**, 217–229.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Vitousek, P.M. & Field, C.B. (1999) Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry*, **46**, 179–202.
- Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, **13**, 87–115.
- Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N.B., Howarth, R.W., Marino, R., Martinelli, L., Rastetter, E.B. & Sprent, J.I. (2002) Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry*, **57–58**, 1–45.
- Wan, S.Q., Hui, D.F., Wallace, L. & Luo, Y.Q. (2005) Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles*, **19**, GB2014.
- Wang, Y.P., Houlton, B. & Field, C.B. (2007) A model of biogeochemical cycles of carbon, nitrogen and phosphorus including symbiotic nitrogen fixation and phosphatase production. *Global Biogeochemical Cycles*, **21**, 1–15.
- Wardle, D.A. (2002) *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Monogr. Population Biol., 34. Princeton University Press, New Jersey.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N. *et al.* (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–1633.
- Wardle, D.A., Bardgett, R.D., Walker, L.R. & Bonner, I. (2009) Among and within-species variation in plant litter decomposition in contrasting long-term chronosequences. *Functional Ecology*, **23**, 442–453.
- Weigelt, A., Bol, R. & Bardgett, R.D. (2005) Preferential uptake of soil nitrogen forms by grassland plant species. *Oecologia*, **142**, 627–635.
- White, M., Thornton, P.E., Running, S.W. & Nemani, R. (2000) Analysis of the BIOME-BGC Terrestrial Ecosystem Model: Net Primary Production Controls. *Earth Interactions*, **4**, Paper 3.
- Williams, M., Rastetter, E.B., Fernandes, D.N., Goulden, M.L., Wofsy, S.C., Shaver, G.R., Melillo, J.M., Munger, J.W., Fan, S.M. & Nadelhoffer, K.J. (1996) Modelling the soil-plant-atmosphere continuum in a Quercus-Acer stand at Harvard forest: The regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell and Environment*, **19**, 911–927.
- Woodward, F.I. (2002) Potential impacts of global elevated CO<sub>2</sub> concentrations on plants. *Current Opinion in Plant Biology*, **5**, 207–211.
- Woodward, F.I. & Lomas, M.R. (2004) Vegetation-dynamics – simulating responses to climate change. *Biological Reviews*, **79**, 643–670.
- Woodward, F.I., Lomas, M.R. & Betts, R.A. (1998) Vegetation-climate feedbacks in a greenhouse world. *Philosophical Transactions of the Royal Society (B)*, **353**, 29–39.
- Woodward, F.I. & Osborne, C.P. (2000) The representation of root processes in models addressing the responses of vegetation to global change. *New Phytologist*, **147**, 223–232.
- Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Brathen, K.A., Cornelissen, J.H.C., Gough, L., Hartley, I.P., Hopkins, D.W., Lavorel, S. & Shaver, G.R. (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of arctic and alpine ecosystems to environmental change. *Global Change Biology*, **15**, 1153–1172.
- Wright, I.J. & Westoby, M. (2003) Nutrient concentration, resorption and life-span: leaf traits of Australian sclerophyll species. *Functional Ecology*, **17**, 10–19.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wutzler, T. & Reichstein, M. (2007) Soils apart from equilibrium - consequences for soil carbon balance modelling. *Biogeosciences*, **4**, 125–136.
- Xu-Ri & Prentice, I.C. (2008) Terrestrial nitrogen cycle simulation with a dynamic global vegetation model. *Global Change Biology*, **14**, 1745–1764.
- Zachle, S. & Friend, A.D. (2006) The role of nitrogen in terrestrial biosphere responses to climate change and CO<sub>2</sub> increase. *Geophysical Research Abstracts*, **8**, 08345.
- Zimmermann, M., Leifeld, J., Schmidt, M.W.I., Smith, P. & Fuhrer, J. (2007) Measured soil organic matter fractions can be related to pools in the RothC model. *European Journal of Soil Science*, **58**, 658–667.

Received 10 March 2009; accepted 22 June 2009  
Handling Editor: Hans Cornelissen